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The effects of geography, habitat, and humans on the ecology and demography of the Gopher tortoise in the southern Lake Wales Ridge region of Florida

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A 35-year (1967–2002) demographic study was conducted on the gopher tortoise (*Gopherus polyphemus*) from two different habitats on Archbold Biological Station located on the southern end of the Lake Wales Ridge in south-central Florida. We found geographic, habitat, and human-mediated effects on several aspects of its biology. Our findings underscore the necessity of long-term demographic data to more accurately answer ecological questions concerning long-lived species, such as how the gopher tortoise detectably might be affected by habitat quality and human activities.

Keywords: Demography, ecology, gopher tortoise

INTRODUCTION

The gopher tortoise (*Gopherus polyphemus*) is a medium-sized inhabitant of sandy uplands of the southern parts of Louisiana, Mississippi, Alabama, Georgia, and South Carolina, extending southward through mainland Florida (Ernst & Lovich, 2009; Powell et al., 2016). Excessive loss and fragmentation of its habitat, coupled with its delayed maturity and human predation, has resulted in the decline of the species throughout its geographic range (McCoy & Mushinsky 1992; McCoy et al., 2006; USFWS, 2013). In 1978, the Gopher Tortoise Council was formed specifically to address conservation of this ancient and ecologically sensitive species. At that time, comprehensive demographic data on the species were uncommon.

In 1967, James N. Layne (JNL) initiated a long, uninterrupted field research programme on Archbold Biological Station (ABS) in Lake Placid, Highlands County, Florida. During the period 1967–2002, ecological, morphological, and population information was gathered on the gopher tortoise from two main sites in sandhill or scrub. The goal was to understand long-term demography of this species as it responded to its geographic location, habitat, and human activity. We provide 35 years of gopher tortoise life history data from ABS. Further, we compare our findings to those of others as they relate to geography, habitat, and human mediation.

STUDY AREA AND METHODS

The Archbold Biological Station, founded in 1941 by Richard Archbold, is a 2101 ha private reserve in Lake Placid, Highlands County, Florida. The station is located on the southern end of the Lake Wales Ridge whose habitats consist of southern ridge sandhills, sand pine scrub, rosemary scrub, scrubby flatwoods, swales, bayheads, seasonal ponds, and areas that are human-disturbed (see FNAI 2010 for descriptions of these habitats). From temperature data collected during 1952–2004, mean-minimum air temperature for January is 8.33˚ C, and mean-maximum air temperature for July is 34.05˚ C. From rainfall data collected during 1932–2004, mean annual rainfall is 136.4 cm (range = 69–195 cm).

The original station property, the East Section, was 431.94 ha. The eight tracts of the West Section were 1204.17 ha. The total area of this study was 1735.48 ha. Beginning August 1967, tortoises were actively captured by hand and individually marked in the field with notches onto the edges of marginal scutes. Tortoises were studied at both the East and West Sections. Survey effort was greatest during the first 20 years by JNL and assistants. At time of capture, individuals were sexed, body mass was recorded, plastron length (PL) and width and straight-line carapace length (CL) were measured in mm. Gular scutes were measured from their base to the notch in mm. Time and location were recorded at capture, as were feeding or reproductive behaviours. Interactions with other

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animals were also noted.

We used a minimum convex polygon to calculate the home range of each individual. We examined a subset of scats defecated by captured animals under a dissecting scope for diet analysis. We used Cormack-Jolly-Seber (CJS) open population models to estimate survivorship (White & Burnham 1999). We measured condition using Fulton's K for analysis (weight/length^3) (Stevenson and Woods, 2006) and Duncan's Multiple Range Test. Sample statistics were calculated using Excel, 2016. Normality was determined using the Anderson-Darlington normality test in MiniTab 13.0 (MiniTab statistical package Inc. State College, Pennsylvania). Means values are followed by standard deviation, and statistical significance was recognized at $P < 0.05$.

RESULTS

Population demographics

Population structure

At the east and west sections, the percent of adults in the population increased over time from as few as 31.6 % up to 69.4 % (Tables 1–2). However, across all years, the percent of adults comprising each of the populations was less than 50 %, the lower value of which was a mere 31.6 % in the East Section (Table 1). The overwhelming numbers of juveniles at both sites was apparent when body size distributions were examined (Figs. 1–2). During the earliest few years of the study (1967–1970) in the East Section, 145 new individuals of known sex and status were captured along with an additional 40 tortoises of unknown status. Of the 145 tortoises, 39.3 % were adults and most of those were very young as evidenced by body size (Fig. 3). Conversely, juveniles ranged widely in size and age (Fig. 3), indicative of an emerging population.

Table 1. Number of first captures of gopher tortoises (*G. polyphemus*) as a percentage of the total during each time period at the East Section site of the Archbold Biological Station, Lake Placid, Florida

Year	Male	Female	Juvenile	Adult
1967–1979	27.0 %	7.8 %	65.2 %	34.8 %
1980–1990	26.9 %	16.3 %	56.8 %	43.2 %
1991–2001	42.8 %	26.6 %	30.6 %	69.4 %
2002	38.5 %	61.5 %	0.0 %	100 %
1967–2002	23.3 %	8.5 %	68.2 %	31.8 %

Table 2. Number of first captures of gopher tortoises (*G. polyphemus*) as a percentage of the total during each time period at the West Section site of the Archbold Biological Station, Lake Placid, Florida

Year	Male	Female	Juvenile	Adult
1969–1979	40.5 %	8.3 %	51.2 %	48.8 %
1980–1990	31.9 %	12.8 %	55.3 %	44.7 %
1991–1998	52.8 %	13.2 %	34.0 %	66.0 %
1969–1998	37.1 %	8.0 %	54.9 %	45.1 %

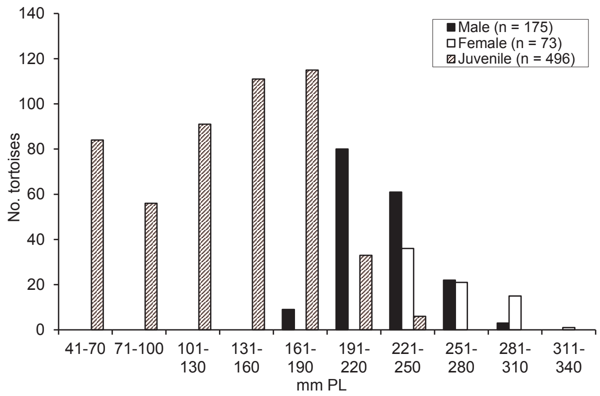

Figure 1. Body size distribution of first time captures of gopher tortoises (*G. polyphemus*) during the entire duration of the study in the East Section of the Archbold Biological Station, Lake Placid, Florida

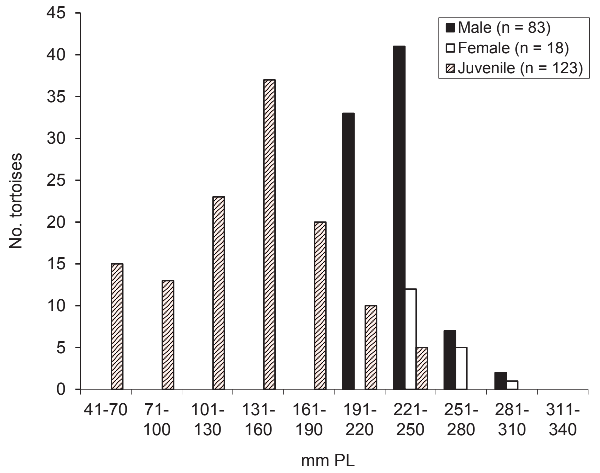

Figure 2. Body size distribution of first time captures of gopher tortoises (*G. polyphemus*) during the entire duration of the study in the West Section of the Archbold Biological Station, Lake Placid, Florida

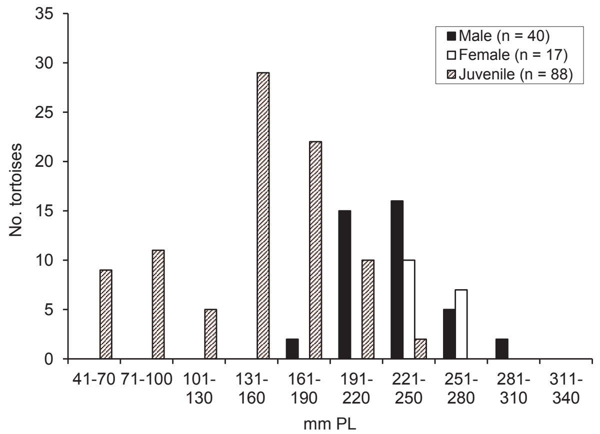

Figure 3. Body size (mm PL) distribution of first time captures of gopher tortoises (*G. polyphemus*) during 1967–1970 in the East Section of the Archbold Biological Station, Lake Placid, Florida

Sex ratio

During nearly all of the time periods and for combined time periods from both sites, adult males outnumbered adult females (Tables 3–4).

Population size

Overall in the East Section, males (Fig. 4) were more numerous than females (Fig. 5), and juveniles (Fig. 6) were more numerous than either sex at adult stage. Over time, numbers of males and females increased, whereas that of juveniles remained stable.

Table 3. Number of first captures of gopher tortoises (*G. polyphemus*) during each time period at the East Section site of the Archbold Biological Station, Lake Placid, Florida

Year	Male	Female	Juvenile	Total	Unknown	Final Total
1967–1979	103	30	249	382	51	433
1980–1990	104	63	220	387	35	422
1991–2001	74	46	53	173	13	186
2002	10	16	0	26	1	27
1967–2002	169	62	498	729	66	795

Table 4. Number of first captures of gopher tortoises (*G. polyphemus*) during each time period at the West Section site of the Archbold Biological Station, Lake Placid, Florida

Year	Male	Female	Juvenile	Total	Unknown	Final Total
1969–1979	34	7	43	84	3	87
1980–1990	30	12	52	94	4	98
1991–1998	48	12	31	91	10	101
1969–1998	83	18	123	224	9	233

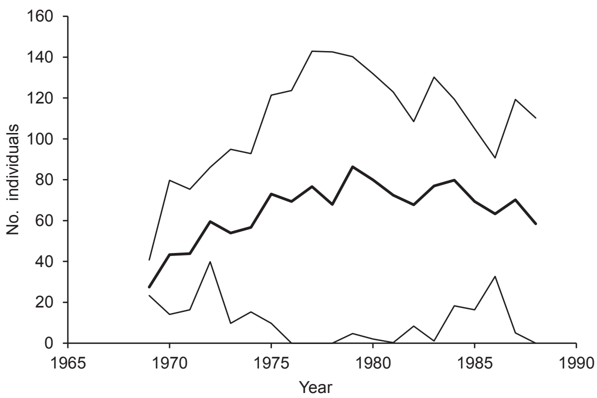

Figure 4. Population estimates of male gopher tortoises (*G. polyphemus*) during 1968–1988 in the East Section of the Archbold Biological Station, Lake Placid, Florida. Estimates are accompanied with upper and lower 95 % confidence levels.

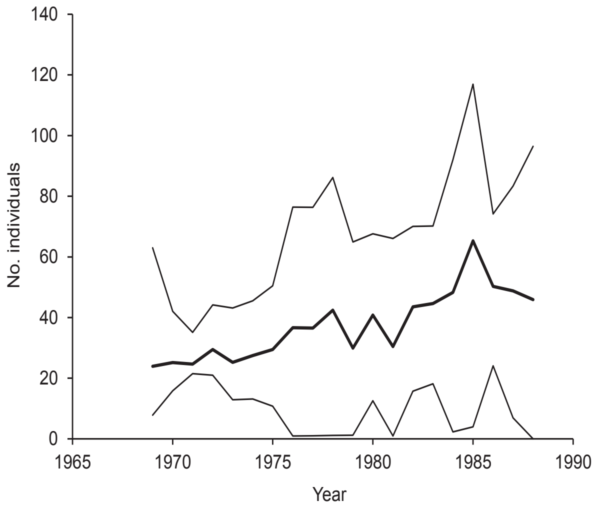

Figure 5. Population estimates of female gopher tortoises (*G. polyphemus*) during 1968–1988 in the East Section of the Archbold Biological Station, Lake Placid, Florida. Estimates are accompanied with upper and lower 95 % confidence levels.

Figure 6. Population estimates of juvenile gopher tortoises (*G. polyphemus*) during 1968–1988 in the East Section of the Archbold Biological Station, Lake Placid, Florida. Estimates are accompanied with upper and lower 95 % confidence levels.

Body size and condition

Minimum body size at sexual maturity

Based on dissections, the smallest male with enlarged testes relative to body size and active sperm in the vasa deferentia measured 186 mm PL. It was at this body size also that the relative length of the gulars was increasing from a minimum of about 12 % to a maximum of about 19 % of body size (Fig. 7). The smallest dissected female containing oviductal eggs was 225 mm PL. Using conversion formulas from regression equations (Fig. 8), we determined that the smallest sexually mature male measured 209.8 mm CL, and smallest sexually mature female measured 253.1 mm CL.

Mean body size at sexual maturity

The data distribution for plastron length (mm) was not

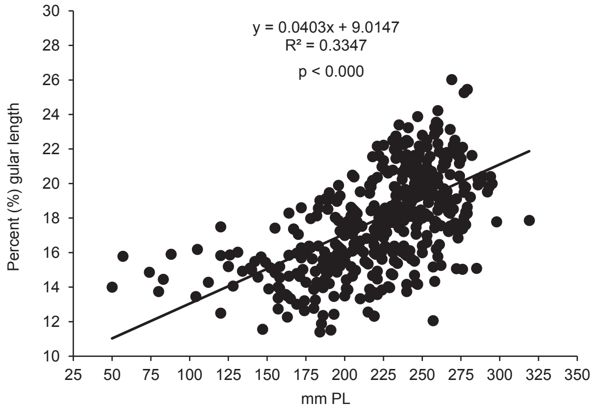

Figure 7. Relative length of the gular plate as a percentage of the plastron length on 415 male gopher tortoises (*G. polyphemus*) from the Archbold Biological Station, Lake Placid, Florida

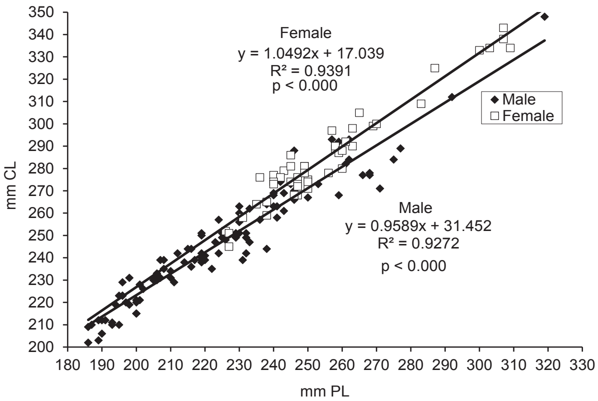

Figure 8. Relationship between body size in mm carapace length (CL) and body size in mm plastron length (PL) in male and female gopher tortoises (*G. polyphemus*) from the East Section of the Archbold Biological Station, Lake Placid, Florida

normally distributed (A^2 = 1.283, *P* = 0.002); therefore, we normalised the data using the normalise function within the MiniTab 13.0 statistical package (MiniTab, Inc. State College, Pennsylvania). The resulting normalised dataset was analysed with a General Linear Model with location and sex set as predictors. Interaction between sex and location was set as a third predictor. Male turtles (mean = 223.7 ± 22.0) were significantly smaller in CL than females (mean = 251.2 ± = 19.4) across study sites (*P* < 0.001). Ignoring gender, CL did not differ between the eastern (mean = 229.7 ± 25.7) and western (mean = 231.24 ± 21.4) study sites (*P* = 0.775). However, PL may have been affected by an interaction between sex of a turtle and location (*F* = 3.15, df = 1, *P* = 0.077). Males from the eastern study site (mean = 221.6 ± 22.6; range = 186–302; N = 163) were similar in size to males (mean = 227.8 ± 20.3; range = 187–305; N = 83) from the western study site. However, females from the eastern (mean = 252.5 ± 19.3; range = 225–309; N = 58) study site were somewhat larger than those (mean = 246.9 ± 19.5 mm PL; range = 225–309; N = 18) from the western study site. However, more data collection is needed to verify whether this is an artefact of smaller sample sizes among females.

Body size dimorphism

Body size dimorphism was weak in both populations. The ratio of mean male body size to mean female body size was high in both the East Section (0.88) and West Section (0.92).

Condition

Using Fulton's K for analysis (weight/length^3) and Duncan's Multiple Range Test, we found significant effects of location (*P* = 0.023, East 2.52 > West 2.46), Sex (*P* = 0.0001, female 2.55, Juvenile 2.54 > male 2.46), but not season (*P* = 0.0855, Winter 2.56, Spring 2.52, Summer 2.509, Fall 2.501) or year (*P* = 0.1350) with respect to body condition of gopher tortoises. In effect, East Section tortoises fared better in condition, even if marginally so, than did their West Section counterparts. Although season did not affect condition of gopher tortoises, the difference among sex and age-class may have reflected the greater energy expenditure by males because of greater movements.

Growth and survivorship

Growth

Von Bertalanffy growth curves generated for both East and West Sections of the ABS assumed a hatchling size of 44 mm PL and minimum body sizes at sexual maturity of 186 mm PL for males and 225 mm PL for females. In the East Section, asymptotic growth was 260.7 mm PL for males (SE = 3.40; 95 % CI = 253.9–267.4) and 272.4 mm PL for females (SE = 4.65; 95 % CI = 263.2–281.6). The time necessary to reach sexual maturity was 7.39 years for males (95 % CI = 6.31–9.31) and 12.74 years for females (95 % CI = 10.08–17.10) (Fig. 9). In the West Section, asymptotic growth was 248.1 mm PL for males (SE = 5.07; 95 % CI = 237.7–258.5) and 257.3 mm PL for females (SE = 8.61; 95 % CI = 239.0–275.5). The time necessary to reach sexual maturity was 8.42 years for males (95 % CI = 5.88–13.45) and 10.27 years for females (5.39–31.51) (Fig. 10). It appears from our findings that the West Section tortoises were growing at rates that were similar to those of the East Section. We are cautious about this comparison in light of the smaller sample sizes in the West Section, as evidenced by the greater confidence intervals.

Survivorship

We estimated survivorship using CJS open population models. Best model estimated equal survival for adult males and females (0.919 ± SE 0.0079). Juvenile survivorship was slightly lower than that of adults but still high (0.826 ± SE 0.014).

Recapture rates

Recapture rates differed by sex, age, and time. Generally speaking, capture probability ranged from about 30–80 % for adults and 15–40 % for juveniles. No annual variation or sex effects were found in transition rates from juvenile

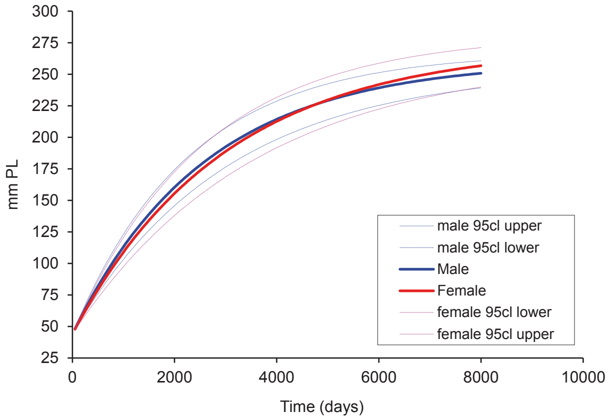

Figure 9. Von Bertelanffy growth curve estimated for gopher tortoises (*G. polyphemus*) of the East Section of the Archbold Biological Station, Lake Placid, Florida

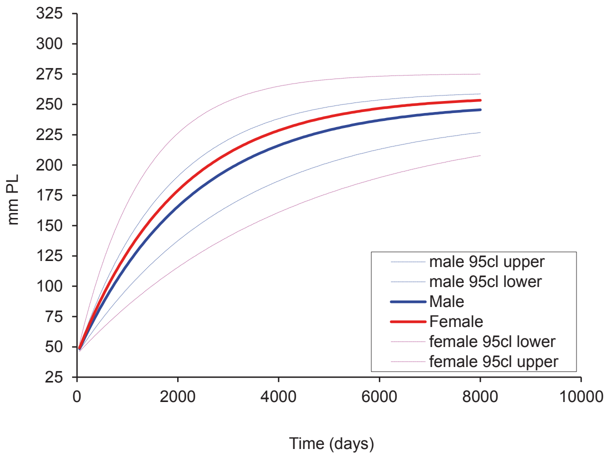

Figure 10. Von Bertelanffy growth curve estimated for gopher tortoises (*G. polyphemus*) of the West Section of the Archbold Biological Station, Lake Placid, Florida

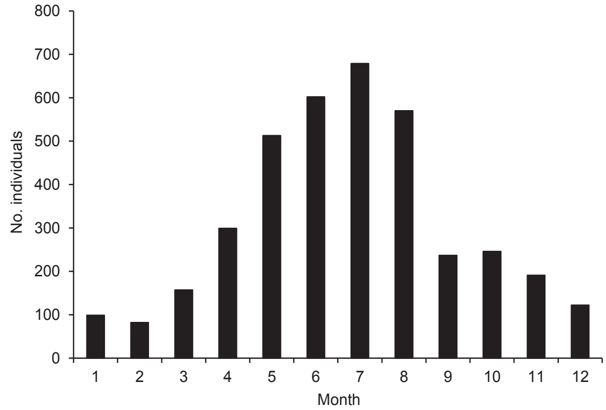

Figure 11. Combined records of all gopher tortoise (*G. polyphemus*) sightings (n = 3,797) for each month during 1967–2002 on the Archbold Biological Station, Lake Placid, Florida.

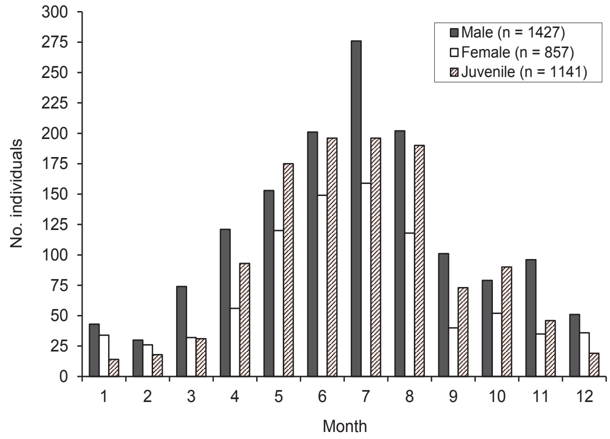

Figure 12. Combined records of all male, female, and juvenile gopher tortoise (*G. polyphemus*) from mark-recapture records for each month during 1967–2002 on the Archbold Biological Station, Lake Placid, Florida

to adult for either sex (0.0399 ± SE 0.005). The 95 % Confidence Intervals were 0.9035 to 0.9345 for adult males and females and 0.7986 to 0.8534 for juveniles. The probability of a juvenile becoming an adult of either sex was about 4 % annually.

Activity

Seasonal

We found continuous activity out of the burrow by the ABS population with most activity occurring during April–August (Fig. 11). Among males, seasonal activity was greatest during April–August. Among females and juveniles, seasonal activity was greatest during May–August (Fig. 12). Indeed, among the marked animals, only 7.6 % of all captures occurred during the three coldest months of December–February.

Diel

On the ABS, the species was diurnal in its activity with activity centred around the warmest parts of the day, consistently avoiding late afternoon and morning during the winter (Fig. 13). Very few records associated with Figure 13 provided an estimation of cloud cover. Consequently, we cannot rule out the possibility that mixing cloudy-cool day with sunny-hot day records could be responsible for the observed peak in distribution of afternoon activity in summer. The range of active hours was greatest during the hottest months.

Movements

Distance moved from original capture and between captures

Movement data for gopher tortoises from the eastern study site (Table 5) were not distributed normally (Anderson-Darling: A^2 = 16.59, P < 0.001). Movements for adult male and female gopher tortoises from the eastern study site (Table 5) were not distributed normally (Anderson-Darling: A^2 = 8.851, P < 0.001). Adult gopher tortoises from the eastern site (mean = 1,498.4 ± 1,499.2 m; N = 162) moved more from site of original capture (two sample t = 5.36, df = 173, P < 0.001) than did juveniles (mean = 781.1 ± 1,063.7 m; N = 89). Adult male gopher tortoises from the eastern study site moved somewhat more from site of original capture than did females

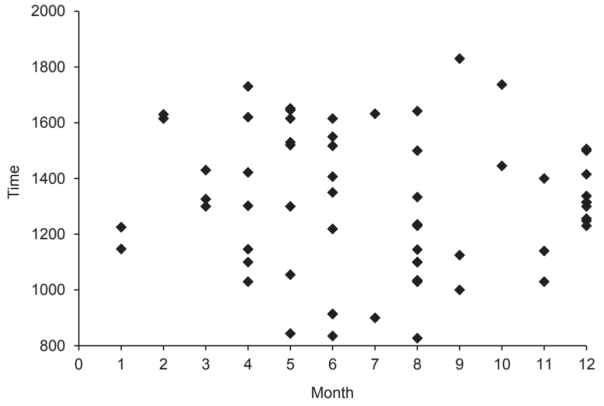

Figure 13. Combined records of all gopher tortoise (*G. polyphemus*) sightings (n = 64) for each hour during 1967–2002 on the Archbold Biological Station, Lake Placid, Florida

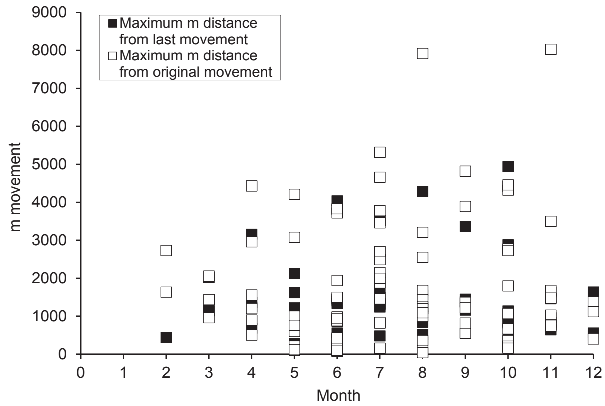

Figure 14. Monthly distance from original capture site and from last capture site for 99 male gopher tortoises (*G. polyphemus*) from the East Section of the Archbold Biological Station, Lake Placid, Florida

Table 5. Mean movements (m) by gopher tortoises (*G. polyphemus*) from the East Section of the Archbold Biological Station, Lake Placid, Florida. Means are followed by standard deviation.

Category	Mean movement (m) from previous site of capture	Mean movement (m) from original site of capture
Male	1,552.5 ± 1,554.8; range = 40–8030; N = 99	1,645.5 ± 1,586.5; range = 40–8030; N = 99
Female	1,202.7 ± 1,223.5; range = 40–5740; N = 63	1,267.3 ± 1,330.2; range = 40–6020; N = 63
Juvenile	768.4.0 ± 1,099.4; range = 0–5000; N = 89	781.1 ± 1,063.7; range = 0–5000; N = 89

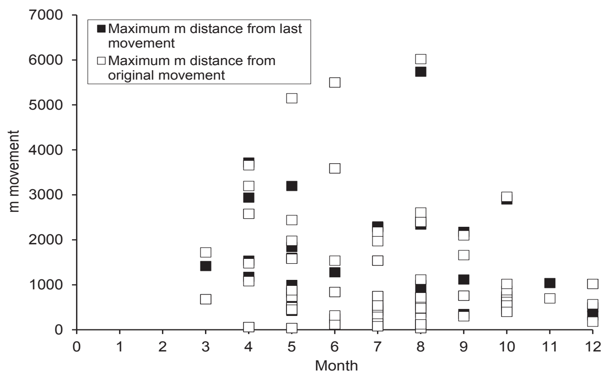

Figure 15. Monthly distance from original capture site and from last capture site for 63 female gopher tortoises (*G. polyphemus*) from the East Section of the Archbold Biological Station, Lake Placid, Florida

(Table 5) but not statistically so (two sample t = 1.79, df = 133. *P* = 0.075). From further analysis using Tukey's pairwise comparison, we found that mature males did not move more than mature females (Tukey: -0.1145, 0.5925); but, juveniles moved significantly less than either adult males (Tukey: 0.4473, 1.0881) or females (Tukey: 0.1676, 0.8899). For males (Fig. 14), females (Fig. 15), and juveniles (Fig. 16), movements were greatest in distance and most numerous during April–October.

Distance moved from previous site of capture

Movements among gopher tortoises were not distributed normally (Anderson-Darling: A^2 = 17.9, $P <$ 0.001). Movements from previous site of capture in the East Section (Table 5) among adults (mean = 1416.5 ± 1441.3 m; range = 40–8030) were significantly larger (two sample t = 3.99, df = 133. $P < 0.001$) than those of juveniles (mean = 768.4 ± 1099.4 m; range = 0–5000). Males, females, and juveniles dispersed differently (Table 5) since the previous encounter (F = 8.20, df1 = 2, df2 = 250, $P < 0.001$). Males moved significantly further (Tukey: 331, 1237) than did juveniles. Female movements were intermediate between those of males and juveniles and not significantly different from males (Tukey: -150, 850) or juveniles (Tukey: -77, 945). Generally, females moved less than males but more so than juveniles from site of last capture.

Home range size- The home range data for gopher tortoises were not normally distributed (A^2 = 8.63, P < 0.001). The home range data for mature male and female gopher tortoises were not normally distributed (Anderson-Darling: A^2= 7.883, $P < 0.001$). The home range sizes of mature gopher tortoises (mean = 6.07 ± 7.0 ha; N = 102) were not significantly different in size (two-sample t = 1.04, df = 188, *P* = 0.31) than those of immature individuals (mean = 1.32 ± 6.7 ha; N = 6). The home ranges of mature males (6.3 ± 7.3 ha; range 0.07–36.5; N = 64) were not significantly different (two-sample t = 1.04, df = 74, *P* = 0.304) from those of mature females (5.6 ± 6.5 ha; 0.1–26.6; N = 38). Collectively, adults occupied larger home ranges than did juveniles (F = 6.55, df = 1, *P* = 0.012).

Habitat use

In the East Section, males, females, and juveniles were most often found in southern ridge sandhill, followed by scrubby flatwoods, and sand pine scrub (Table 6). More specifically, gopher tortoises were found more often in turkey oak phase sandhill than in hickory phase (Table 7). In scrubby

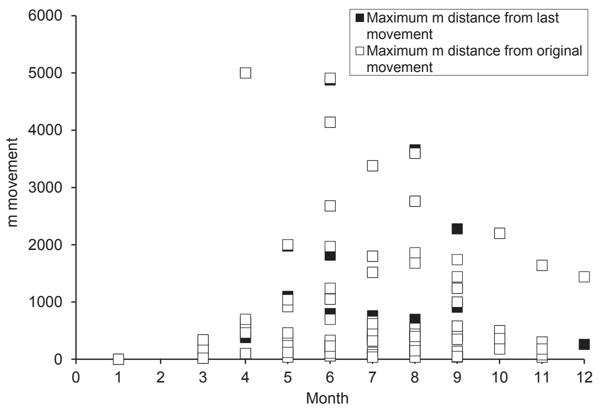

Figure 16. Monthly distance from original capture site and from last capture site for 81 juvenile gopher tortoises (*G. polyphemus*) from the East and West Sections of the Archbold Biological Station, Lake Placid, Florida

Table 6. Number of records of individuals for each general habitat type used by gopher tortoises (*G. polyphemus*) from the East Section of the Archbold Biological Station, Lake Placid, Florida

Habitat	Male	Female	Juvenile	Total
Bayhead	1	0	2	3
Flatwoods	83	49	84	216
Improved pasture	1	0	0	1
Ruderal	84	56	49	189
Sand pine scrub	186	104	148	438
Scrubby flatwoods	236	148	228	612
Seasonal Pond	4	4	3	11
Southern Ridge sandhill	401	278	331	1010
Total	926	595	776	2297

Table 7. Number of records of individuals for each specific habitat type used by gopher tortoises (*G. polyphemus*) from the East Section of the Archbold Biological Station, Lake Placid, Florida.

Habitat	Male	Female	Juvenile	Total
Bayhead	1	0	2	3
Flatwoods-cutthroat grass phase	4	4	2	10
Flatwoods- gallberry phase	9	1	13	23
Flatwoods- palmetto phase	70	44	69	183
Improved pasture	1	0	0	1
Human-modified oldfield	66	53	43	162
Human-modified garden	18	3	6	27
Human-modified land-scape	28	24	37	89
Sand pine scrub-mature oak phase	186	104	148	438
Scrubby flatwoods-live oak phase	187	98	158	443
Scrubby flatwoods-inopina oak phase	49	50	70	169
Seasonal pond	4	4	3	11
Southern Ridge sandhill-hickory phase	160	93	160	413
Southern Ridge sandhill-turkey oak phase	241	185	171	597
Total	1,024	663	882	2,569

flatwoods, gopher tortoises were found more often in live oak phase than in the inopina oak phase (Table 7). Of the remaining habitats, flatwoods and ruderal habitats were used extensively by gopher tortoises. Far and away, palmetto phase was the preferred flatwoods type, and old field was used most often by gopher tortoises in human-modified habitats (Tables 6–7).

Burrow dynamics

Tortoise use

Over the 24-year period, only three (1.6 %) of 192 active burrows initially detected were still active, the steep decline of which was evident the following year of the study (Fig. 17). Likewise, of 16 inactive burrows, only one (6.3 %) burrow subsequently became home to a gopher tortoise (Fig. 17), suggestive of little competition for burrows. The burrow widths co-varied significantly ($P < 0.000$) with the shell width of the largest resident at each of the three distances from the burrow entrance (Fig. 18).

Commensal vertebrate species

On the ABS, the following vertebrates were observed by JNL entering or leaving gopher tortoise burrows: Florida gopher frog (*Lithobates capito aesopus*), southern black racer (*Coluber constrictor priapus*), eastern indigo snake (*Drymarchon couperi*), eastern coachwhip (*Masticophis flagellum flagellum*), Florida pine snake (*Pituophis melanoleucus mugitus*), Florida mouse (*Podomys floridanus*), cotton mouse (*Peromyscus gossypinus*).

Reproduction

Fertility

Males dissected in May (193 mm PL) and October (186 mm PL) had enlarged yellowish-coloured testes with abundant sperm in the ducts (Fig. 19), indicating fertility at least during May–October for which we have data (Fig. 19).

Nesting

On the ABS, a female with enlarged ova (32 mm) was found on 29 April 1977. Females with shelled eggs were found during May (N = 3), and nests were found in May (N = 1) and June (N = 2).

Clutch size

Five shelled eggs were recovered from a dissected 225 mm PL female. Two nests excavated in the field contained five and six eggs.

Annual clutch production

From a single dissected female, no evidence existed for the production of more than one clutch for the season.

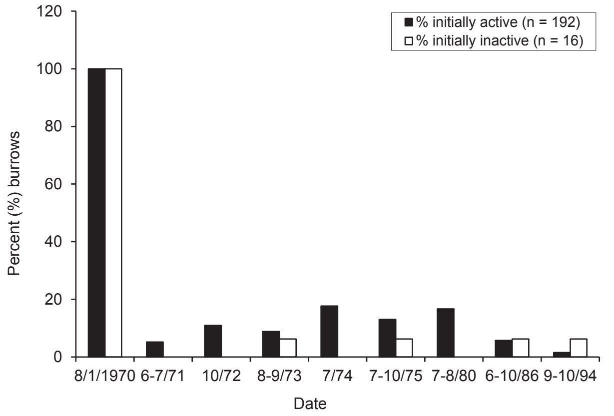

Figure 17. Temporal changes in the status of gopher tortoise (*G. polyphemus*) burrows on the Archbold Biological Station, Lake Placid, Florida

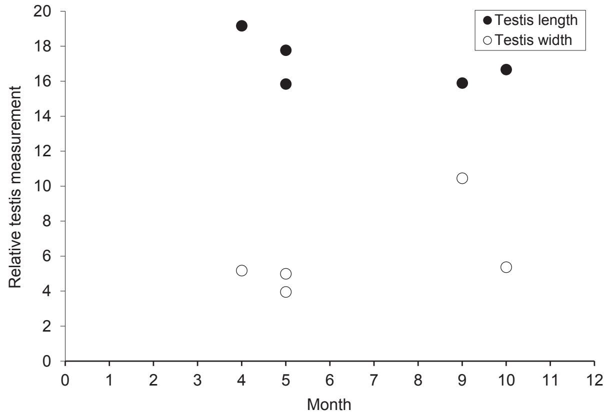

Figure 19. Monthly distribution of right testis lengths and widths as a percent of body length in five male gopher tortoises (*G. polyphemus*) on the Archbold Biological Station, Lake Placid, Florida

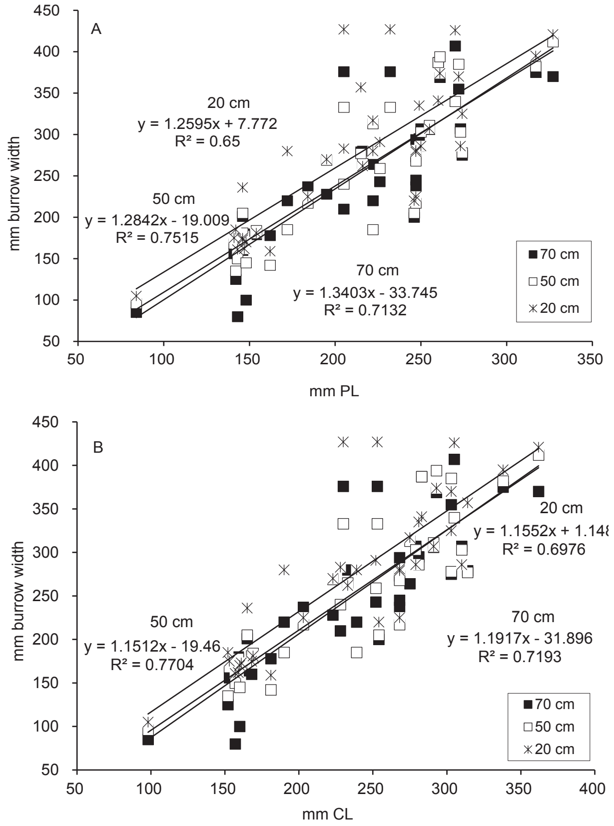

Figure 18. Relationship between burrow diameter at three different distances from the burrow entrance and body size in gopher tortoises (*G. polyphemus*) (n = 37) on the Archbold Biological Station, Lake Placid, Florida. **A** = plastron length, **B** = carapace length. All regression analyses were significant to $P < 0.000$.

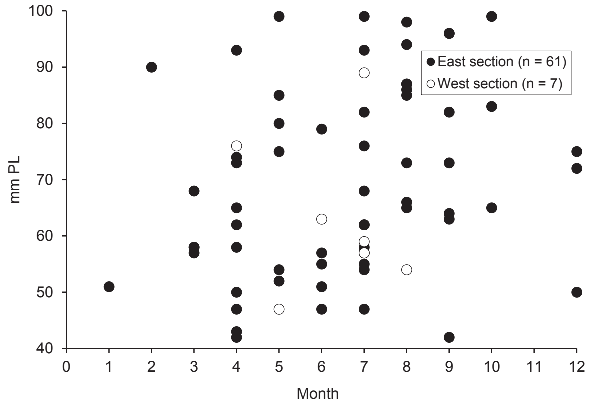

Figure 20. Monthly distribution body sizes of small gopher tortoises (*G. polyphemus*) captured in the East Section and West Section of the Archbold Biological Station, Lake Placid, Florida

Egg dimensions

Shelled egg dimensions for a five-egg clutch dissected from a 225 mm PL female found 12 June 1983 were 44.5 X 38.9 mm, 42.8 X 38.5 mm, 44.0 X 37.5 mm, 47.4 X 37.1 mm, 49.2 X 36.3 mm. Shelled egg dimensions for a six-egg clutch dug from the field 25 June 1979 were 44.5 X 43.2 mm, 46.3 X 41.0 mm, 46.0 X 42.7 mm, 45.4 X 44.0 mm, 48.2 X 42.1 mm, 46.6 X 42.8 mm.

Hatching season

On the ABS, the smallest individuals were found during April–September (Fig. 20).

Hatchling body size

On the ABS, the smallest individuals we found measured 42 mm PL (Fig. 20).

Diet

General

On the ABS, gopher tortoises were primarily, but not exclusively, herbivorous and ate a wide range of primarily plant items (Table 8). To that end, grasses (both native and landscape), saw palmetto, and pusley (*Richardia* spp.) were prominent in their diet as were various parts of pines and bromeliads (Table 8).

Coprophagy

Four instances of coprophagy by one female (263 mm PL) and three juveniles (163, 182, 192 mm PL) took place while the tortoises were being held for processing and had immediate access to the conspecific scats. In one of these instances, the scat was old and dry but was sought

Table 8. Diet as reported by numbers of tortoises associated with 203 records of 83 food categories from field observations, scat observations, and scat analysis of 127 gopher tortoises (G. *polyphemus*) on the Archbold Biological Station, Lake Placid, Florida

Food item	No. tortoises with food item
Richardia spp. (includes *R. brasiliensis* and *R. scabra*)	50
Paspulum setaceum	33
Tillandsia spp.	32
P. notatum	22
Serenoa repens	19
Grass (unknown seeds and leaves)	16
Plant (unknown leaves, stems)	15
Pinus elliottii (needle)	13
Euphorbiaceae (includes *Euphorbia maculata*)	11
Vaccinium spp. (includes leaf, capsule, seed, stem)	11
Quercus spp. (leaf)	9
Andropogon (seed, stalk)	8
Pinus spp. (needle)	8
Gopherus polyphemus feces	5
Opuntia (seed)	5
Palmetto (seeds)	5
Rock	5
Seed unknown	5
Selaginella spp.	5
Diodella rigida	4
Pinus spp. (cone petal)	4
Carya sp.	3
Chapmannia floridana	3
Coleoptera (parts)	3
Commelina erecta var. *angustifolia*	3
Diodella teres	3
Eremochloa ophiuroides	3
Lupinus spp. (leaves, seeds)	3
Prosapia	3
Sabal etonia (includes berries)	3
Schrankia spp.	3
Tragia urens	3
Bird feathers	2
Cenchrus spp.	2
Panicum	2
Parthenocissus quinquefolia	2
Sciurus carolinensis (bones, fur, teeth)	2
Setaria corrugata	2
Sida cordifolia	2
Smilax auriculata	2
Vitis spp.	2
Ampelopsis arbores	1
Asimina triloba (seeds)	1
Atrenius fattigi	1
Berosus	1
Camaechrista fasiculata	1
Campsis radicans	1
Cassia chamaecrista	1
Chrysopsis graminifolia	1
Citrus spp. (seed)	1
cocoon	1
Cyperaceae (*Fimbistylis* or *Bulbostylis*)	1
Danthonia spicata	1
Dasypus novemcinctus (rib bones)	1
Dermestidae	1
Diachlorus ferrugatus	1
Drymarchon corais (scutes)	1
Froelichia floridana	1
glass chunks	1
Gnaphalium falcatum	1
Gnaphalium purpuresceus	1
Heterotheca scabrella	1
Hydrocanthus spp.	1
Lactarius volenus	1
Lycania michauxii	1
Myrica sp.	1
Oldamlandia corymbosa	1
Opuntia (spine)	1
Oxalis spp.	1
Paspalum spp.	1
Persea spp. (leaves)	1
Polygonella fimbriata	1
Quercus geminata (leaf)	1
Quercus myrtifolia (cap)	1
Quercus virginianus (whole acorns)	1
Sand	1
Schinia rivulosa	1
Serenoa repens (berries)	1
Serica frosti	1
Solanum spp.	1
Thrinax microcarpa	1
Ximenia americana	1

out and eaten by the 192 mm PL juvenile. In the field, a 281 mm PL female was observed eating an old dry conspecific scat. Besides potential nutritive value, we are unsure of the extent to which coprophagy helps or hinders subsequent germination of seeds already passed through once in its digestive system.

Predators

On the ABS, black bear (*Ursus americanus*) and Raccoon scat were found by JNL to have contained remnants of juvenile gopher tortoise.

Mortality factors

On the ABS, hog wire fence trapped and sometimes killed adults, and humans harvested active tortoises found alongside the road and inactive tortoises in burrows near the road.

DISCUSSION

Population Demographics

Population structure

The low percentage of adults in our two sites, particularly in the East Section, stood in sharp contrast to values reported elsewhere in Florida. For example, at a coastal location in south-western Florida, adults comprised 56.5 % of the captures (McLaughlin, 1990), and in 2013 at a south-eastern Florida coastal site in Jupiter, Florida, adults comprised 65 % of the censused population (Jon A. Moore, pers. comm.). Adult composition was high for both a pine flatwoods/hardwood hammock site (70 %) and a mostly pasture and some upland hammock site (77.1 %) in west-central Florida (Godley, 1989). At one sandhill and two modified habitats studied during 1981–1987 in northern Florida, adults comprised 40–54 % of the population (Diemer, 1992a). In a follow-up survey in 2009 (Diemer Berish et al., 2012), fewer juveniles were captured resulting in a different population structure. A population decline or difficulty in detectability of juveniles because of floristic changes was thought to be responsible for fewer captures of juveniles in 2009 (Diemer Berish et al., 2012). In north-central Florida adults comprised 80.6 % of populations (Smith, 1995). We are unsure to what extent the duration of this study affected the estimate of adult composition, whereby a long period of time of search would offset the difficulty of detecting small, inconspicuous members of the population. Compared to these other studies, habitat did not seem to control the composition of adults in the population. At least for the East Section, which borders a road and was also bisected partially by a road, we wonder if harvesting pressure on adults, particularly evident in the early years, resulted in more space for juvenile animals. To that end, the temporal trend in adult composition was to increase, such that by 1999, the adult composition (Table 1) was on par with that of other studies (op. cit.). In contrast, the West Section population was buffered from the road by unburned, low quality habitat thereby providing more, even if not complete, protection to a comparatively smaller population from harvesting. Consequently, the earliest values for adult composition were higher than those of the East Section, and by contemporary times, the adult composition was likewise on par with others (Table 2).

Sex ratio

At both of our sites, males tended to greatly outnumber females. In light of the intensive search effort during the early years of this study, the duration of this study, and the corroborative sex ratio values at different time intervals, we believe the male-biased sex ratio on the ABS to be affirmed. This finding was in keeping with many, but not all, other populations. For example, males outnumbered females in south-eastern Florida (Fucigna & Nickerson, 1989). The same was true at one sandhill and two modified habitats in northern Florida during 1981–1987 (1.00:1.31) (Diemer, 1992a) but differed (1.00:0.73) in a follow-up survey in 2009 (Diemer Berish et al., 2012). In a west-central Florida pine flatwoods/hardwood hammock site, males outnumbered females, but were outnumbered by females at another site comprised primarily of pasture and secondarily by upland hammock (Godley, 1989). In west-central Florida (Linley, 1986) and in north-central Florida (Smith, 1995), the sex ratio was even. In coastal south-western Florida, the overall sex ratio was even but was female-biased at one site (McLaughlin, 1990). In Jupiter, Florida, females dominated slightly (0.88:1:00) in a 2013 census (Sano, 2014).

Habitat preference

Based on counts of animals and our model, findings on the ABS conformed to the findings that the gopher tortoise preferred grasslands or grassland analogues (Ashton & Ashton, 2004, 2008), such as the sandhill of the east section more than the eastern desert scrub of the west section on the ABS.

Population size

Population densities on the ABS were low, perhaps because of the poor quality of habitat, especially in the scrub of the west section. In the east section with 431.94 ha of living space, densities scarcely reached one tortoise/ha. Elsewhere in Florida, population densities averaged 16.7 tortoises/ha (range = 4.2–24.9 tortoises/ha) in four south-western Florida sites (McLaughlin, 1990).

On the ABS, adults could use more than one burrow (Douglass & Layne, 1978), tortoise body size and burrow widths were strongly correlated (Martin & Layne, 1987), and the burrows excavated by juveniles were shorter than those of adults and the widths of the burrows reflected the size of the juvenile (Meshaka & Layne, 2015).

Numbers of burrows provided a different measure of abundance. For example, burrow counts yielded a population estimate of 11.3 tortoises/ha in 1979 on Cape Sable (Kushlan & Mazzotti, 1982). Surveys on Cape Sable by McCoy & Mushinsky (1992) showed no changes during 1978–1979 or 1987–1988. Follow-up surveys in 2001(Waddle et al., 2006) detected a sharp decline in estimated density of active burrows from 14.5/ha in 1979 to 4.4/ha in 2001 although the overall number of burrows remained relatively stable.

Mushinsky & McCoy (1994) noted that although population densities as estimated by number of burrows from many sites in Florida were less than 10 tortoises/ha, densities of two sites exceeded 30 tortoises/ha. Small parcels of suitable quality can support large populations. For example, more than 40 tortoises were found on a 1.21 ha coastal strand site near Vero Beach, Florida, indicating a population density of 27.5 tortoises/ha (Jon A. Moore, pers. comm.).

In Florida, a strong relationship was detected between numbers of active plus inactive burrows and area for both mainland and island sites, but density of gopher tortoises decreased as habitat increased on mainland but not islands perhaps because insular populations were forced to make do with what was available instead of dispersing to optimal habitat (Mushinsky & McCoy, 1994). Interestingly, 65 burrows/ha were calculated for a 1.21 ha coastal strand site in Vero, Beach, Florida

(Jon A. Moore, pers. comm.). In south-central Florida, densities of active burrows were lower in scrub (0.6/ha) and flatwoods/plantations (0.21/ha) (Castellón et al., 2012). Habitat quality varied with up to 2.7 tortoises/ha in disturbed habitat in east-central Florida (Breininger et al., 1994) to 7.6 tortoises/ha in northern Florida pine-oak habitat (Diemer, 1989). In north-central Florida, mean burrow densities for two sandhills were 2.4 burrows/ha and 10.6 burrows/ha, and mean densities for two old fields were 6.0 burrows/ha and 7.6 burrows/ha (Smith, 1995). In South Carolina, 1.8 tortoises/ha inhabited pine-turkey oak and 0.4 tortoises/ha were found in turkey oak-hawthorn (Wright, 1982).

Body size at sexual maturity

Minimum body size at sexual maturity

The body size at which the gopher tortoise reached sexual maturity appeared to have varied more by location than by latitude (Table 9). This finding was especially evident in females, whereas in males the largest values were to be found in the northernmost sites. At least among males complicating this topic were the varying criteria used for determining sexual maturity. For example, using fertility as the criterion, ABS males reached maturity at smaller body sizes (this study; White et al., 2018) than those of south-western Georgia (Landers et al., 1980). Among males in west-central Florida, plastral concavity was detected at 200 mm CL and full concavity at 240–250 mm CL, which yielded a minimum size at sexual maturity of 240 mm CL (Mushinsky et al., 1994). In northern Florida, the smallest males measured 177 mm CL based on development of gulars and plastral concavity (Diemer & Moore, 1994). Gular projections were found to be a sexually-dimorphic trait, with those of adult males being relatively longer and more deeply-notched than those of adult females (Meshaka & Layne, 2015). In south-western Georgia, males were sexually mature at 230–240 mm CL, and all males visiting females were at least 240 mm CL (Landers et al., 1982). However, males with active sperm were as small as 203 mm CL.

Mean adult body size

Body sizes of adult gopher tortoises were found to be largest in northern and southern populations and smallest at sites of intermediate latitude, temperature, productivity, and seasonality (Ashton et al., 2007) (Table 9). Data from this study corroborated findings by Ashton et al. (2007), who also used data from the ABS.

Sexual dimorphism in body size

Across its geographic range, degree of body size dimorphism tended to be stronger at minimum body size at sexual maturity than at mean adult body size, which was generally near unity (Table 9). Still, among the 20 largest adults of each sex, males were smaller and weighed less than did females (Meshaka & Layne, 2015). Predation was found to shape body size and body size dimorphism in this species. For example, females were larger than males at a pine flatwoods/hardwood hammock site in west-central Florida (Godley, 1989). Both sexes from that site were larger than the equal-sized males and females from a primarily pasture with some upland hammock site in west-central Florida (Godley, 1989). The smaller size and lack of sexual dimorphism at the latter site was thought to be a result of human harvest pressure on large adults (Godley, 1989). Estimated by burrow width, northern Florida tortoises (Alford, 1980) were smaller than those of Cape Sable, a coastal strand in extreme southern Florida (Kushlan & Mazzotti, 1982, 1984). The largest tortoises from Alford's (1980) study were those from ruderal settings. Difference in body size dimorphism between the two ABS sites seem best explained by differential human predation, whereby males of the roadside colony were smaller perhaps because of differential susceptibility to harvest than those of the protected west section population. Geographic variation in sexual dimorphism in this species has not been restricted to body size. Mushinsky et al. (1994) noted greater dimorphism not only in carapace length, but also in bridge width and bridge thickness in Georgia populations than in gopher tortoises in Tampa.

Body condition

In general, condition values were higher among individuals of the more productive East Section than the West Section. In contrast, females did not differ in condition between scrub and flatwoods habitats at the Avon Park Air Force Range in south-central Florida (Rothermel & Castellón, 2014). Condition of individuals from neither our study nor those of Rothermel & Castellón (2014) was affected by season. Our findings of overall lower values among males appeared to have been related to their greater movements regardless of location.

Growth and survivorship

Generally speaking, the gopher tortoise took longest to mature in northernmost latitudes (Table 9). Our findings conformed to that pattern. However, habitat quality may have played a role in the differences in age of sexual maturity between two populations from nearby sites (Godley, 1989; Mushinsky et al., 1994). For example, in southern Alabama and south-western Georgia, differences in growth and survivorship were related to land management practices in populations located not far from on another (Tuberville et al., 2014). In slash pine plantations in south-central Alabama, gopher tortoises required 20 years to mature, presumably because of human disturbance of the site that resulted in loss of forbs (Aresco & Guyer, 1999a). Notwithstanding natural or human-mediated differences in habitat quality to explain differences in growth rates among sites, geographic differences exist in growing seasons. In that regard, most growth occurs during May-September in northern Florida (Auffenberg & Iverson, 1979) as compared to April–October in south-western Georgia (Landers et al., 1982).

The asymptotic body size of the gopher tortoise on the ABS was reached at smaller sizes in males (260.7 mm PL, 281.4 mm CL) than in females (272.4 mm PL, 302.8 mm CL). The same trend was evident in south-central Alabama, where asymptotic body size was smaller in males (270.6 mm CL) than in females (322.6 mm CL)

Table 9. Summary of body size values and age at maturity for the gopher tortoise (*G. polyphemus*) across its geographic range

Location	Minimum adult body size - Male (age at maturity)	Minimum adult body size - Female (age at maturity)	Mean adult body size - Male	Mean adult body size - Female	Mean male body size : mean female body size
SW Florida *(McLaughlin 1990)*	225 mm CL (9–13 yrs)	282 mm CL (14 yrs)	288.4 mm PL/ 284.7 mm CL	302.8 mm PL/ 302.9 mm CL	0.95
SE Florida *(Ashton et al. 2007)*				308 mm CL	
SE Florida Jon A. Moore, pers. comm)			290 mm CL	310 mm CL	0.94
SE Florida (Sano 2014)	>240 mm CL (7–9 yrs)	>240 mm CL (7–9 yrs)			
SC Florida This study	186 mm PL/ 209.8 mm CL (7.4 yrs)	225 mm PL/ 253.1 mm CL (12.7 yrs)	East = 221.6 mm PL West = 227.8 mm PL	East = 252.5 mm PL West = 246.9 mm PL	East = 0.88 West = 0.92
SC Florida (White et al., 2018)	209 mm CL		275.6 mm CL		
SC Florida *(Rothermel and Castellón 2014)*		251 mm PL/ 254 mm CL		274.7 mm PL/ 278.4 mm CL	
WC Florida (Mushinsky et al. 1994)	240 mm CL (probably 9–10 yrs)	242–315 mm CL (9–10 yrs)			
WC Florida (Godley 1989)	(16–19 yrs)	255 mm CL (16–19 yrs)	275.1 mm CL	299.8 mm CL	0.92
WC Florida *(Godley 1989)*			244.4 mm CL	247.4 mm CL	0.99
WC Florida (Small and MacDonald 2001)		187 mm CL (5–12 yrs)			
WC Florida (Linley 1986)		(13 yrs)			
N Florida (Auffenberg and Iverson 1979)	230 mm CL	238 mm CL			
N Florida (Iverson 1980)		220–230 mm PL (10–15 yrs)			
N Florida (sandhill) (Diemer 1992)			234.1 mm CL	258.8 mm CL	0.91
N Florida (modified habitat) *(Diemer 1992)*			238.9 mm CL	266.7 mm CL	0.90
N Florida (modified habitat) (Diemer 1992)			234.8 mm CL	262.4 mm CL	0.89
N Florida *(Diemer and Moore 1994)*	177 mm CL (9–13 yrs)	232 mm CL (14–18 yrs)			
N Florida (Smith 1995)			244.3 mm CL	255.2 mm CL	0.96
SW Georgia (Landers et al. 1980)	230–240 mm CL; active sperm at 203 mm CL	+ 255 mm CL			
SW Georgia *(Landers et al. 1982)*	(16–18 yrs)	250–265 mm CL (19–21 yrs)			
SC Alabama *(Aresco and Guyer 1999a)*		(20 yrs)			
South Carolina (Wright 1982)	(12 yrs)				

(Aresco & Guyer, 1999a).

Survivorship in the gopher tortoise was lowest in the earliest life history stages. For example, 89 % of nests were destroyed in south-western Georgia, with a success rate of about one clutch per 9.5 nests (Landers et al., 1980). During a two-year period at a site in South Carolina 70.8 % of gopher tortoise nests were destroyed, and annually, 70 % of hatchlings were lost to predation (Wright, 1982). In southern Mississippi, 28.8 % of nests hatched (Epperson & Heise, 2003), the success rate of which did not vary between ruderal and forested sites.

Mortality during the first year of life was over 90 % in central Florida (Witz et al., 1992), and bimonthly survival rates of hatchlings in central Florida exceeded 60 % (Wilson, 1991). Mortality during the first year of life exceeded 90 % in northern Florida (Alford, 1980), and in southern Mississippi, 65 % of hatchlings were dead within 30 days of life (Epperson & Heise, 2003).

Among adult tortoises on the ABS, residents fared better than relocated individuals. Eleven percent of resident tortoises on the ABS were still alive after 15 years and 64 % survived at least one month, whereas all relocated tortoises were gone by 14 years and only 41 % survived for more than one month (Layne, 1989).

In this study, we found no difference in modelled annual survival of males and females. The estimates across the population agreed well with the known animals and empirical data outlined above as modelled survival would lead to a 25 % survival over 15 years. Capture probabilities differed over time, sex, and age, however, were relatively high. Given that the searches were conducted by the same biologist over the entire study, knowledge of individual habitats, tortoise patterns, and search image may have increased capture rates. In south-western Georgia, some tortoises were thought to live 80–100 years (Landers et al., 1982). Using the 12.7-year age at maturity from the East Section and a survival rate of 0.919 from this study, approximately 0.3 % of the adult population could be expected to reach 80 years of age.

Recapture Rates

On the ABS, males were captured more often than females during most of the year (this study; Douglass & Layne, 1978). To that end, south Florida males foraged and moved about between female burrows, while females generally remained closer to their own burrows (Karlin, 2002). However, the finding of greater male movements in south and south-central Florida contrasted with findings in north-central Florida, where recapture rates increased over time but were still generally low and similar between sexes (Smith, 1995). At a sandhill and two modified habitats in northern Florida, recapture rates were generally higher for adults than juveniles (Diemer, 1992a).

Activity

Seasonal

On the ABS, we found the gopher tortoise to be active throughout the year, especially during April–August, and least active during the winter. Likewise, continuous activity with reduction during the winter in this species was found on the ABS (Douglass & Layne, 1978), on Sanibel Island in south-western Florida (McLaughlin, 1990), in Jupiter, Florida, where it also breeds throughout the year (Moore et al., 2009), a coastal strand in Vero Beach, Florida (Jon A. Moore, pers. comm.), and farther north in Brevard (Hollister, 1951) and Putnam (Hubbard, 1893) counties. In north-central Florida, individuals were active continuously, especially during March–November, with most captures during May–October (Smith, 1995). However, in north-central Florida, individuals could also be active during late November–late-February (Clements, 1956). Similarly, in the northern edge of its geographic range, the species has an overwintering period (Speake & Mount, 1973). In south-western Georgia, most activity occurred during May–August, and tortoises were dormant during December– March (Landers et al., 1982). In south-western Georgia, little activity occurred during November–February and all individuals were active by 1 April when maximum air temp was at least 27˚C (McRae et al., 1981).

Diel

In agreement with others (Pope, 1939; Oliver, 1955), the species was diurnal on the ABS (this study; Douglass & Layne, 1978). However, foraging at dusk occurred during hot weather (Oliver, 1955), adults would occasionally leave their burrows at night (Alexy et al., 2003), and nocturnal forays by juveniles occurred after storms (Pike & Grosse, 2006). On the ABS, the gopher tortoise exhibited a unimodal diel pattern throughout the year, having peaked during the hottest times (1300–1600hrs) (Douglass & Layne, 1978). Our findings were similar to those of Douglass & Layne (1978), but the ranges were greater during the hottest months. We also qualify this conclusion with the possibility that analysis of diel activity that accounts for cloud cover and microhabitat could result in differences in patterns of its diel pattern of activity. Hubbard (1893) also reported unimodality in diel activity in Florida.

Individuals from a Jupiter, Florida, population exhibited a unimodal activity pattern during the colder months and switched to a bimodal activity pattern in the summer, foraging early in the morning and near dusk to avoid the hottest times of the day (Jon A. Moore, pers. obs.). In South-western Georgia, diel pattern of activity varied seasonally whereby the pattern was unimodal during May-June and September–October and was bimodal during March–April and June–August (McRae et al., 1981).

Average body temperature of active gopher tortoises was 34.7˚ C (Douglass & Layne, 1978). Apparently, daytime temperatures on the ABS did not exceed limits for activity, even if individuals were in the shade. However, males were active earlier and later in the day than were females, which was thought to be in response to more opportunities for mating (Douglass & Layne, 1978). In south-eastern Florida, activity was associated with mean temperatures of 31.8˚ C carapace surface temperature and 32.3˚ C cloacal temperature (Schaffner, 2015). Carapace surface temperature averaged 27.6˚ C among individuals basking on the apron of the burrow and 26.4˚ C among individuals inside the burrow tunnel (Schaffner, 2015).

Movements out of burrows in south-eastern Florida are typically associated with air temperatures ranging 21–34˚ C (Jon A. Moore, pers. comm.) but avoided foraging when air temperatures > 32˚ C (Schafffner, 2015).

Movements

All segments of the gopher tortoise population that we studied moved most often and farthest during the warmer months, and movements of adults were significantly greater than those of juveniles. Somewhat surprisingly, only the variance in distance between captures was greater in males than females, which was presumably in response to courtship activities of wandering males. Similar long movements between the sexes on the ABS may have been a response to localised sources of high-quality food on the East Section and overall lower productivity of the West Section.

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Home range size-
Home range size averaged larger among males, females, and juveniles on the ABS than elsewhere. For example, in south-western Florida, home range size was significantly larger in males (1.10 ha) than in females (0.06 ha) McLaughlin, 1990. In central Florida, overall home range size averaged 1.1 ha (Doonan, 1986), with a follow-up at that site of 0.63 ha for males and 0.21 ha for females (Bard, 1989). In northern Florida, roadside strip surrounding a mature slash pine plantation, average home range size varied among males (0.88 ha), females (0.31 ha), subadults (0.05 ha), and juveniles (0.01 ha) (Diemer, 1992b). Female home range size in north-central Florida females averaged 0.48 ha in sandhill and 0.11 ha in old field (Smith 1995). Males made many courtship-related short distance movements in the spring in south-western Georgia (Landers et al., 1980). In south-western Georgia, home range size was bigger in males (0.45 ha) than in females 0.08 ha) but thought to be larger if studied for longer time (McRae et al., 1981). Home range size was thought also to have increased with a decrease in herbaceous biomass (Auffenberg & Iverson, 1979), and ultimately it was influenced by habitat quality (Diemer, 1992b). Roads were found to have the ability to elongate the home range size (McRae et al., 1981; Douglass, 1986; Diemer, 1992b). All three of the aforementioned factors affecting home range size in the gopher tortoise appeared to have influenced our findings on the ABS. First, the long-term nature of the study could capture a great deal of the variability in seasonal and annual movements. Second, although the East Section sandhill was associated with better forage than the West Section scrub, overall, the infrequently burned sandhill and the frequently burned scrub were not high-quality habitats from a food productivity standpoint. Third, the road bisecting the two sections provided a unique linear habitat that was exploited by males, females and juveniles.

Habitat use
We found that, in descending order, sandhill, flatwoods, sand pine scrub, and human-modified habitats were used most by the gopher tortoise on the ABS. Along a small mammal trapping grid on the ABS, gopher tortoises were more frequently encountered in low flatwoods-palmetto and mature sand pine scrub-oak phase, and in scrubby flatwoods- inopina oak phase, low flatwood- grass, or bayhead (Meshaka & Layne, 2015). Fire periodicity was shown to affect burrow density on the ABS (Ashton et al., 2008). A preference by this species for open sandy habitat that is naturally maintained by fire on the ABS conforms to findings across its geographic range. In south-eastern Florida, burrows were most associated with bare sand and were most numerous and regularly dispersed in wet prairie associations, which was richest in forbs among their sites (Stewart et al., 1993). This species was most abundant in grassy, open canopy habitat, higher in sandhills and low in sand pine scrub (Auffenberg & Franz, 1982) and was considered primarily a sandhill grazing species (Landers, 1980). The importance of open canopy was such that in association with increasing canopy cover over time, burrow abandonment was recorded at a rate of 22 % each year over a five-year period in a pine plantation (Aresco & Guyer, 1999b).

<u>Burrow dynamics</u>
Tortoises
On the ABS, hatchlings used existing burrows or would hide in debris until the following spring, at which time they began making their own burrows (Douglass, 1978). Body size correlated very closely with burrow size on the ABS (this study; Martin & Layne, 1987), in south-western Florida (McLaughlin, 1990), and in northern Florida (Alford, 1980).

Commensal vertebrate species
Far and away, the most numerous species found in gopher tortoise burrows across treatments on the ABS was the exotic greenhouse frog, *Eleutherodactylus planirostris* (66.2 %) (Lips, 1991). Species richness and abundance varied among habitats. The numbers of species inhabiting burrows were similar among turkey oak (n = 10), sand pine scrub (n = 11), and scrubby flatwoods (n = 13) sites, with fewest numbers of species in unburned scrubby flatwoods (n = 5) as compared to burned scrubby flatwoods (n = 12) (Lips, 1991). The highest number of individual animals found in burrows was in turkey oak (n = 139), followed by sand pine scrub (n = 97) and scrubby flatwoods (n = 83) (Lips, 1991). Again, fewer individual animals occurred in unburned scrubby flatwoods (n = 37) than in burned scrubby flatwoods (n = 46) (Lips, 1991). Thus, gopher tortoise burrows are important to a wide range of species on the ABS as they are elsewhere (Jackson & Milstrey, 1989; Ashton & Ashton, 2004.)

<u>Reproduction</u>
Male combat
Male-male combat on the ABS was observed in January and described in detail (Hailman et al., 1991).

Courtship and mating
Courtship and mating occurred during more months in southern Florida populations than in northerly populations. Testes from gopher tortoises that we examined on the ABS during May–October indicated fertility during those months. Courtship was observed in the field in May (Layne in Douglass, 1976) and during March–November among captives (Douglass, 1976). In south-eastern Florida, courtship and mounting was observed year-round, the peak incidence of which occurred during August–December (Moore et al., 2009). On Sanibel Island in south-western Florida, mating was observed 12 times during 18 May–27 June, three times during 3 July–23 August and once in September (McLaughlin, 1990). In north-eastern Florida, reproductive activity occurred during April–November and males head-bobbed at the burrow mouths of females most commonly in September (Butler & Hull, 1996). Courtship occurred during September–October in northern Florida (Diemer, 1992b) and during spring–fall in south-western Georgia (Landers et al., 1980). In

south-western Georgia, mating appeared to be restricted to late April–early-June when chin glands were active in females (Landers et al., 1980).

Nesting

Southern Florida populations of the gopher tortoise nested over a longer period than those of northerly sites. On the ABS, two dissected females containing shelled eggs were found in May, a nest was found in May, and two additional nests were found in June (Meshaka & Layne, 2015). On the ABS, nesting was observed during May–June (Douglass, 1976), and the 32 mm follicle we found in an April female on the ABS fit within the ovarian cycle of northern Florida gopher tortoises (Iverson, 1980). On 11 May in Florida, a female was observed digging a nest on a mound of old peat mulch. In south-western Florida, shelled eggs were also present in females during April–May; however, inferentially nesting may have been possible from Fall through Spring as well (McLaughlin, 1990), partially-shelled oviductal eggs and ovulated follicles were found in a female from Palm Beach County on 3 April (Iverson ,1980), and shelled eggs were detected in females as early as 7 April in Jupiter, Florida (Moore et al., 2009).

North of the ABS, studies showed that the nesting season began later and ended by early- to mid-summer; no nesting was observed during 5 March–19 April in northern Florida (Hallinan, 1923); field records showed nesting during May–June in northern Florida (Iverson, 1980); nesting records during late May–early June (Hallinan, 1923; Iverson, 1980); nesting in early-June (Diemer & Moore, 1994) and the month of June (Smith, 1995) in northern Florida; nesting during mid-May–late-June in south-western Georgia (Landers et al., 1980); nesting during mid-May–mid-July with peak nesting during late-May–early-June in southern Mississippi (Epperson & Heise, 2003); and nesting during late-May–June in South Carolina (Wright, 1982).

Clutch size-Clutch sizes of the gopher tortoise were thought to be larger in southern Florida than in northern Florida (Iverson, 1980). Subsequently, clutch size was found to be largest in the southern portion of its geographic range in association with greater productivity of resources and less seasonality (Ashton et al., 2007). This is particularly evident along the southern coast. To that end, mean clutch size was 6.9 eggs in south-western Florida (McLaughlin, 1990), 6.3 eggs on the ABS (Ashton et al., 2007), 5.8 eggs at the Avon Park Air Force Range (Rothermel & Castellón, 2014), 8.2 eggs at Okeechobee County Park in Palm Beach County (Ashton et al., 2007), 7.46 eggs on Merritt island (Demuth, 2001), and 10.1 eggs (range = 8–13) from Jupiter, Florida, where the largest clutch radiographed was 13 eggs, although a nest with 18 eggs was later found (Moore et al., 2009).

Northward, mean clutch size of the gopher tortoise was shown to have decreased in size. In central Florida, mean clutch size was 7.6 eggs (Godley, 1989). In west-central Florida, the mean clutch size of 8.5 eggs did not differ significantly between resident and trans-located tortoises but increased with an increase in female body size (Small & MacDonald, 2001). In west-central Florida, the mean clutch size was 7.8 eggs (Linley, 1986). In Northern Florida, mean clutch size based on a combination of estimates (all similar) was 5.2 (Iverson, 1980). In northern Florida, mean clutch size was 5.8 eggs (Diemer & Moore, 1994). In north-central Florida, mean clutch size was 5.76 eggs (Smith, 1995). In north-eastern Florida, mean clutch size was 5.04 (Butler & Hull, 1996). In southern Mississippi, mean clutch size was 4.8 eggs (Epperson & Heise, 2003). In south-western Georgia, clutch size averaged 7.0 eggs (Landers et al., 1980). Average clutch size in north Florida (mean = 5.3; range = 1–9) and egg dimensions were smaller than those of south-western Georgia and thought by Landers et al. (1980) to be explained by the smaller body size of those animals. In South Carolina, mean clutch size was 3.8 eggs (Wright, 1982). Body size and clutch size were not positively related on the ABS (Ashton et al., 2007) but were so at Okeechobee County Park (Ashton et al., 2007), at Avon Park Air Force Range (Rothermel & Castellón, 2014), in northern Florida (Iverson, 1980; Diemer & Moore, 1994; Smith, 1995), and in south-western Georgia (Landers et al., 1980). At Okeeheelee County Park, the largest clutch sizes were produced by intermediate-sized females, indicating age-related reproductive senescence (Ashton et al., 2007).

Annual clutch production

No evidence of multiple clutch production was found in a single dissected female from ABS, which was in keeping with findings of single annual clutch production in this species from northern Florida (Iverson, 1980; Taylor, 1982; Diemer & Moore, 1994; Smith, 1995), south-western Georgia (Landers et al., 1980), and South Carolina (Wright, 1982).

Incubation times

Incubation times were not measured on the ABS; however, in general eggs of the gopher tortoise took approximately three months to hatch: 101 days in the aforementioned peat mound (Meshaka & Layne, 2015), an average of 88.5 days (88 and 89 days) in south-western Florida (McLaughlin, 1990); a 91-day incubation time for a clutch laid in April 2013 in south-eastern (Vero Beach) Florida (Jon A. Moore, pers. comm.); a range of 91–105 days (Linley & Mushinsky, 1994) and 56–102 days (Small & MacDonald, 2001) in west-central Florida; an average of 87.4 days in north-central Florida (Smith, 1995); an average of 105 days in north-eastern Florida (Butler & Hull, 1996); a probable range 80–90 days in northern Florida (Iverson, 1980); and an average of 102 days in south-western Georgia (Landers et al., 1980). Incubation time averaged 88 days in southern Mississippi in both forested and ruderal sites (Epperson & Heise, 2003). If a geographic trend in incubation time exists for the gopher tortoise, it was not apparent from these aforementioned studies.

Hatching season

On the ABS, hatchlings appeared during late August–early October (Douglass, 1978). In this study, the smallest individuals appeared during April–September, the earliest of which were presumed to have hatched late the previous fall. In south-western Florida, the hatching season was during late-May–late-September, suggestive of extended reproduction, with most hatching ending by late August (McLaughlin, 1990). Farther north, hatching was restricted to late summer and fall as reported in the following studies; at least mid-August–September in northern Florida (Iverson, 1980); late-August–early-October in north-eastern Florida (Butler & Hull, 1996); and the month of September (Arata, 1958) and during late-August–early-October in north-central Florida (Smith, 1995).

Hatchling size

Mean hatchling size on the ABS was 47.7 mm PL (Douglass, 1978) and smallest hatchlings measured 42 mm PL (this study) and 43 mm PL (Douglass, 1978). The means of the following data were recorded from four hatchlings from a single clutch from the ABS: 31.1g, 46.6 mm CL, 41.8 mm CW, 43.0 mm PL, 36.5 mm PW, and 5.1 mm anterior projection of the gular scute (Meshaka & Layne, 2015). In west-central Florida body size of hatchlings ranged 45.9–47.7 mm PL (Small & MacDonald, 2001), and in north-central Florida, mean hatchling size differed between two years (48.0 vs. 42.3 mm CL) (Smith, 1995).

Diet

On the ABS, the gopher tortoise ate a wide range of vegetation but foraged primarily on grasses (this study; Meshaka & Layne, 2015). An interest in grasses and nutritious forbs was evident in adults and juveniles in many parts of its geographic range. Pusleys and bromeliads were also found in many stomachs. In west-central Florida (MacDonald & Mushinsky, 1988) and south-western Georgia (Garner & Landers, 1981), individuals also ate a lot of grasses but preferred the more nutrient-rich forbs. In South Carolina, wiregrass also comprised much of its diet (Wright, 1982). Among adults, Aristida was important in many places (Auffenberg, 1969; Fletcher, 1899; Wright, 1982), perhaps in relation to its abundance. In a west-central Florida sandhill, adults ate a wide range of plant taxa (MacDonald & Mushinsky, 1988). Scat analysis revealed *Aristida* and Poaceae at the genus and family level, respectively, to be the most abundant food items in a west-central Florida population (MacDonald & Mushinsky, 1988). Also commonly eaten at MacDonald & Mushinsky's (1988) site were *Pinus*, *Quercus*, *Galactia*, *Cnidoscolus*, *Tillandsia*, *Pityopsis*, and *Richardia*. Differentially chosen plants were *Galactia* and *Tephrosia*, *Cnidoscolus*, *Pinus*, *Quercicus*, *Vaccinium*, *Richardia*, and *Rubiaceae*, thereby eating *Aristida* at its occurrence (MacDonald & Mushinsky 1988). More so than smaller individuals, adults ate plants with some form of chemical protection (MacDonald & Mushinsky, 1988). Likewise, in south-western Georgia Garner and Landers (1981) noted that *Aristida* was poorly exploited in areas where more nutritious forbs were available. Ingestion of calcium-rich stones, fossil shells, and small mammal bones was reported in females whose developing eggs were undergoing calcium deposition (Moore & Dornburg, 2014). The importance of calcium in the diet could explain the rocks and squirrel bones found in the ABS individuals. In southern Florida, scavenging for animal protein in carcasses was also reported for the gopher tortoise (Meshaka & Layne, 2015) which may have been associated in part with a search for bones as is known to be the case with ingestion of mammalian scats (Moore & Dornburg, 2014).

Juvenile gopher tortoises in a west-central Florida sandhill generally ate forbs when seasonally abundant then switched to grasses, often to the level of its availability (Mushinsky et al., 2003). Overall, juveniles elected on average less than ½ the genera that they would encounter on a given foraging bout and avoided all together *Aristida*, a very common grass (Mushinsky et al., 2003). Coprophagy was observed by members of the ABS population. Among juveniles, coprophagy was found to inoculate their gut with microbial symbionts helpful in digestion of plants (Bjorndal, 1987; Moore & Dornburg, 2014). To that end, the cellulolytic microflora that degrades cellulose and hemicellulose resulted in a high (73 %) digestibility of cell walls in the diet of the gopher tortoise (Bjorndal, 1987)

Seed dispersal- On the ABS, gopher tortoise-dispersed seeds of the exotic Bahia Grass (*Paspalum notatum*) germinated at lower frequencies than those of its native congener, *P. setaceum* (Carlson et al., 2003). Both of these grasses were most common in gopher tortoise scats on the ABS but were accompanied by a wide range of other plants, especially *Pinus elliotti*, *Galactia* sp., *Vaccinium myrsinites*, *Quercus geminata*, *Gaylussacia dumosa*, and roots (Carlson et al., 2003). The relative frequency of seed species found in scats was highest for *P. notatum*, *P. setaceum*, and *Diodia teres* (Carlson et al., 2003).

<u>Predators</u>

Eggs

On the ABS, nest predators were the eastern indigo snake (Layne & Steiner, 1996), raccoon (*Procyon lotor*), gray fox (*Urocyon cinereoargenteus*), and especially the nine-banded armadillo (*Dasypus novemcinctus*) (Douglass & Winegarner, 1977; Meshaka & Layne, 2015). Also on the ABS, an egg fragment and other food remains were found beneath the nest of a Cooper's hawk (*Accipiter cooperii*) (Meshaka & Layne, 2015). The raccoon was an important nest predator as reported by Hallinan (1923) and individuals depredated nests in north-central Florida (Smith, 1995). Nest predators in south-western Georgia were the raccoon, gray fox, striped skunk (*Mephitis mephitis*), and opossum (*Didelphis marsupialis*) (Landers et al., 1980).

Hatchlings

On the ABS, recently hatched tortoises were found in the diet of the eastern indigo snake (Layne & Steiner, 1996) and the remains of a fall hatchling were recovered from the stomach of an eastern coachwhip the following May (Douglass & Winegarner, 1977). The red-tailed hawk (*Buteo jamaicensis*) was reported as a predator of juvenile gopher tortoises on the ABS (Fitzpatrick & Woolfenden, 1978). In St. Petersburg, Florida, remains of a juvenile were removed from a wild-caught savannah monitor (*Varanus exanthematicus*) (Owens et al., 2005). Geographically expanding populations of the Argentine giant tegu (*Salvator merianae*) and the Nile monitor (*Varanus niloticus*) (Meshaka, 2013) provide novel threats to eggs or young of the gopher tortoise. In Jupiter, Florida, remains of a juvenile were recovered from coyote (*Canis latrans*) scat (Moore et al., 2006). In north-central Florida, hatchlings were killed by ants (*Solenopsis geminata*, *S. invicta*, *S. pergandei*, and *Conomyrma bossuta*) (Smith, 1995). In south-western Georgia, fire ants were predators of hatchlings (Landers et al., 1980). In southern Mississippi, hatchlings were killed primarily by mammals and secondly by fire ants (*S. invicta*) (Epperson & Heise, 2003). In Alabama, a hatchling was removed from the stomach of an Eastern Indigo Snake (Mount, 1975).

Adults

On the ABS, the gopher tortoise was subject to poaching at varying intensities (Meshaka & Layne, 2015). Sub-adults were attacked by dogs (Douglass & Winegarner, 1977). Dogs were considered to be responsible for the scarcity of gopher tortoises at one of the more developed sites in a south-western Florida study (McLaughlin, 1990). In west-central Florida, three juvenile gopher tortoises were lost presumably to raptors (Wilson, 1991). Adults were eaten by canids (Causey & Cude, 1978) and Black Bears (Landers et al., 1982).

Unnatural sources of mortality

Railroad-related mortality was observed on the ABS, whereby animals were trapped between the rails and presumably died of heat exposure and by vehicles (Meshaka & Layne, 2015). Railroad mortality was also observed in St. Lucie, which involved a 230 mm CL male (Engeman et al., 2007).

Summary

McCoy & Mushinsky (1992) found that protection of even large parcels of land was in and of itself no guarantee of population health of the gopher tortoise, and their difficulty in making temporal comparisons of abundance based on earlier surveys by others underscored the need for more systematic approaches to population census. Long-term study sites such as the ABS, with multiple habitat types and a diverse fire management schedule have provided the conditions necessary to examine the natural and human-mediated responses of the gopher tortoise to spatial differences in habitat type and quality as well as to temporal responses at a scale that is meaningful to this long-lived species. To that end, the growth to maturity, reproductive aspects, and seasonal activity were found to fit within geographic trends. We suggest that habitat quality affected population size, body condition, and home range size of this large, grassland species. Although extensive human predation appeared to best explain differences in the population structure on the ABS, body size was found to conform to predictions based on a combination of geography, climate, seasonality, and productivity.

Two human-mediated threats to the integrity of the biotic community of the ABS are likely threats to its gopher tortoise population - isolation and the exotic Argentine giant tegu. The ABS is an island of an archipelago of protected lands on the Lake Wales Ridge. Ever more separated from other islands by habitat destruction, populations of many of its species risk increasing isolation from other populations. For the gopher tortoise, this threat alone warrants dedicated continuation of monitoring of the ABS population. The Argentine giant tegu is an established member of the exotic herpetofauna of Florida (Meshaka, 2013). It occurs in two disjunct regions of Florida: Hillsborough and Polk counties and in Miami-Dade County. In the former range, this lizard occurs in xeric uplands of the Balm-Boyette Scrub Preserve and the Mosaic phosphate lands, where individuals use gopher tortoise burrows (Enge, 2007). Males can grow to an excess of 1.22 m in total length. The species is omnivorous and a documented predator of crocodilian and chelonian eggs in southern Florida (Mazzotti et al., 2015). The Argentine giant tegu represents a threat to the gopher tortoise as a predator of its eggs and hatchlings and, more broadly, represents a threat to other sandy upland species that it can capture and eat. The Argentine giant tegu will inevitably disperse onto the Lake Wales Ridge and will have a high likelihood of colonisation success on the ABS. Establishment of this species on the ABS will bring with it a high likelihood of significant alteration of the community structure and population sizes of many of the station's vertebrate species. Gopher tortoise surveys should include monitoring burrow entrances in part by periodically sweeping burrow entrances to detect the presence of resident tegus.

Our findings examined responses of the gopher tortoise to natural processes and human-mediated perturbations that were uniquely combined on the ABS. Continued study of this population can reveal the kind and extent of responses to various land management treatments, effects of isolation, and the inevitable colonization of a predatory exotic species in a well-documented site.

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