Nest site characteristics, nesting movements, and lack of long-term nest site fidelity in Agassiz's desert tortoises at a wind energy facility in southern California

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Nest site selection has important consequences for maternal and offspring survival and fitness. Females of some species return to the same nesting areas year after year. We studied nest site characteristics, fidelity, and daily pre-nesting movements in a population of Agassiz's desert tortoises (*Gopherus agassizii*) at a wind energy facility in southern California during two field seasons separated by over a decade. No females returned to the same exact nest site within or between years but several nested in the same general area. However, distances between first and second clutches within a year (2000) were not significantly different from distances between nests among years (2000 and 2011) for a small sample of females, suggesting some degree of fidelity within their normal activity areas. Environmental attributes of nest sites did not differ significantly among females but did among years due largely to changes in perennial plant structure as a result of multiple fires. Daily pre-nesting distances moved by females decreased consistently from the time shelled eggs were first visible in X-radiographs until oviposition, again suggesting some degree of nest site selection. Tortoises appear to select nest sites that are within

their long-term activity areas, inside the climate-moderated confines of one of their self-constructed burrows, and specifically, at a depth in the burrow that minimizes exposure of eggs and embryos to lethal incubation temperatures. Nesting in "climate-controlled" burrows and nest guarding by females relaxes some of the constraints that drive nest site selection in other oviparous species.

Key words: Agassiz's desert tortoise, *Gopherus agassizii*, nest site selection, nest fidelity, pre-nesting movements, renewable energy, Sonoran Desert

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Nest site selection (NSS) is important because it affects the survival and fitness of offspring, ultimately affecting the fitness of mothers as well. In some species, maternal selection of a nest site is the only form of post-ovipositional "parental care" provided to offspring. The "maternal manipulation hypothesis" posits that females enhance the fitness of their offspring by selecting nest sites with conditions that enhance survival and performance phenotypes in those offspring (Shine 2012). Females select sites for nests when their placement is non-random with respect to a particular area (Wilson 1998) based on differences in microhabitat (Valenzuela and Janzen 2001). Nest site location influences the microhabitat for incubation and can affect incubation duration and thus time of emergence (Ennen et al. 2012a, Lovich et al. 2012), survival from abiotic factors like flooding (Pignati et al. 2013), survival from biotic factors like predators (Spencer and Thompson 2003, Micheli-Campbell et al. 2013), and parasitoids of eggs (Iverson and Perry 1994) and hatchlings. NSS also influences gene flow in metapopulations (McGuire et al. 2013). Experimental results demonstrate increased survival of hatchlings in nest sites selected by females relative to random sites (Wilson 1998, Hughes and Brooks 2006).

Various performance measures of hatchlings show the benefits of nest sites selected by females versus random sites, thus potentially improving fitness of the offspring (Shine 2012), the parent (Schwarzkopf and Andrews 2012), or both. NSS contributes to neonates hatching earlier with fewer developmental or teratological anomalies and greater mobility (Peet-Pare and Blouin-Demers 2012). In addition nests selected by mothers affect the behavior and activity of neonates in ways that may enhance their survival (Shine and Harlow 1996, Peet-Pare and Blouin-Demers 2012). Shine and Harlow (1996) were quick to point out that putative fitness advantages of a particular physical or behavioral phenotype were not established for their study organism (the Australian lizard, *Bassiana duperreyi*). However, subsequent studies demonstrated that NSS resulted in offspring traits under strong positive selection in a snake species (Brown and Shine 2004). NSS also affects animals with environmental sex determination, like many turtles (Ernst and Lovich 2009), through the influence of the temperature regime experienced by developing embryos. In fact, nest site philopatry (discussed further below) has been used as an explanation for the evolution of environmental sex determination (Reinhold 1998), although not without some controversy (Valenzuela and Janzen 2001). Nest site philopatry has also been invoked as an explanation for female-biased sex ratios in turtles since it is a sex-specific, culturally inherited trait (Freedberg and Wade 2001). Females of some turtle species select nest sites based on egg size, placing clutches of larger eggs in warmer environments more likely to produce females

(Roosenburg 1996). Conversely, clutches of smaller eggs are oviposited in cooler sites more likely to produce males due to growth and maturity benefits accrued differentially by the sexes.

Assuming that NSS is under strong natural selection, then it stands to reason that females might return to the same nest site year after year if it continues to meet the requirements for improving their fitness and that of their offspring (Lindeman 1992). As a group, turtles exhibit varying degrees of nest site fidelity at different spatial and generational scales. For example, females of many marine and freshwater species return to the same nesting beaches or areas repeatedly (see reviews in Ernst and Lovich 2009). In some cases, females even exhibit natal homing or philopatry, returning to their place of birth to nest when they are mature (Meylan et al. 1990, Valenzuela and Janzen 2001, Freedberg et al. 2005, Sheridan et al. 2010, Watanabe et al. 2011). Other species nest in the same general area year after year (Loncke and Obbard 1977, Obbard and Brooks 1980, Lindeman 1992, Tucker 2001, Walde et al. 2007, Micheli-Campbell et al. 2013), but it is unknown if that represents true natal homing. Still other species appear to nest in proximity to their previous nest but with no particular fidelity to a specific location (Nordmoe et al. 2004). In theory, terrestrial species, like Agassiz's desert tortoise (*Gopherus agassizii*) are not limited to narrow fringes of nesting areas surrounding aquatic habitats as are aquatic turtles. However, selective forces are expected to drive NSS in *G. agassizii* for all the theoretical and empirically verified survival and fitness benefits discussed above.

We examined characteristics of nest sites, nest site fidelity, and pre-nesting movements in a population of *G. agassizii* at a wind energy generation facility near Palm Springs, California in two field seasons, separated by more than a decade, a time period that is consistent with the duration of nest site fidelity reported by other turtle species (Mitrus 2006). We did not explicitly test nest site selection with spatial hypotheses (e.g., Hays et al. 1995) or by comparing actual nest sites to available nest sites as done previously at our study site for nesting burrows by Ennen et al. (2012a). Rather, we provide a detailed description and comparison of nest sites of the same cohort of females over time. The landscape at the study site is spatially diverse, presenting females with a wide range of slopes, aspects, elevations, plant communities (Lovich et al. 2011b), and burned or unburned areas (Lovich et al. 2011c) for nesting. A previous analysis suggested that NSS was not observed at the landscape level, but possibly at the level of a tortoise burrow, in which most nests are located (Ennen et al. 2012a). We tested the hypothesis that females exhibited nest site fidelity, returning to nest in the same general microsite or locality (sensu, Leibold et al. 2004) of their known activity area (Lovich et al. 2011c). We hypothesized that the mean distances within and between years would be similar if interdecadal nest fidelity was observed. That is, nests in the same year are expected to be close together due to the small activity area size of female desert tortoises, and if nest site fidelity is exhibited, the distances between years would be expected to be similarly proximate. In addition, based on prior field observations, we hypothesized that once shelled eggs were detected in individual female tortoises, they would move shorter distances each day as the date of oviposition approached, possibly as a result of narrowing down their search for a suitable nest site. Although our sample size of nests from the same females in both 2000 and 2011 is small, no other long-term data on nest fidelity are available for this species in the wild.

MATERIALS AND METHODS

Study site and field techniques.—The study site, known locally as the Mesa wind farm, is located approximately 13 km northwest of the city of Palm Springs, California (33° 57' N, 116° 40' W), at the western edge of the Sonoran Desert (Lovich et al. 2011b). The site has been a focus of long-term research on behavior and habitat use (Lovich and Daniels 2000; Lovich et al. 2011c, Ennen et al. 2012b), reproductive ecology (Lovich et al. 1999; Lovich et al. 2012, Ennen et al. 2012a, Agha et al. 2013), and other aspects of the ecology of *G. agassizii* (Lovich et al. 2011a). A large wind energy generation facility has operated at the site since 1983 and currently includes 460 turbines and an associated infrastructure of roads, transformers, and substations. Habitat utilized by *G. agassizii* in the area ranges from 600 to 900 m elevation and is characterized by a semi-desert chaparral vegetation community, with plants representative of coastal sage scrub, chaparral, Sonoran Desert, and Mojave Desert ecosystems. Both large and small fires have affected the landscape, with little measurable effect on individual activity areas, body condition indices, or annual reproductive output of female *G. agassizii* (Lovich et al. 2011c). Additional details of the study site and tortoise population are given in references cited immediately above.

Although detailed data on reproduction were collected from 1997 to 2000, 2009 to 2011 and during 2013, actual nest locations were determined only in 2000 and 2011. Changing project priorities resulted in reduced nest finding efforts in 2011. The field procedures we used were previously described by Ennen et al. (2012a). For the sake of convenience, we describe the basic techniques here and refer the reader to that publication for more information. Adult female *G. agassizii* were outfitted with small radio transmitters and tracked at approximately 7–10 day intervals during March –August, a period that bracketed the production of shelled eggs and oviposition (Lovich et al. 2012). At each capture females were X-radiographed (Hinton et al. 1997) in the field to determine the presence of shelled eggs, clutch size, and clutch number (up to three clutches are produced by a female in a given year) before being released at the point of capture. If shelled eggs were visible, females were also fitted with thread-trailing devices that allowed discrimination of fine-scale movements. Females were then tracked daily until a substantial weight loss indicated oviposition. We then followed the thread trail to find nest sites, concentrating on tortoise burrows since females at this site normally nest in their burrows (Ennen et al. 2012a). During the year 2000 we identified both first- and second-clutch nests of 23 females. In 2011, only a single nest was located for each female (*n* = 8) that included both first and second clutches. This allowed comparison of nest sites and tests of nest site fidelity for five females with known nest locations in both 2000 (two nests each) and 2011 (one nest each).

At each nest site we collected GPS locations and measured distance to the nearest living perennial plant (m) and burrow orientation in degrees. In 2000 we also measured burrow dimensions (Table 1). Using GIS we quantified slope angle, elevation, and slope aspect of each nesting location.

Statistical analyses.—To measure dispersion of nest sites within and between years we used GIS-based analyses to estimate three-dimensional landscape distance (m) between clutch locations of each female within and between sampling years, similar to the analysis of Lindeman (1992). Of the 22 adult females we monitored during the study, only five met the following criteria: 1) they had known nest locations in both 2000 and 2011, and 2) they produced at least two clutches in 2000. Only one nest was detected for each female in 2011

TABLE 1.— Summary statistics for environmental attributes of nest sites used by Agassiz's desert tortoises (*Gopherus agassizii*) near Palm Springs, California, 2000 and 2011. Means are followed by range, *SD* and (sample size). Means and *SDs* for slope aspect and burrow orientation are calculated as circular statistics. Burrow dimensions were only available for 2000. Data include nests in both years other than those for the five females discussed in the text with known nest locations in both years and two clutches in 2000.

				Environmental attribute				
Year	Slope angle (degrees)	Elevation (m)	Slope aspect (degrees)	Distance to nearest perennial plant (m)	Burrow orientation (degrees)	Burrow length (cm)	Burrow height (cm)	Burrow width (cm)
2000	13.7	757.5	170.9	0.55	166.0	55.4	13.8	32.4
	2.4–28.3	683.7–	74.5–	0–2.0	12.0–312.0	28.0–105.0	11.0–18.0	27.0–49.0
	8.4 (23)	841.1	331.7	0.65 (21)	80.0 (23)	23.4 (22)	1.6 (22)	5.3 (22)
		40.1 (23)	77.9 (23)					
2011	14.8	755.1	188.4	3.14	160.2			
	1.1–32.0	682.7–	120–240	0-6.25	110.0–225.0			
	10.9 (8)	844.0	40.7 (8)	2.23 (8)	40.5 (8)			
		57.2 (8)						

but again, our sample included both first and second clutches. Within-year distances were calculated as the distance between first and second clutches of each individual in 2000 (*n* = 5 distances) only. Between year distances were calculated as the distance from both first and second clutches in 2000 to the same female's single clutch in 2011 (*n* = 10 distances). Mean distances were tested using a paired *t*-Test.

For all relocations after a female was identified to be carrying eggs we calculated the distance moved over the previous day and the number of days since the female was originally identified as carrying eggs. If the female had not been located on the previous day, the interval was not explicitly included in our analysis. In order to test the hypothesis that tortoises move ever shorter distances in the days prior to laying eggs, we fit a Cox (1972) proportional hazards regression model with distance moved on the prior day as the predictor. Cox proportional hazards regressions combines a nonparametric model of the probability of laying eggs (in this application) as a function of the time since the individual was known to be gravid, with a parametric model of how covariates alter this nonparametric model. Based on our hypothesis, we expected the sign of the coefficient associated with distance moved since the prior day to be negative. We tested for statistical significance based on a Wald test.

All data were tested for normality and transformed as necessary prior to analysis. Circular data were analyzed with Oriana® statistical software. Statistical analyses were conducted using SYSTAT version 13.00.05 and R version x64 3.0.2. Statistical tests were considered significant at probabilities ≤ 0.05. All tests were *a posteriori* as the primary focus of the research was not on nest site fidelity. Research was conducted under permits from the U.S. Fish and Wildlife Service, California Department of Fish and Wildlife, and the Bureau of Land Management. We are grateful to the Institutional Animal Care and Use Committee of Northern Arizona University for reviewing and approving our research procedures.

RESULTS

The locations of nests by year and female tortoise are shown in Figure 1. None of the females returned to the exact spot to nest twice but most nested in the same general area within and between years. An exception was female #69 in the western portion of the
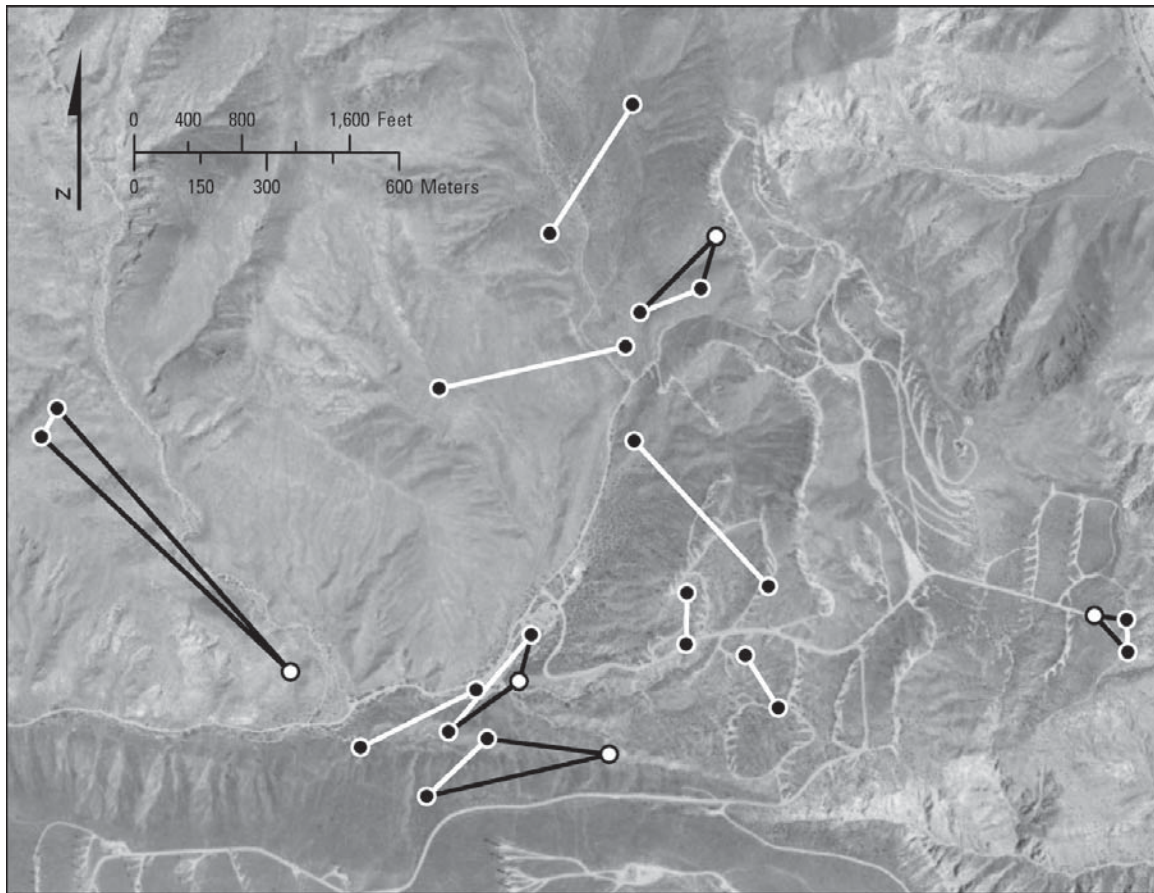
Figure 1.—Aerial photograph of study area showing locations of Agassiz's desert tortoise (*Gopherus agassizii*) nests in the years 2000 (black dots) and 2011 (white dots). White lines connect first and second clutches of each female in 2000. Black lines connect nests from 2000 to a single nest for each of the same females in 2011. For the year 2000, only verified locations for nests of females that produced a first and second clutch are shown. None of the nest locations shown contained a known triple clutch. Triangles detail the nest locations of the five females discussed in the text with known nest locations in both years and two clutches in 2000. The other white lines and black dots show the nests of other females in 2000 without known nest locations in 2011. Wind turbine access roads can be seen as "tic-marks" off the main roads on the right side of the photo. Center of map is approximately 13 km northwest of Palm Springs, Riverside County, California.

study area because her nest in 2011 was far from her nests in 2000. First- and second-clutch nests of each female in 2000 ranged from 73.1 to 291.0 m apart (x = 157.3, SD = 91.1). Distances between first and second clutches of a female in 2000 and her single nest in 2011 ranged from 73.8 to 822.0 m (x = 321.4, SD = 279.4). Comparing nest site differences within and between years using $\log_{10}$-transformed distances and a two-sample *t*-Test with pooled variance failed to reject our null hypothesis that the means were the same (t_{13} = 1.26, P = 0.23).

Summary statistics for the environmental attributes we measured at nests are shown in Table 1. The mean direction of nesting burrow orientation in 2000 was not statistically different from the mean for 2011 using the Watson-Williams *F*-test for circular data ($F_{1, 29}$ = 0.05, P = 0.83). Similarly, the slope aspect of nesting burrow locations between the years was not statistically different using the same test ($F_{1, 29}$ = 0.42, P = 0.52). Using the three non-circular variables (elevation, slope angle, and $\log_{10}$-transformed distance to nearest perennial plant) in a MANOVA revealed a significant difference in the attributes between

years (Wilks' Lambda = 0.28; *F-ratio* = $11.15_{3,13}$, *P* = 0.001). Somewhat paradoxically, individual univariate *F*-tests on the same variables were insignificant with the exception of $\log_{10}$-transformed distance to nearest perennial plant ($F_{1,15} = 21.98$, $P < 0.001$). A MANOVA for the same variables, this time comparing attributes among females, was insignificant as were all univariate tests.

As we hypothesized, the coefficient associated with daily distance a female moved after detection of shelled eggs and prior to nesting was negative (untransformed value of -0.009 with standard error of 0.003) and statistically significant according to a Wald test (7.1 on 1 *df*, $P < 0.01$). Figure 2 illustrates how different values of distance moved and days since an individual was known to be carrying shelled eggs change the expectation of whether a female is likely to continue to carry her eggs or oviposit.
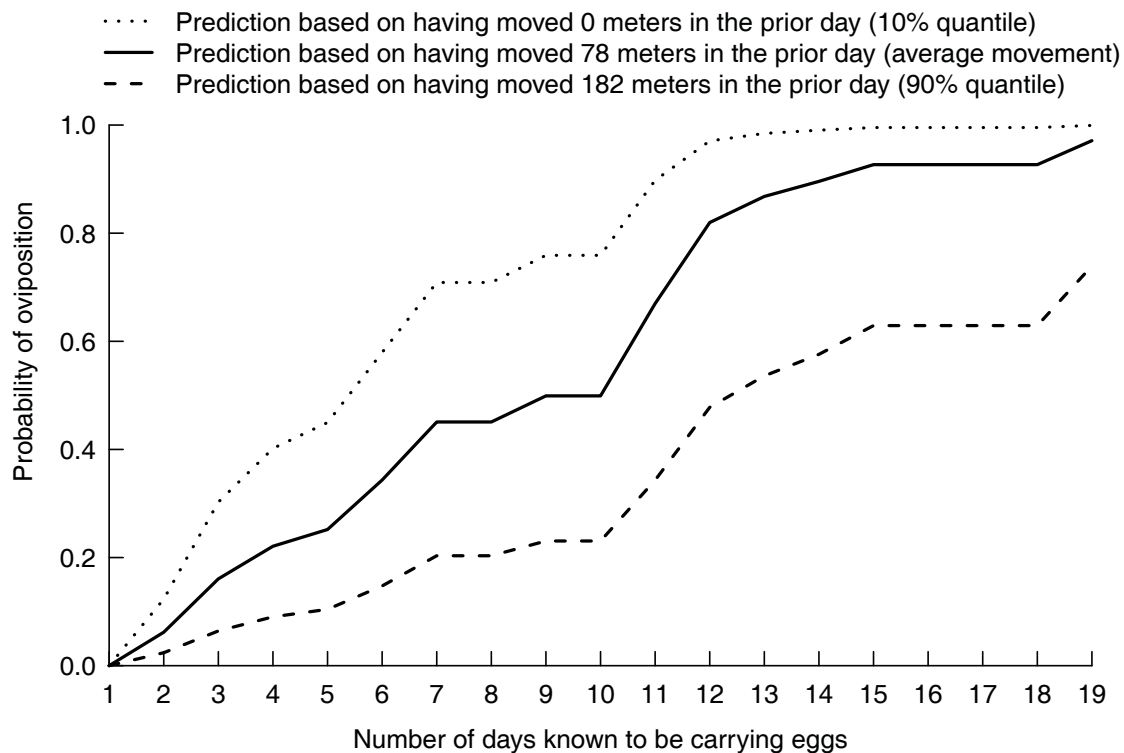

Figure 2.— Daily movements and the number of days that Agassiz's desert tortoises (*Gopherus agassizii*) are known to have been carrying shelled eggs jointly predict the probability of oviposition. For example, tortoises that are known to have been carrying shelled eggs 12 days or more and cease moving are highly likely (>95%) to oviposit. Study site was approximately 13 km northwest of Palm Springs, Riverside County, California.

Discussion

Nest site fidelity has been reported in a diversity of turtle species (e.g., Christens and Bider 1987, Szerlag-Egger and McRobert 2007). For example female green sea turtles (*Chelonia mydas*) return to their natal beaches at least 70% of the time (FitzSimmons et al. 1997, Mortimer and Portier 1989). Another example of an aquatic species that also displays nest site fidelity is the European pond turtle *Emys orbicularis* (Najbar and Szuszkiewicz 2007). During a three year period, nests of individual females were found within 0.75 – 8.5 m of each other. Another study of the same species found that two individual turtles

displayed nest site fidelity to within a distance of less than 20 m over more than 10 years (Mitrus 2006). However, during that 15 year study, other females had nest locations that measured up to 840 m apart. Painted turtles (*Chrysemys picta*) in Idaho demonstrated nest site fidelity both within and among years during a three-year study (Lindeman 1992). The issue of spatial scale (Levin 1992) needs to be considered as the nesting beach for sea turtles can be much larger than suitable nesting areas available to a freshwater turtle living in a smaller wetland habitat.

We found little evidence to support the concept of nest site fidelity in Agassiz's desert tortoises at our study site over an 11 year period. Previous researchers noted that "Desert tortoises do not migrate in California, although some females move from habitual areas to other sites to lay eggs" without providing details about fidelity (Turner et al. 1986). At our study site, distances between a given female's nests in one year and her nests 11 years later ranged from 73.1 to 822.0 m. Wide variation in the degree of nest site fidelity has been observed in other turtle populations (Rowe et al. 2005, Mitrus 2006). With the exception of female #69 mentioned above, all nest sites fit largely within the core activity areas (measured as minimum convex polygons of capture locations; Lovich et al. 2011c) of each female from 1997 to 2010. Those activity areas ranged from an estimated 2.85 – 42.63 ha during two time intervals: 1997 to 2000 and 2001 to 2010 (Lovich et al. 2011c). It appears that a female's choice of nest sites is more a reflection of the boundaries of her activity area (Jackson and Walker 1997), than it is to deliberate searching outside that zone of familiarity. In fact, previous research suggested that although tortoises at our study site appear to select burrow locations that differ from random locations (Lovich and Daniels 2000), they do not exhibit nest site selection when comparing environmental attributes of burrows with nests to burrows without nests (Ennen et al. 2012a).

We are not suggesting that nest site selection is unimportant to *G. agassizii*. Our earlier research also demonstrated that the location and depth of nests in tortoise burrows varied predictably. The microhabitat of the burrow is typically cooler and higher in humidity and, therefore, aids in reducing water loss at certain times of day (Bulova 2002, Walde et al. 2009), and may account for why nests located farther into the burrow were shallower than nests located closer to the burrow entrance (Ennen et al. 2012a). Previous researchers suggested that nest site selection inside the burrow increases tortoise embryo survival by protecting them from lethal incubation temperatures (Baxter et al. 2008). It is also likely that this behavior affects sex determination in hatchling *G. agassizii* since warmer nests produce females and cooler nests produce males (Spotila et al. 1994). Thus, females appear to select nest sites more at the microsite scale (Leibold et al. 2004) inside the burrow rather than larger scales like the landscape. However, it is possible that females select nest sites at multiple scales. For example, females may select nest sites that are a tradeoff between predation risk in the overall environment and local vegetation cover (Spencer and Thompson 2003). Similarly, females of some sea turtles demonstrate individual consistency in their nest placement above the highest spring tide line, but very little consistency in nest placement and fidelity on an axis parallel to the shoreline or even the same nesting beach (Kamel and Mrosovsky 2004). Ultimately, the nest site selected is expected to optimize the minimization of risk at multiple scales.

Nest site environmental attributes we measured were consistent among females based on MANOVA and ANOVA, but varied between years, due mainly to differences in distance to the nearest perennial plant. We suggest that the difference is due to the effects

of multiple fires at our study site during the period of study, resulting in high mortality of widely-spaced, long-lived, dominant plant species like creosote bush (*Larrea tridentata*) and their replacement by closely-spaced, fast-growing, successional species like brittlebush (*Encelia farinosa*) (Lovich et al. 2011c). These changes affect the spatial distribution of perennial plants based on their sensitivity to fire (Brown and Minnich 1986, Abella 2009).

Nest site selection is also important in reducing vulnerability of eggs and embryos to predation as discussed above. Desert tortoise nests are exposed to a wide variety of predators (Ernst and Lovich 2009) and from 12 to 70% of nests are destroyed annually (Ennen et al. 2012a). Vulnerability of tortoise nests to predators may be minimized by two factors. First, desert tortoises at the site typically nest inside their burrows (Ennen et al. 2012a) where nests are better protected. Burrows at our site can be over 3 m in length but most are less. Second, predation risk might be mitigated by female nest guarding. Desert tortoises protect nests at our study site, either passively by sitting over the top of them and blocking the entrance to the burrow by turning sideways, or aggressively by pushing perceived predators away (Agha et al. 2013).

Nesting in the "climate controlled" conditions of tortoise burrows also mitigates against the temperature extremes in the larger scale of a desert landscape and, in conjunction with nest defense, relaxes some of the constraints that drive NSS in other turtle species. Based on analysis of our data it appears that tortoises nest within their activity areas on the broader landscape. This is in contrast to some turtle and tortoise species (e.g., Obbard and Brooks 1980, Stubbs and Swingland 1985), especially sea turtles, that leave foraging areas and migrate for considerable distances to nesting beaches (Hart et al. 2012). Desert tortoises then appear to select specific locations for their burrows (Lovich and Daniels 2000). Our data showing the shortening of daily movements as the date of oviposition approaches suggest that females are narrowing down their search for a suitable burrow. This is in contrast to the conclusion of Ennen et al. (2012a) that there was no evidence of nest site selection among burrows, perhaps due to the fact that the suite of environmental attributes used in the earlier analysis did not adequately reflect those that are important to females. After selection of an appropriate burrow, females then select nest locations within the burrow (Ennen et al. 2012a) that increase survivorship of hatchlings (Baxter et al. 2008). Since tortoises use multiple burrows during a single season (Bulova 1994, Rautenstrauch et al. 2002, Harless et al. 2009), any of which might have suitable microclimates for nest development and protection, returning to the same one to nest repeatedly may be unnecessary. However, finer-resolution data (e.g., annual) might reveal more or less fidelity than our data spanning 11 years between the nests of individual females.

providing accommodations during our research. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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