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Factors Affecting the Thermal Environment of Agassiz's Desert Tortoise (*Gopherus agassizii*) Cover Sites in the Central Mojave Desert during Periods of Temperature Extremes

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ABSTRACT.—Agassiz's Desert Tortoises (*Gopherus agassizii*) spend >95% of their lives underground in cover sites that serve as thermal buffers from temperatures, which can fluctuate >40°C on a daily and seasonal basis. We monitored temperatures at 30 active tortoise cover sites within the Soda Mountains, San Bernardino County, California, from February 2004 to September 2006. Cover sites varied in type and structural characteristics, including opening height and width, soil cover depth over the opening, aspect, tunnel length, and surficial geology. We focused our analyses on periods of extreme temperature: in summer, between July 1 and September 1, and winter, between November 1 and February 15. With the use of multivariate regression tree analyses, we found cover-site temperatures were influenced largely by tunnel length and subsequently opening width and soil cover. Linear regression models further showed that increasing tunnel length increased temperature stability and dampened seasonal temperature extremes. Climate change models predict increased warming for southwestern North America. Cover sites that buffer temperature extremes and fluctuations will become increasingly important for survival of tortoises. In planning future translocation projects and conservation efforts, decision makers should consider habitats with terrain and underlying substrate that sustain cover sites with long tunnels and expanded openings for tortoises living under temperature extremes similar to those described here or as projected in the future.

Agassiz's Desert Tortoise (*Gopherus agassizii*, hereafter referred to as Desert Tortoise or tortoise; Murphy et al., 2011) is a state and federally listed threatened species with designated critical habitat (U.S. Fish and Wildlife Service [USFWS], 1990, 1994; California Code of Regulations, 2013). Desert Tortoises occupy numerous habitat types throughout their geographic range in the Mojave and western Sonoran deserts of California, southern Nevada, northwestern Arizona, and southwestern Utah (Berry et al., 2002; Murphy et al., 2011). These habitats are characterized by highly variable environmental conditions, which may have played a role in the evolution of numerous adaptations and exaptations for coping with temperature extremes and unpredictable food and water resources (Morafka and Berry, 2002).

Desert Tortoises escape temperature extremes, aridity, and predators through behavior: They spend >95% of their lives underground in winter hibernation (Nussear et al., 2007), summer estivation (McGinnis and Voight, 1971), or daily cycles of emergence and retreat (Woodbury and Hardy, 1948; Nagy and Medica, 1986). They can tolerate droughts through physiological adaptations for conserving water (Nagy and Medica, 1986; Henen et al., 1998; Christopher et al., 1999) and by behavioral responses (Ruby et al., 1994; Duda et al., 1999). For example, when rain falls, these tortoises emerge to drink from water catchments, increase metabolic activity, and eat dried plants (Medica et al., 1980; Nagy and Medica, 1986; Henen et al., 1998). These adaptations are particularly important given recent projections of climate change.

The 2007 Intergovernmental Panel on Climate Change (IPCC) predicted increased warming is virtually certain for the 21st century (Intergovernmental Panel on Climate Change [IPCC], 2007). Moreover, a more arid climate, driven by higher temperatures and decreased precipitation, has been predicted for southwestern North America (Seager et al., 2007). Recent models, using these projections, show climate change is likely to reduce suitable habitat for Desert Tortoises (Barrows, 2011). The overall effects of climate change will be a complex interaction of

direct and indirect impacts, including decreased food resources, increased predation, and reduced reproduction rates (Fig. 1). However, the risk of local extirpations may be dampened by availability of quality cover sites.

Cover sites (e.g., burrows, caves, rock shelters, or pallets) are an integral part of tortoise habitat. These permanent to semipermanent shelters act as thermal buffers between tortoises and temperatures above the critical thermal maximum (39.5–43.0°C; Brattstrom, 1965) in summer and lethally cold temperatures in winter (Woodbury and Hardy, 1948; Nussear et al., 2007). Despite the importance of cover sites, data are limited on structure and other factors affecting thermal characteristics, including the geology that supports cover-site development.

Cover sites in the western and northeastern part of the Mojave Desert range have been described generally by McGinnis and Voight (1971), Burge (1978), and Bulova (1994), and more specifically relating to temperature by Woodbury and Hardy (1948) and Zimmerman et al. (1994). Our objectives were 1) to compare temperatures between different cover-site types, 2) to determine the structural characteristics that best explain variance in temperature extremes and fluctuations inside cover sites, 3) to model temperature change with distance inside cover sites, 4) to describe the geology that supports cover-site development, and 5) to postulate potential suitable habitat that may enhance survival given predicted conditions of climate change.

MATERIALS AND METHODS

Study Site.—Situated on the edge of a military installation, the ~8-km² study site is located in the Soda Mountains, San Bernardino County, California (Fig. 2). The site was undisturbed by anthropogenic activities during the study and has been the subject of several biological and geological research projects (e.g., Berry et al., 2006; Miller et al., 2009). At elevations of 459–795 m, the topography is composed of north–south trending, steep-sided ridges, 30–60 m in height; the ridges are separated by large and small ephemeral, generally dry stream channels (washes), which flow south into the main stream channel at Red Pass (Fig. 2). The old alluvial fan deposits are roughly 550,000–1,000,000 yr old and

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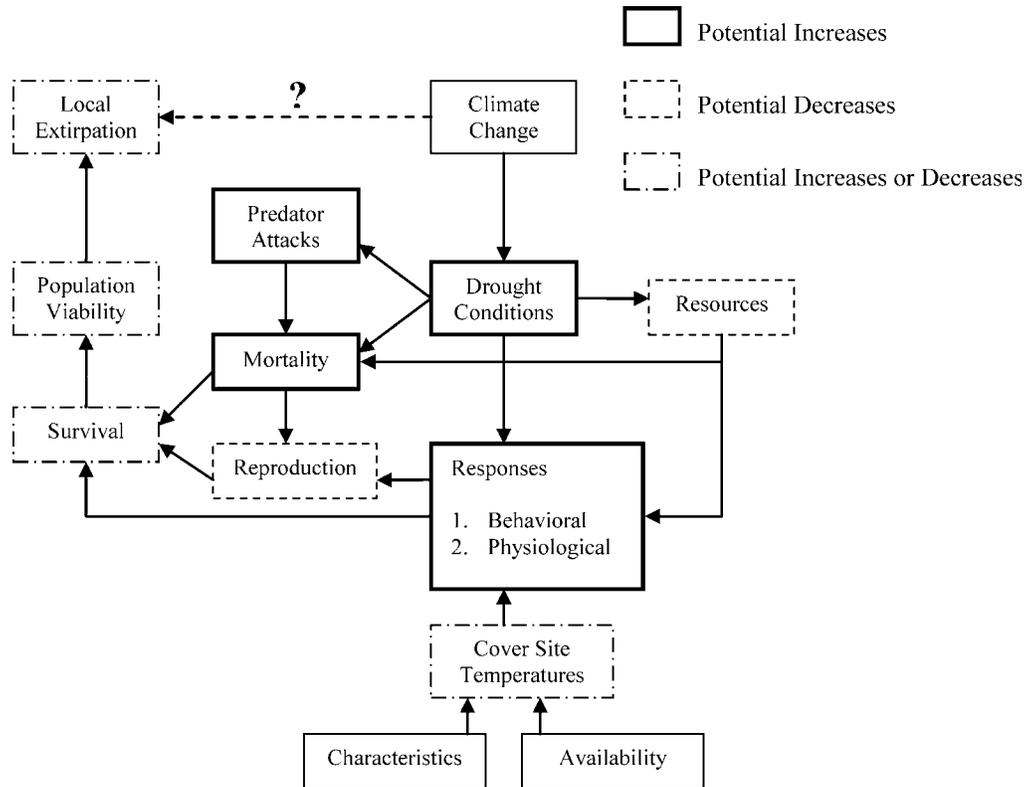


FIG. 1. Conceptual diagram displaying potential effects of climate change on Desert Tortoise populations and responses that may occur. Potential increases or decreases are indicated by mixed dashed lines. Here we pose the possible question whether climate change could lead to local extirpations if available cover sites inadequately provide relief from increased drought conditions.

overlie Miocene-age sandstone, shales, and conglomerates (Miller et al., 2009). Slope debris (colluvium) covered old deposits in many places. The predominant vegetation was creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), cheesebush (*A. salsola*), desert tea (*Ephedra californica*), and sweetbush (*Bebbia juncea*) associations (Berry et al., 2006).

Cover-Site Selection and Characteristics.—Between 2002 and 2004, we marked 60 tortoises as part of a long-term research project (Berry et al., 2006). Tortoise population density in 2003 was estimated with the use of mark–recapture techniques to be 28 km⁻². We fitted 28 adult tortoises with radio transmitters, monitored them at least once per month, and recorded their locations and cover-site associations. We noted that most cover sites were either completely contained in the old alluvial fan deposits of gravelly sand that ranged in calcite cementation from dense and cement-like to loosely cemented, or the roofs of the cover sites were in contact with the old alluvium (Miller et al., 2009). Some cover sites were in underlying strongly cemented to friable Miocene rock, in specific durable beds that formed roofs of cover-site tunnels. A few cover sites were developed in colluvium consisting of loose gravelly sand to moderately cohesive gravelly sand, similar to that described for “intermediate age” deposits of Miller et al. (2009).

We grouped the cover sites into five types, based on surficial geology: 1) caliche caves, defined here as natural or excavated caves with tunnels generally >1 m in strongly consolidated gravel and sand or rock with various levels of calcic development (old alluvial fan deposits or the roof was old alluvium) and persisting for several years if not decades (similar to dens described by Woodbury and Hardy, 1948); 2) consolidated gravel caves—natural or excavated caves in

consolidated gravel and sand and persisting for many years; 3) burrows—excavated in sand and gravels showing little soil development (colluvium), generally <1 m in length, and persisting one season or less; 4) rock shelters—natural or excavated crevices under rocks and persisting for >1 yr; and 5) pallets—shallow depressions under a shrub or excavated shallow burrows, barely covering the tortoise shell and persisting from a few days to months. Tortoises used 390 cover sites, including 314 caliche caves (80%), 39 soil burrows (10%), 16 rock shelters (4%), 11 consolidated gravel caves (3%), and 10 pallets (3%).

We selected 30 cover sites for the study in the proportion occurring on the site: 24 caliche caves, 3 soil burrows, 2 consolidated gravel caves, and 1 pallet. Additional selection criteria included frequent use by at least one tortoise, variation in cover-site size, and sufficient space for placing a temperature probe without disturbing tortoises. We did not monitor rock shelters, because use was temporary and rarely repeated; whereas pallets, another temporary shelter, have shown consistent use previously (Bulova, 1994). For each cover site, we recorded type, opening height, and width (m), depth of soil cover (m) at cover-site opening, probe length (m) in tunnel, and aspect (cardinal direction of opening: E, W, N, or S) (Fig. 3A,B).

To ensure that temperature probes were not obstructing the tunnel and tortoise activities, we limited placement to points where we could see the distal end. Probes were placed at or near the end of the tunnel in cover sites with shorter tunnels, whereas probes did not extend to the end when tunnels were long or had sharp bends. Despite placement limitations, we decided that probe length was an appropriate metric of tunnel length (i.e., longer probe lengths were associated with longer tunnels and

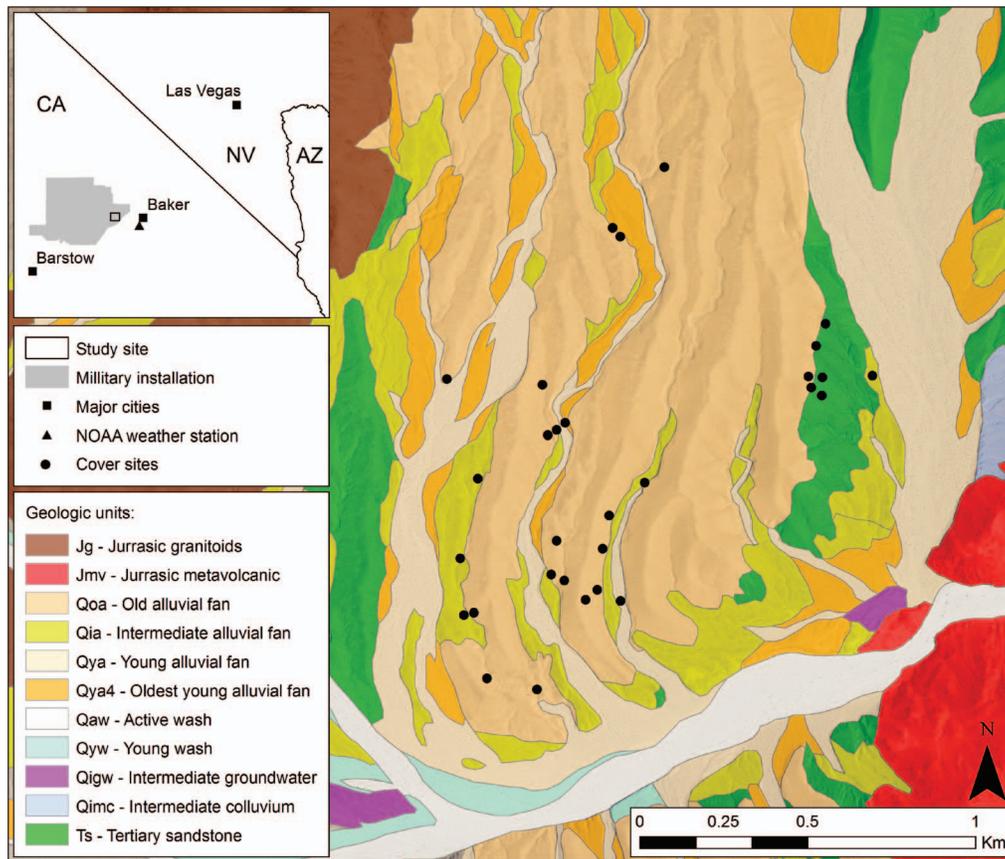


FIG. 2. Map of Soda Mountains study plot, San Bernardino County, California, showing geological units and cover-site locations. Map base layer was a 1-m NAIP image downloaded from USGS National Map Viewer.

shorter lengths with shorter tunnels). Each structural characteristic was measured at the onset of probe placement and subsequently measured for quality control and to record any natural (i.e., excavations by tortoises or other users) or anthropogenic alterations.

Temperature Measurements.—We measured external and cover-site temperatures at prespecified intervals of 30 or 60 min, with the use of three types of HOBO temperature loggers (Fig. 3C–E; Onset Computer Corporation, Bourne, Massachusetts): HOBO Temp Series (Model H01-001-01) measured temperatures at a single location; HOBO Pro Series (Model H08-031-08) measured temperatures at two locations; and HOBO Outdoor/Industrial 4-Channel External Series (Model H08-008-04) measured temperatures at four locations. The manufacturer's specifications indicated consistent performance throughout the range of expected temperatures (0–60°C), with a $\pm 0.2^\circ\text{C}$ accuracy.

Before the probes were placed in the field, we protected selected parts from weather and rodent chewing. Temp Series loggers, which lacked waterproofing, were wrapped tightly in plastic and duct tape, attached to a copper or polyvinyl chloride (PVC) tube, and placed in the tunnel with the probe on the distal end (Fig. 3C). Copper tubing was bent to follow the contour of a curved tunnel, whereas PVC was appropriate for a straight tunnel. The Pro Series base probe was placed at the cover-site opening, and the secondary probe, which extended from the base, was threaded through tubing and placed within the tunnel (Fig. 3D). One four-channel HOBO was placed under a shrub canopy (*Ambrosia dumosa*), with probes on the soil surface ~ 0.25 m from the shrub base, at four cardinal directions (Fig. 3E). The canopy was moderately dense, typical of the

environment, and exposed the probes to partial sun throughout the day.

HOBOs were monitored monthly between 4 and 5 February or 23–26 March 2004 and 15 and 16 September 2006. Data were downloaded with a HOBO Shuttle Data Transporter and uploaded with Boxcar 4.3 software package (Onset Computer Corporation, Bourne, Massachusetts). Data were exported in two formats: temporal (30 or 60 min) and daily minimum and maximum values. Abnormal data caused by animal chewing or probe removal were removed. Data gaps also resulted from equipment malfunction (e.g., battery failure), flash flood, or cover-site collapse.

We collected additional daily maximum and minimum air temperature data from the Baker weather station, located ~ 20 km east of the study site, at an elevation of 284 m (National Oceanic and Atmospheric Administration [NOAA] database: National Climate Data Center, 2011). Flagged data (i.e., problematic records) were removed from the database and analysis. We applied a standard lapse rate (1°C per 100 m) correction to correct weather station data for elevation.

Data Analysis.—We focused our analyses on extreme temperature periods, i.e., in summer, between July 1 and September 1, and late fall and early winter, between November 1 and February 15. We used daily maximum (T_{max}) and minimum (T_{min}) temperatures and calculated daily temperature fluctuations (T_{flux}) by taking the difference between daily maximum and minimum ($T_{\text{flux}} = T_{\text{max}} - T_{\text{min}}$). We then averaged over seasonal periods of interest. Extreme periods were identified with the use of temperatures recorded below the shrub and those from the Baker weather station.

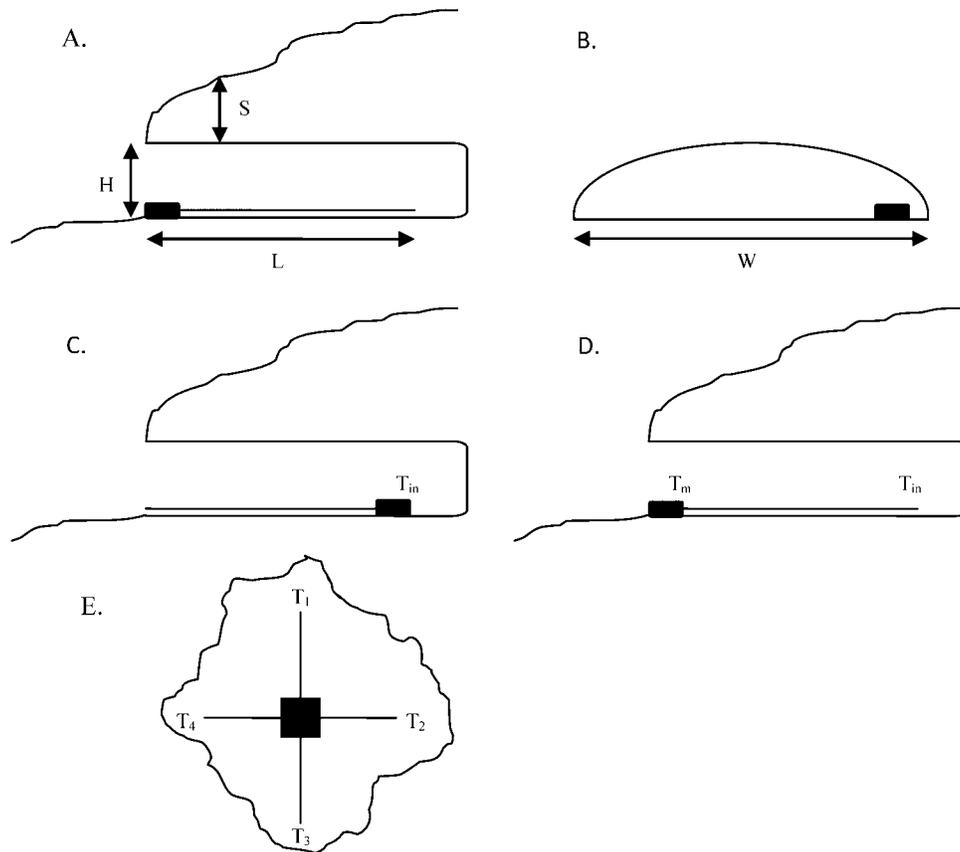


FIG. 3. Diagram of cover-site characteristics (A,B) and temperature probes used (C–E) at the Soda Mountains study plot, San Bernardino County, California. Characteristic abbreviations are S: soil cover, H: opening height, W: opening width, and L: probe length. Three models of probes used: (C) HOBO Temp Series loggers measured temperatures inside the tunnel (T_{in}), (D) HOBO Pro Series temperature probe measured temperatures at opening (T_m) and inside and (E) HOBO Outdoor/Industrial 4-Channel External Series measured temperatures at four locations (T_{1-4}) on the soil surface beneath the shrub canopy.

We used Kruskal-Wallis tests to compare temperatures between cover-site types, aspects, probe locations (opening vs. tunnel) in cover sites containing two probes, and to test for differences in cover-site characteristics between cover-site types. We applied nonparametric analyses because our data contained uneven sample sizes and deviated from the normal distribution assumed by most parametric tests. Previous studies have also found temperature data to be nonnormally distributed (Harmel et al., 2002). Prior to comparing cover-site types, we removed the pallet from the data set because there was only one replicate. We addressed limited sample sizes and unbalanced design by comparing Kruskal-Wallis H statistics with critical values from an exact probability table provided by Meyer and Seaman (2013). By doing this, we improved confidence in our results by avoiding use of large-sample chi-square approximations, which have been shown to be sensitive both to small and unbalanced sample sizes (Spurrier, 2003; Meyer and Seaman, 2013).

We performed a multivariate regression tree analysis to determine which cover-site characteristics were best predictors of inside temperature. The analysis was performed on four response variables: seasonally averaged maximum summer and minimum winter temperatures and seasonally averaged summer and winter temperature fluctuations. Six predictor variables were used: soil cover depth at cover-site opening, width and height of opening, probe length, aspect, and cover-site type. Categorical variables included four cover-site types and four cardinal directions (i.e., aspect). Regression trees were grown to

maximum size and subsequently pruned to optimal number of splits by tenfold cross validation to avoid overfitting.

Regression trees were tested for significance with a simulated permutation test, following methods described by Rejwan et al. (1999). Briefly, the amount of variance explained by the tree (r^2) was calculated for 2,000 random associations between response variables and cover-site characteristics. These values were then compared to the r^2 value obtained from the original tree. The original tree was considered significant and could be extrapolated outside the sample if the obtained r^2 value was among the top 5% of the random tree r^2 values.

We further quantified the relationship between probe length and cover-site temperature by fitting a linear regression model. Three classes of temperature data (summer maximum and summer and winter fluctuations) were log transformed to linearize the relationship and satisfy model assumptions (i.e., normality and constant variance). Summer maximum temperatures had a constant baseline subtracted to satisfy the assumptions. Winter minimum temperatures were not transformed because raw data exhibited a linear pattern and met the regression assumptions.

All statistical analyses were performed in R 2.15.3 (R Development Core Team, 2013). Regression trees were implemented with the use of the *rpart* package (Therneau et al., 2012). Post hoc multiple comparisons were conducted with the use of the *kruskalmc* function in *pgirmess* package (Giraudeau, 2013).

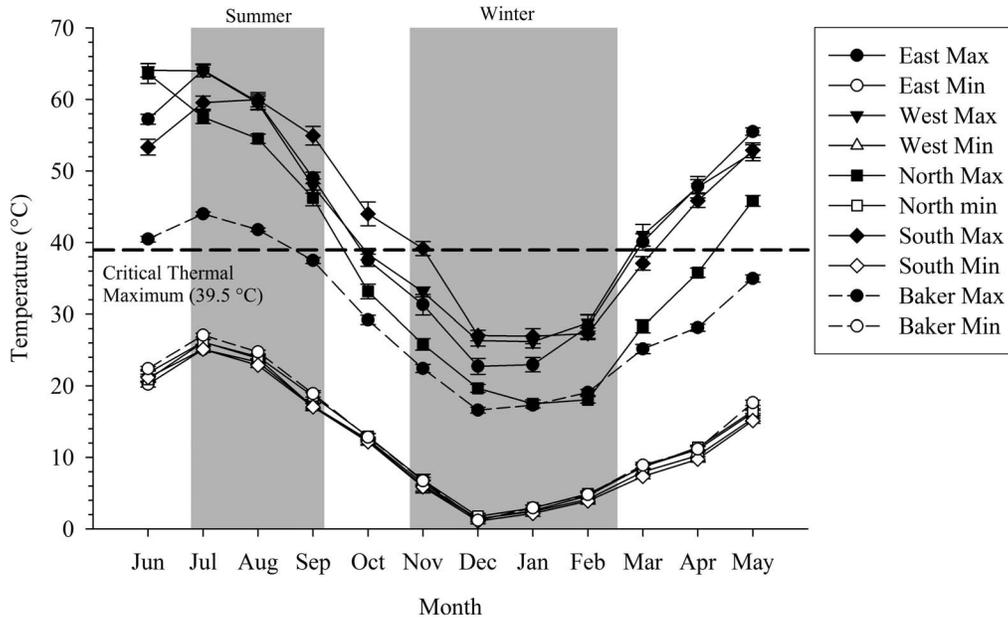


FIG. 4. Average monthly maximum and minimum temperatures calculated from daily temperature extremes recorded by probes placed on the soil surface under a white-bursage shrub canopy (*Ambrosia dumosa*) at the Soda Mountains study plot, and collected by a NOAA weather station in Baker, San Bernardino County, California. Probes were placed at four cardinal directions (N, S, E, W). Gray boxes indicate periods of summer (July 1–September 1) and winter (November 1–February 15) extremes. Error bars represent \pm standard error.

RESULTS

Temperatures under Shrub and Baker Weather Station.—Temperatures below the shrub were measured for an average duration of 636 ± 6 days (SD). Equipment issues increased variability in the number of measurements at each location. The temperature pattern under the shrub was similar to temperature measurements at the Baker weather station (Fig. 4). Summer maximum temperatures were slightly higher under the shrub compared to Baker air temperature.

General Characteristics of Cover Sites.—Average cover-site characteristics differed slightly when compared between types (Table 1). Probe length was the only characteristic significantly different (Kruskal-Wallis test; $\chi^2 = 8.45$, $P < 0.05$, $df = 3$). The median probe length for caliche caves was significantly longer than for soil burrows (critical probability level for post hoc set at $P = 0.05$).

Cover-Site Temperatures.—Differences in average summer maximum temperatures were significant between types (Kruskal-Wallis test; $\chi^2 = 7.10$, $P < 0.05$, $df = 2$; Table 2). Post hoc comparisons showed that median average summer maximum temperature in soil burrows was higher than caliche caves (critical probability level for post hoc set at $P = 0.05$). No

significant differences in average winter minimum temperatures were observed among types (Kruskal-Wallis test; $\chi^2 = 1.35$, $P = 0.51$, $df = 2$; Table 2) or between aspects (Kruskal-Wallis test; $\chi^2_{\text{summer}} = 6.37$, $P = 0.09$, $df = 3$; $\chi^2_{\text{winter}} = 2.74$, $P = 0.43$, $df = 3$). There was also no difference in average seasonal temperature fluctuations between types (Kruskal-Wallis test; $\chi^2_{\text{summer}} = 4.45$, $P = 0.11$, $df = 2$; $\chi^2_{\text{winter}} = 2.78$, $P = 0.25$, $df = 2$) or aspects (Kruskal-Wallis test; $\chi^2_{\text{summer}} = 3.54$, $P = 0.32$, $df = 3$; $\chi^2_{\text{winter}} = 3.15$, $P = 0.37$, $df = 3$).

When analysis focused on cover sites with two temperature probes ($n = 12$), significant differences were observed between probe locations (Table 2). Median average summer maximum temperature was significantly higher at the cover-site opening compared to inside the tunnel (Kruskal-Wallis test; $\chi^2 = 16.33$, $P < 0.001$, $df = 1$). Conversely, median average winter minimum temperature was significantly lower at the opening than inside (Kruskal-Wallis test; $\chi^2 = 14.08$, $P < 0.001$, $df = 1$).

Regression Tree Analysis.—The final (i.e., pruned) regression-tree model for summer maximum temperature had four terminal nodes and an r^2 of 0.75 ($P < 0.05$) (Fig. 5A). Three of six predictor variables were included. Probe length caused the first split and explained 50% of variance. Soil cover and opening width caused subsequent splits and respectively explained 13% and 12% of

TABLE 1. Characteristics (mean \pm SD; range) of cover sites monitored for temperature between 2004 and 2006 at the Soda Mountains study plot, San Bernardino County, California.

Type	n	Characteristics (m)			
		Probe length	Soil cover over tunnel roof	Width at opening	Height at opening
Caliche cave	24	1.47 \pm 0.44 (0.40–2.32)	0.76 \pm 0.26 (0.34–1.43)	0.47 \pm 0.22 (0.26–1.04)	0.22 \pm 0.08 (0.12–0.40)
Soil burrow	3	0.56 \pm 0.27 (0.34–0.85)	0.44 \pm 0.14 (0.27–0.55)	0.33 \pm 0.03 (0.30–0.36)	0.16 \pm 0.01 (0.15–0.16)
Consolidated gravel	2	1.17 \pm 0.93 (0.52–1.83)	0.78 \pm 0.02 (0.76–0.80)	0.35 \pm 0.06 (0.31–0.40)	0.15 \pm 0.02 (0.14–0.16)
Caliche pallet	1	0.64	0.67	0.37	0.15

TABLE 2. Temperatures (mean \pm SD; range) of cover sites monitored between 2004 and 2006 at the Soda Mountains study plot, San Bernardino County, California.

	<i>n</i>	Temperature ($^{\circ}$ C)			
		Summer maximum	Summer fluctuation	Winter minimum	Winter fluctuation
Cover-site type					
Caliche cave	24	33.70 \pm 1.93 (29.2–38.3)	1.11 \pm 1.05 (0.2–5.3)	13.50 \pm 2.38 (9.1–20.2)	1.67 \pm 1.95 (0.2–9.8)
Soil burrow	3	36.61 \pm 0.36 (36.3–37.0)	2.69 \pm 1.64 (1.2–4.5)	11.90 \pm 2.19 (10.5–14.4)	2.27 \pm 0.48 (1.7–2.6)
Consolidated gravel	2	34.23 \pm 0.20 (34.1–34.4)	1.23 \pm 0.83 (0.6–1.8)	12.74 \pm 2.68 (10.8–14.6)	0.83 \pm 0.62 (0.4–1.3)
Caliche pallet	1	35.26	1.30	8.92	1.52
Probe location					
Inside	12	33.39 \pm 1.83 (29.2–35.9)	0.87 \pm 0.43 (0.2–1.8)	14.18 \pm 2.56 (10.8–20.2)	1.20 \pm 0.88 (0.2–3.0)
Mouth	12	43.67 \pm 6.81 (35.1–57.7)	13.95 \pm 8.90 (2.0–29.5)	7.66 \pm 2.05 (4.5–11.0)	10.61 \pm 5.97 (0.9–18.9)

variance. The highest average summer maximum temperature (36.69 $^{\circ}$ C) was found in cover sites with probe length <1.34 m and soil cover <0.70 m. Conversely, the lowest average summer maximum temperature (32.21 $^{\circ}$ C) was found in cover sites with probe length \geq 1.34 m and opening width \geq 0.36 m.

Winter minimum temperature also contained four terminal nodes (Fig. 5B), with an r^2 of 0.54 ($P < 0.05$). Probe length

caused the first split and a subsequent split that accounted for 37% and 6% of variance, respectively. Opening width also caused a secondary split and accounted for 11% of variance. The lowest average winter minimum temperature (10.97 $^{\circ}$ C) was found in cover sites with probe length <0.91 m. The highest average winter minimum temperature (16.27 $^{\circ}$ C) was found in cover sites that were \geq 1.58 m, with an opening width \geq 0.50 m.

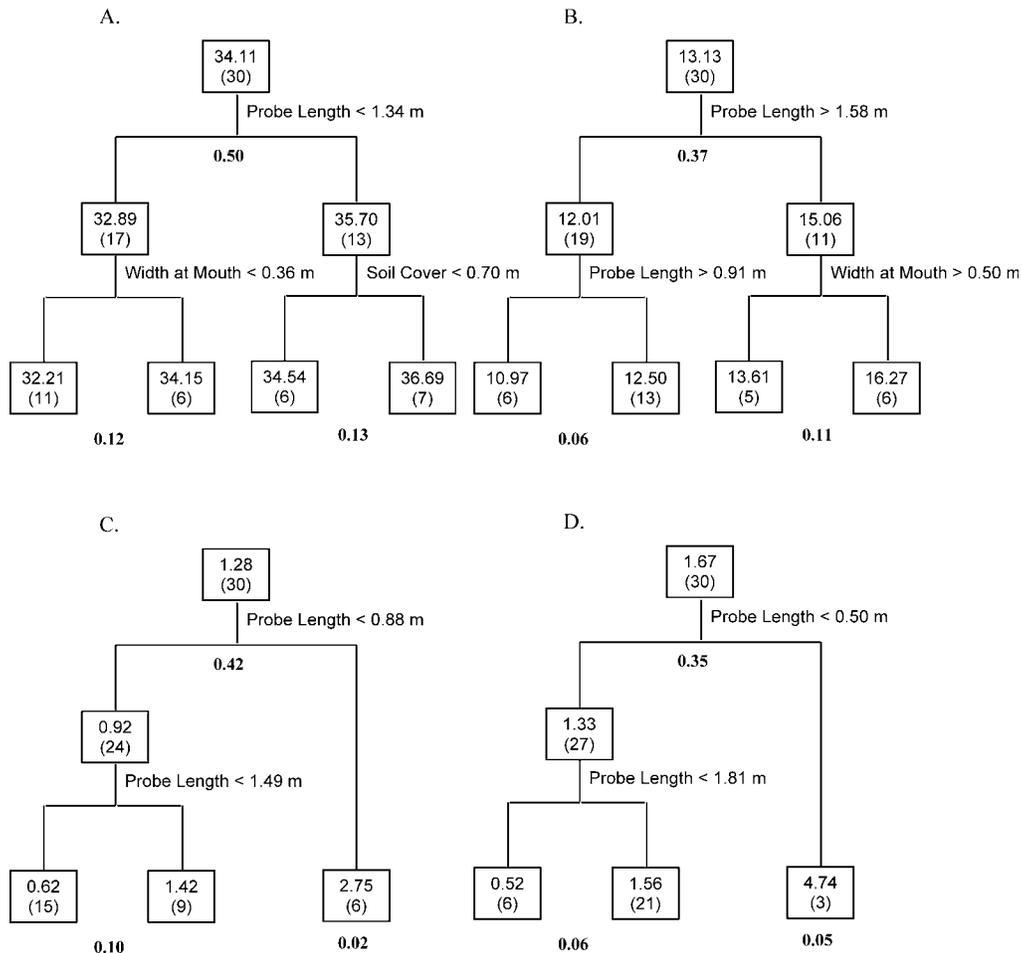


FIG. 5. Regression tree models generated for (A) maximum summer and (B) winter minimum temperatures, and (C) summer and (D) winter temperature fluctuations recorded inside tunnels of 30 Desert Tortoise cover sites at the Soda Mountains study plot, San Bernardino County, California. The number of cover sites is shown in parentheses and r^2 of the split is in bold.

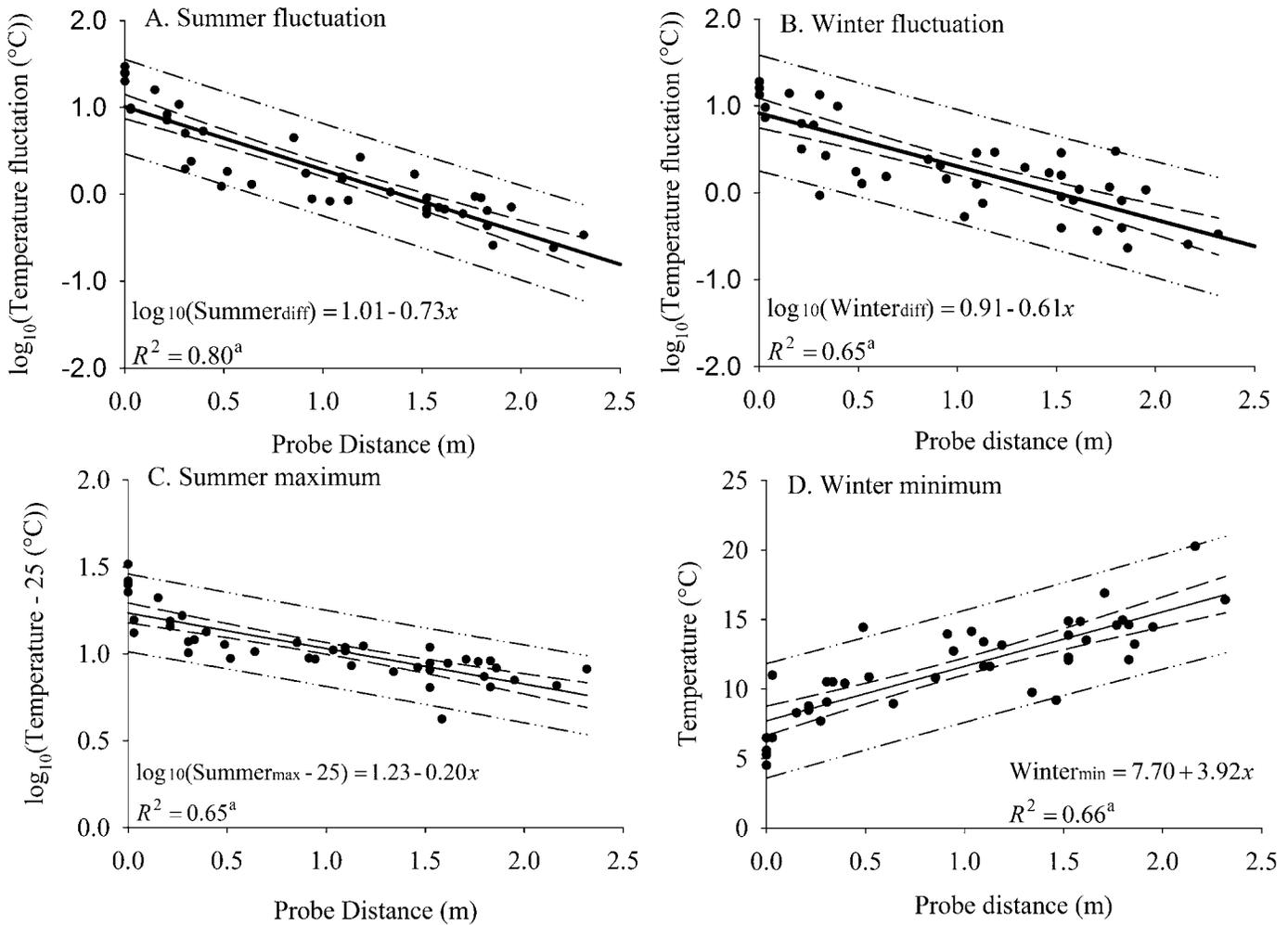


FIG. 6. Relationship between probe length and \log_{10} temperature fluctuations ([A] summer and [B] winter), and temperature extremes ([C] summer maximum and [D] winter minimum) inside Desert Tortoise cover sites at the Soda Mountains study plot, San Bernardino County, California. Solid lines represent least-squares linear regression for all data points. The dashed and dashed-dotted lines represent 95% confidence and prediction intervals, respectively.

Final regression trees for summer and winter temperature fluctuations contained three terminal nodes caused by probe length splits (Fig. 5C,D). The largest average temperature fluctuations (summer = 2.75°C, winter = 4.74°C) were in cover sites with probe length <0.88 m in summer and <0.50 m in winter. Conversely, the smallest average fluctuations (summer = 0.62°C, winter = 0.52°C) were in cover sites with probe length >1.49 m in summer and >1.81 m in winter. Overall, probe length accounted for 54% and 46% of variance ($P < 0.05$), in summer and winter, respectively.

Final regression trees for extreme seasonal temperatures and daily seasonal temperature fluctuations indicated that tunnel length was the greatest influence on cover-site temperatures. Cross-validation analysis indicated that this relationship would likely maintain predictability outside of the sample for both seasonal extremes (median $r^2_{\text{summer}} = 0.48$, median $r^2_{\text{winter}} = 0.26$, $n = 2,000$ permutations) and seasonal fluctuations (median $r^2_{\text{summer}} = 0.42$, median $r^2_{\text{winter}} = 0.24$, $n = 2,000$ permutations).

Regression Analysis of Probe Length.—Temperature had a significant linear relationship with probe length for all four response variables (Fig. 6A–D). The relationship was negative for both average summer and winter temperature fluctuation. The relationship with average summer maximum temperature was

also negative, whereas average winter minimum temperature exhibited a positive relationship.

DISCUSSION

Cover-Site Temperatures and Characteristics.—We evaluated structural characteristics that influence thermal environments of Desert Tortoise cover sites. We focused our analysis on periods of time when extreme temperatures are peaked and likely lethal upon prolonged exposure, thereby increasing necessity of cover-site refuge. Temperature extremes recorded under a shrub in summer were as much as 30°C above the critical thermal maximum identified for tortoises. These temperatures were also greater than local air temperatures, highlighting increased near-to-ground temperatures experienced by tortoises.

In previous studies, tortoises were observed to use cover sites with longer tunnels during summer (Burge, 1978) and winter (Woodbury and Hardy, 1948; Burge, 1978). Other desert reptiles, such as Gila Monsters (*Heloderma suspectum*), exhibit similar behavior, retreating to deeper, warmer sites in winter and cooler, moister sites in summer (Beck and Jennings, 2003). Our study suggested that tunnel length (i.e., probe length) was the key

characteristic of cover sites that regulated thermal environments.

The importance of tunnel length was correlated previously with temperature stability. Woodbury and Hardy (1948) described longer winter “dens” as being advantageous because of lags between outside and inside temperatures, creating lower daily peaks and minimizing fluctuations. Our results supported this distance–stability relationship. Probe length was the only variable identified in the analysis for temperature fluctuation, accounting for 54% and 46% of variance in summer and winter, respectively. Probe length also correlated inversely with daily temperature fluctuations as a logarithmic-linear function (Fig. 6A,B). Seasonal relationship was more pronounced in summer, which was reasonable given probe length accounted for more variance in summer temperature than in winter.

Although not the only variable identified in the analysis for extreme temperatures, probe length accounted for the most variance (50% summer maximum, 37% winter minimum). Additional variation was explained by opening width (summer and winter) and soil cover (summer). Others have theorized larger openings increase air circulation, making cover-site temperature more susceptible to outside extremes (Woodbury and Hardy, 1948). However, our models indicated the opposite—cover sites with larger openings had cooler summer temperatures and warmer winter temperatures. We observed that tunnels often narrowed after the opening, indicating that opening width may not be indicative of tunnel width. Other factors not measured in this study, such as rodent middens and backfill, can also impact air circulation.

Cover-site type and aspect are characteristics that can provide certain thermal advantages (Burge, 1978; Berry and Turner, 1986); however, both type and aspect were statistically unimportant variables in the regression tree analysis. Conversely, Kruskal-Wallis tests showed significant differences between types—median summer maximum temperature was significantly lower in caliche caves compared to soil burrows. Given the unbalanced design and small sample sizes, caution should be used when interpreting these results beyond the sampled cover sites. For example, regression tree analysis divides data into increasingly smaller partitions, which may underrepresent groups with small sample sizes, making it less likely to identify an effect.

Small sampling distributions for cover-site type and aspect were limited by the landscape. The distribution of sampled cover sites represented the availability of cover sites: caliche caves were numerous and more permanent, whereas consolidated gravel caves, pallets, and soil burrows were fewer in number or, in the latter two cases, tended not to persist from season to season. Aspect was limited by north-trending ridges, which promoted excavation on east–west facing slopes. These limitations reinforced the influence that surficial geology has on construction and maintenance of certain cover-site characteristics—most notably tunnel length.

The geological characteristics associated with caliche and consolidated gravel caves, the types most strongly associated with persistence and also with tunnel length, were strongly cemented old alluvial fan deposits and Miocene sandstone and conglomerate. These substrate materials apparently are durable enough to resist collapse and yet sufficiently friable for digging. Cover sites in colluvium and alluvial fan deposits with little or no soil development were observed to be less persistent and prone to collapse.

Cover-Site Temperatures and Climate Change.—Climate change poses dual threats to Desert Tortoises. The interactive effects of increased temperature and reduced precipitation may threaten populations with extinction, similar to those modeled for other ectotherms (Sinervo et al. 2010). Tortoises typically respond to drought conditions by decreasing time above ground (Ruby et al. 1994; Duda et al., 1999) and physiologically reducing water and energy expenditures (Henen et al., 1998; Bulova, 2002). The effectiveness of these responses is temperature dependent and strongly coupled with cover-site temperatures.

Although our study was limited to temperature, soil moisture should also be investigated. Reduced soil moisture has been shown to amplify temperature extremes (Hirschi et al., 2011) and climate predictions for the desert (warmer and drier) would lead to less energy used by latent heat flux (i.e., evapotranspiration) and more for near-surface heating (Seneviratne et al., 2010). Subsurface impacts are difficult to project because soil-moisture retention is strongly dependent on particle-size distribution and soil structure (e.g., Miller et al., 2009), and may vary widely in the deposits we investigated. However, given the connection between soil moisture, temperature, and potential feedback loops (see Fig. 10; Seneviratne et al., 2010), further work is needed to investigate effects on cover-site temperatures.

Management Implications.—Tortoise translocations are on the rise. In 2008, for example, several hundred tortoises were translocated from critical habitat on military land in the central Mojave Desert (Esque et al., 2005), and, in 2013, USFWS and U.S. Bureau of Land Management announced plans to translocate an estimated 1,000 tortoises a year from the Desert Tortoise Conservation Center in Las Vegas, Nevada. In addition, human-mediated migrations of tortoises to higher elevations or more northerly habitats may become an essential recovery tool (Camacho, 2010; Thomas, 2011).

Successful translocations may be limited by availability of suitable cover sites (Bulova, 1994). Riedle et al. (2008), for example, noted that populations of the closely related Morafka’s Tortoise (*Gopherus morafkai*) were strongly influenced by the availability of cover sites, in particular caliche caves. Our findings further suggest that during periods of extreme temperatures, suitable cover sites should contain long tunnels and larger openings and that the ability for locations to sustain such cover sites may rely on terrain and underlying substrate.

Habitats similar to the Soda Mountains study site (i.e., surficial geology supporting caves in old alluvial fans and conglomerate) can be found in the northern Mojave Desert in deeply dissected Basin and Range topography of high mountains and down-dropped valleys. The >3,000-m range in elevations from valley floor to mountain peaks supports many different vegetation associations and habitats, some of which may provide shelters for tortoises. In addition, caves often occur in limestone and dolomite formations, and these formations are common in parts of the Basin and Range.

This study provides information on how the characteristics of cover sites affect the well-being of individual tortoises (e.g., temperature stability). Still, more data are needed to understand relationships between cover-site structure, tortoise ecophysiology, and recovery of populations (Fig. 1). We also need to develop geographical distributions of geological formations likely to support optimal cover sites. Such information is essential to predicting the long-term persistence of populations and supporting risk and benefit analyses of assisted migrations and translocations (Camacho, 2010).

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