

Spatial Organization of Desert Tortoises and their Burrows at a Landscape Scale

JEFFREY J. DUDA^{1,2}, ANTHONY J. KRZYSIK^{3,4}, AND JOEL M. MELOCHE¹

¹Department of Biological Sciences, Wayne State University, Detroit, Michigan 48202 USA;

²Present Address: USGS, Biological Resources Division, Western Fisheries Research Center,
6505 NE 65th, Seattle, Washington 98115 USA [E-mail: jeff_duda@usgs.gov];

³U.S. Army-ERDC-CERL, P.O. Box 9005, Champaign, Illinois 61826 USA;

⁴Present Address: Ecological Research Institute, Prescott College, 220 Grove Ave, Prescott, Arizona 86301 USA

ABSTRACT.— We thoroughly surveyed two 9 km² study plots using 624 km of transect lines in the south-central Mojave Desert, California, mapping with a precision global positioning system the location of desert tortoises (*Gopherus agassizii*) and their burrows. We found 98 desert tortoises and 1463 tortoise burrows. Three separate geospatial methods (quadrat-variance, nearest neighbor, and 3 geospatial functions) confirmed that active and total desert tortoise burrows were aggregated on the landscape at multiple spatial scales. Desert tortoises also displayed an aggregated pattern, although results were not consistent between the two plots. We also found a significant positive association between desert tortoises and their burrows using Type II linear regression and Ripley's $K_{12}(t)$ function. A strong positive association between active burrows/km² and tortoises/km² ($r^2 = 0.88$) and between total burrows/km² and tortoises/km² ($r^2 = 0.80$) and the supporting results of Ripley's $K_{12}(t)$ geospatial function suggest that, within a given year and locality, desert tortoise burrows can be used to determine relative desert tortoise density patterns.

KEY WORDS.— Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; burrows; geospatial statistics; Mojave desert; Ripley's functions; spatial pattern; USA

The excavation of subterranean burrows is an essential adaptation of the desert tortoise (*Gopherus agassizii*), a species of the Mojave and Sonoran Deserts currently listed as threatened over ca. 30% of its geographic range (U.S. Fish and Wildlife Service, 1990; Berry, 1997). As a relatively stable temperature and humidity microhabitat, a burrow provides refuge from the daily and seasonal temperature extremes typical of a desert environment (McGinnis and Voight, 1971; Gregory, 1982; Ruby et al., 1994; Zimmerman et al., 1994; Rautenstrauch et al., 1998). Burrows also serve as focal locations for predator avoidance, courtship, reproduction, and nesting (Woodbury and Hardy, 1948; Patterson, 1971; Turner et al., 1986; Bulova, 1994; 1997). A narrow seasonal window of suitable weather forces tortoises to spend up to 95% of their lifetime inactive in their burrows or pallets (shaded, above ground depressions) (Nagy and Medica, 1986).

During their activity season, tortoises use a number of different burrows, displaying acute navigational ability and fidelity to well-used travel routes (Berry, 1986; Bulova, 1997). They typically place the entrance of their burrows under shrubs in specific microhabitats, such as washes or vegetative ecotones (Burge, 1977; Baxter, 1988), presumably to take advantage of food resources or soils amenable to burrowing behavior (Jennings, 1997; Lovich and Daniels, 2000). Mojave Desert tortoises use from 1 to 20 burrows per year, although average numbers vary between genders, geographic locations, seasons, and years (Bulova, 1994; Burge, 1978; Duda et al., 1999; Freilich et al., 2000). The interaction between the number of burrows used, the distance between burrows, and switching patterns and fre-

quency, plays a central role in determining an individual's annual home range (Duda et al., 1999).

Published data on landscape scale spatial distribution patterns of desert tortoises and their burrows are unavailable in the literature. Here, we detail the results of an intensive survey of desert tortoises and tortoise burrows on two 9 km² study plots designed to determine: 1) the spatial pattern of desert tortoises and their burrows at a landscape scale; 2) whether a positive association exists between the density of desert tortoises and the density of tortoise burrows and, if so, at what scale this relationship is strongest; and 3) the structural dimensions and vegetative associations of tortoise burrows. We then discuss these data and analyses in an ecological context designed to supplement the management and conservation of this species.

METHODS

Study Area.— All data were collected at the Sand Hill Training Area (Sand Hill) of the Marine Corps Air Ground Combat Center (MCAGCC), 28 km northwest of Twentynine Palms, California. Sand Hill is a 111 km² area in the southwest corner of MCAGCC where light military training occurs in a low relief landscape of gentle, rolling hills dominated by creosote-bursage scrub (*Larrea tridentata* – *Ambrosia dumosa*). Elevation at Sand Hill ranges from 555 to 883 m, but most of the contours lie between 732–829 m. Soils are finely sorted and consist mostly of sandy-loams, with some loose sands.

As part of a population density assessment (Krzysik, 2002), we established 5 study plots, 3 km x 3 km square,

throughout Sand Hill. Here, we detail the results of an extensive survey of desert tortoise burrows that occurred over two contiguous plots with a 2 km common boundary. Hereafter, we refer to these as the north and south study plots.

We estimated shrub community composition and density at Sand Hill during the summer of 1994 as part of another study. We randomly placed four 800 m reference transects at Sand Hill. At regular intervals along this transect (100, 300, 500, and 700 m), we established a 100 m x 4 m transect following a random compass bearing (0–359°) originating on the reference transect. Within these sixteen 400 m² strip transects we measured the maximum height and diameter of all shrub species and used these data to estimate species composition, total shrub cover, and total intershrub space.

Locating and Measuring Tortoise Burrows. — We surveyed the north and south study plots for desert tortoises and their burrows. Two observers, spaced 30 m apart, surveyed two parallel 3 km transect lines along a north-south compass bearing. Each observer was responsible for surveying 15 m on each side of the transect line. We deemed a 30 m transect appropriate for two surveyors to efficiently cover 18 km² within a reasonable sampling time frame. Using precision military global positioning system (GPS) receivers in navigation mode with “real time” 5 m accuracy, a sighting compass, and landmarks on the horizon, we were able to remain on transect lines for the entire 3 km. When a set of transect lines was completed, we surveyed the adjacent pair in the opposite direction. In this manner, each 9 km² study plot was surveyed with 104 transects. Sampling was completed in 24 days between 3 March and 1 May 1996, during the season of peak above-ground tortoise activity.

We recorded a suite of parameters upon finding each tortoise or tortoise burrow. The spatial locations of tortoises and their burrows were recorded with GPS and burrows were marked with high visibility flagging to ensure they would not be mistakenly resampled on adjacent transects. For all burrows, we recorded the presence of perennial vegetation ≤ 1.0 m from the burrow’s entrance. Also, for burrows found in good condition (see below), we measured maximum height of tunnel floor to roof, maximum width, and maximum depth. We estimated the maximum depth of burrows by guiding a retractable steel measuring tape as far into the burrow as possible.

We ranked the condition of tortoise burrows on an ordinal scale (classes 1–5) as a function of condition and maintenance. Condition class 5 burrows were considered active (i.e., currently in use by a tortoise, although not necessarily at the time of sampling), having a characteristic dome shape with a rounded roof and flat floor, and the entrance with obvious signs (e.g., foot prints, plastron scrapes) of recent tortoise activity. Class 4 burrows were similar in all respects to class 5 burrows, yet they lacked signs of recent activity. Class 3 burrows were losing their characteristic dome shape and had some structural damage near the entrance. Class 2 burrows were in a general state of disrepair,

with much debris, caving in, and some loss of interior and exterior integrity. Class 1 burrows were collapsed, yet obvious, tortoise burrows. For ease of presentation, we refer to the above classes in the text as: active, excellent, good, poor, and collapsed.

Statistical Analyses. — We used three separate techniques, quadrat-variance, nearest neighbor, and geospatial functions, to analyze the spatial pattern of desert tortoises and their burrows in the two study plots. First, we superimposed a grid measuring 100 m x 100 m (resulting in 900 “quadrats” for each plot) upon a distribution map of each study plot and tallied the number of tortoises and the number of tortoise burrows in each quadrat. This routine was repeated using 200, 300, 500, and 1000 m grid sizes (resulting in 225, 100, 36, and 9 quadrats/plot, respectively). We then calculated frequency distributions of occupied quadrats for tortoises, active burrows, and total burrows at each grid size. Only burrows rated as active, excellent, or good were included in the “total burrows” tabulation. We assumed that burrows rated as poor or collapsed, obviously having not been in use for some time, would contribute additional error variance into the analysis of spatial pattern and were not reflective of current burrow use by the resident tortoise population.

We tested the null hypothesis that the spatial pattern of desert tortoises, active burrows, and total burrows did not differ from complete spatial randomness (CSR), defined by Diggle (1983) to describe an array of points that are distributed independently. We used the per grid cell means and variances from 100, 200, 300, 500, and 1000 m to calculate a variance:mean ratio. A characteristic of the Poisson (random) distribution is equality between the mean and variance; we used this relationship to test for CSR (Ludwig and Reynolds, 1988). Thus, a variance:mean score not significantly different from 1 suggests spatial randomness. We tested for departure from unity in our data using a t-test, following the method described by Greig-Smith (1983), where the standard error of the estimate, calculated independent of density, is

$$\sqrt{2/(n-1)} .$$

Variance:mean scores > 1 indicate a clumped or aggregated spatial pattern, whereas scores < 1 indicate a uniform pattern. A drawback of the quadrat-variance approach, pointed out by many authors (Greig-Smith, 1983, and references therein), is the sensitivity to quadrat size. At small quadrat sizes, there is a bias towards random patterns, and as quadrat size increases (up to a point) there is a bias towards clumped patterns.

We used the computer program SPATIAL (Fisher, 1990) to calculate nearest neighbor and geospatial functions. The nearest neighbor routine of SPATIAL, derived from the Clark-Evans (1954) statistic and independent of quadrat size, calculates the average minimum distance from one individual (or burrow) to its nearest neighbor for each individual in the data set. The actual nearest neighbor

distance (r_A) is then compared to an expected average nearest neighbor distance (r_E), computed as:

$$r_E = \left(2\sqrt{\rho}\right)^{-1}$$

where ρ = density (Clark and Evans, 1954). We calculated r_E with a correction for edge effects (Donnelly, 1978). Under CSR the ratio r_A / r_E does not differ significantly from unity. Unlike the variance:mean ratio, R scores < 1 indicate a clumped, whereas scores > 1 indicate a uniform pattern.

We calculated three univariate geospatial functions, Ripley's $K(t)$ function (Ripley, 1981) and Diggle's $F(x)$ and $G(y)$ functions (Diggle, 1983), also using program SPATIAL (Fisher, 1990). As with nearest neighbor statistics, geospatial functions are based on the total nearest neighbor distances in an area. The Clark-Evans statistic is a first order statistic, based on a mean, whereas Ripley's $K(t)$ is a second order statistic based on the variance of the nearest neighbor data (Haase, 1995). Thus, the utility of $K(t)$ is that it uses all possible event-event distances within a given search radius, instead of just a single nearest neighbor distance (Fisher, 1990). In practice, the $K(t)$ function centers a circle of radius t around a point and determines the number of nearest neighbors that lie within the circle. An iterative routine calculates this value for all points in the data set and determines the mean and variance for each value of t evaluated between $t = 0$ and t_{max} . The unbiased estimator of $K(t)$ used by program SPATIAL, with corrections for edge effects, is:

$$\hat{K}(t) = n^{-2}A \sum_{i \neq j} w_{ij}^{-1} I_t(u_{ij})$$

where t = distance, n = number of events in area A , w_{ij} = proportion of the circumference of the circle of radius t centered on one event (i) passing through another event (j) that lies within A , u_{ij} = distance between i_{th} and j_{th} events, and I_t is a counter variable defined to be 1 if $u < t$ and 0 otherwise (Fisher, 1990:312).

$G(y)$ is an empirical distribution function of nearest neighbor distances for each point in the area and $F(x)$ is an empirical distribution function that examines the distribution of point-individual distances based on a predefined, uniform sample grid (see Fisher, 1990, for equations and unbiased estimates of these functions; Ripley [1981] and Diggle [1983] provide theoretical discussions and derivations). The functions have different sensitivities in detecting different spatial patterns and Diggle's functions, based on nearest neighbor measures, are sensitive to sample size (Barot et al., 1990). Here, we focus on $K(t)$ (because of sample size robustness and the fact that our data tended towards spatial aggregation) and use $G(y)$ and $F(x)$ in a complementary fashion.

We determined departure from CSR by generating minimum, maximum, and mean values of each function through the univariate Monte Carlo simulation option of SPATIAL. Under CSR, the function $K(t) = \pi t^2$ and thus positive values of $K(t) - \pi t^2$ indicate an aggregated pattern and negative values indicate a uniform pattern. The Monte

Carlo routine generates function values based on hypothetical distributions of the data generated for the same number of events in the same size area using a uniform random process (this process is actually pseudorandom because it relies upon a computer-based random number generator). The minimum and maximum values, when plotted against t , constitute a confidence envelope with which to determine significant departures from CSR. We ran 99 Monte Carlo simulations per data set (i.e., for tortoises, active burrows, and total burrows in each plot), which provided expected values and 99% confidence intervals.

We also examined the interaction between desert tortoises and both active and total burrows using type II regression and Ripley's $K_{12}(t)$ function. We ran type II linear regression on the number of tortoises and either active or total burrows per grid cell from the data collected for quadrat-variance techniques mentioned above. A type II linear regression is appropriate when both the dependent and independent variables are measured with error (Sokal and Rohlf, 1995), although type I regression may be used when the purpose of the regression is prediction of the independent variable (in this case, tortoises). We decided to use the more conservative type II regression for our data. We excluded data obtained with the 100 and 200 m grids because at such small scales most of the data points were either 0, 1, or 2 for both the dependent and independent variables. We used a FORTRAN program to calculate type II regression (written by J. Emlen) that minimized the residual variance perpendicular to the regression line. We determined the standard deviation of regression parameters using 10,000 bootstraps. Significance was evaluated at $p < 0.05$.

Ripley's $K_{12}(t)$ function, a bivariate analog of $K(t)$, examines spatial association between two variables that occur within the same area. The estimator of $K_{12}(t)$, corrected for edge effects, is:

$$\hat{K}_{12}(t) = (n_1 + n_2)^{-1} \{n_1 \tilde{K}_{12}(t) + n_2 \tilde{K}_{21}(t)\}$$

where

$$\tilde{K}_{12}(t) = (n_1 n_2)^{-1} A \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij}^{-1} I_t(u_{ij})$$

and

$$\tilde{K}_{21}(t) = (n_1 n_2)^{-1} A \sum_{i=1}^{n_2} \sum_{j=1}^{n_1} w'_{ij}^{-1} I_t(v_{ij})$$

The notation above follows that of $K(t)$, except that subscripts 1 and 2 refer to the two types of events, u_{ij} = distance between the i th type 1 event and the j th type 2 event, v_{ij} = distance between the i th type 2 event and the j th type 1 event, and w_{ij} and w'_{ij} are the proportions of the circumference of circles of radius t centered on an event of one of the point types and passing through an event of the other point type (Fisher, 1990:314). Significant positive values of $K_{12}(t)$ indicate spatial association, whereas negative values indicate spatial repulsion of the two variates.

RESULTS

Abundance of Desert Tortoises and Burrows. — We located 1463 tortoise burrows at the north and south study plots (Fig. 1). Of these, 592 (65.6/km²) were found in the north plot and 871 (96.8/km²) in the south plot. There were 111 active, 147 excellent, 117 good, 82 poor, and 135 collapsed burrows in the north plot. In the south plot, the series was 171, 205, 186, 127, and 182 burrows. The two plots contained nearly identical proportions of burrows in each condition class ($= 1.54, p > 0.75$). When we combined the plots, excellent burrows accounted for 20.0% of all burrows; there were more good burrows (24.2%) and fewer poor burrows (14.2%) than expected from a uniform distribution.

Burrows were associated with perennial vegetation 67.6% of the time (creosote bush, 52.1%; white bursage, 8.5%; big galleta grass [*Pleuraphis rigida*], 5.3%; other 1.7%), and 32.4% were located in open, intershrub spaces. The other shrub taxa associated with tortoise burrows were, in order of importance: *Krameria grayii*, *Hymenoclea salsola*, *Ephedra* sp., and *Psorothamnus* sp. We estimated the total shrub cover at Sand Hill to be 15.2% and intershrub spaces accounted for 84.8% of the total cover. The co-dominant shrubs, creosote bush and bursage, comprised 7.9% and 7.1% of the total shrub cover. Thus, it appears that tortoises did not locate their burrows randomly, but preferentially placed them underneath or near vegetation, especially creosote bushes.

We analyzed the depth of tortoise burrows, pooled from the north and south plots, using only those burrows rated as

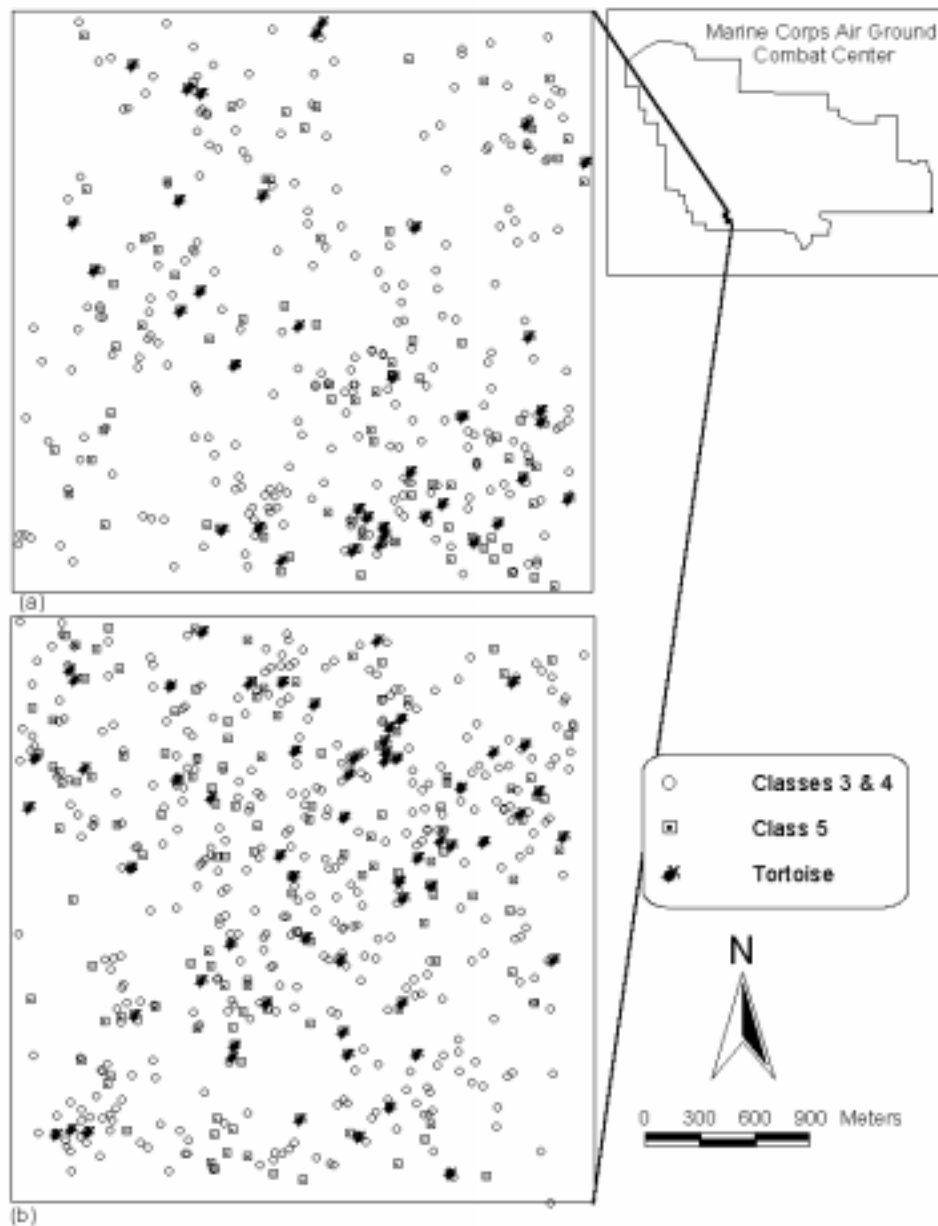


Figure 1. Map of the spatial location of desert tortoises, active tortoise burrows (squares), and total desert tortoise burrows (circles+squares) at two 9 km² study plots (a = north, b = south) at Sand Hill, Marine Corps Air Ground Combat Center, Twentynine Palms, California.

active, excellent, or good ($n = 937$) because these burrows were structurally sound. However, some could not be measured because there was a tortoise occupying them. In all, 851 burrows were measurable. Burrow depth had a mean of 0.82 m and a distribution positively skewed in favor of shallow burrows. Nearly 75% of the burrows measured were < 1 m in length. Deeper burrows between 1–2 m were less common (22%) and burrows > 2 m were rare. Burrows that were rated as active ($\bar{x} = 1.1$ m) were significantly deeper than those rated as excellent ($\bar{x} = 0.88$), which in turn were significantly deeper than burrows rated as good ($\bar{x} = 0.56$) (Kruskal-Wallis: $H_{2,851} = 169.9$, $p = 0.001$; multiple comparisons, all $p < 0.001$).

We located 98 tortoises, with 37 at the north plot and 61 at the south plot. A drought during 1996 caused tortoises to reduce their above-ground activity (Duda et al., 1999), resulting in 86.0% of the desert tortoises being found underground, sheltered in burrows. Partly because of this, we were able to determine sex for only 55.0% of the animals (35 males and 18 females). The others were unavailable for sex determination because they were either too far underground or immature and lacking the morphological characteristics needed for distinguishing gender.

Spatial Pattern Analyses. — In general, the spatial patterns of desert tortoises, active burrows, and total burrows were aggregated, regardless of the algorithm used to determine departure from CSR. However, there were some inconsistencies, especially with the variance:mean ratio. The variance:mean ratio for desert tortoises was > 1 for all grid sizes examined (Table 1). This difference was significant for tortoises at the north plot, but not significant at all grid sizes for the south plot, where burrow abundance was 64% greater. Both active and total desert tortoise burrows displayed variance:mean ratios significantly > 1 (with the exception of active burrows using 100 m grid cell sizes at the south plot), with the ratio increasing steadily with increased grid size (Table 1). An increase of the variance:mean ratio with increased grid size (and resultant decrease in grid number) is expected, based both on theoretical and empirical studies, and may be an artifact of the technique (Greig-Smith, 1983).

Results from the Clark-Evans nearest neighbor analysis also suggested that active and total tortoise burrows were aggregated, although the results were not significant for the tortoises themselves (Table 2). The mean nearest neighbor distance for desert tortoises was 231.8 m at the north plot and

Table 1. Descriptive statistics and significance tests of quadrat-variance scores used for desert tortoises, active burrows, and all burrows at the north and south study plots (for a description of burrow types, see text). Significant differences denote a departure from complete spatial randomness, and \bar{x}/σ values > 1.0 imply an aggregated spatial distribution.

Grid (m)	N	Plot	\bar{x}	σ^2	σ^2/\bar{x}	t	p^1
Tortoises ($N_n = 37, N_s = 61$)							
100	900	N	0.04	0.05	1.18	3.71	***
100	900	S	0.07	0.07	1.06	1.34	0.09
200	225	N	0.16	0.22	1.32	3.41	***
200	225	S	0.27	0.29	1.06	0.60	0.28
300	100	N	0.37	0.53	1.44	3.10	**
300	100	S	0.61	0.66	1.08	0.55	0.29
500	36	N	1.03	1.69	1.65	2.71	**
500	36	S	1.69	2.32	1.37	1.55	0.08
1000	9	N	4.11	9.88	2.40	2.80	**
1000	9	S	6.78	11.95	1.76	1.53	0.1
Active Burrows ($N_n = 111, N_s = 171$)							
100	900	N	0.12	0.14	1.17	3.66	***
100	900	S	0.19	0.19	1.02	0.44	0.33
200	225	N	0.49	0.72	1.46	4.89	***
200	225	S	0.76	0.91	1.19	2.00	*
300	100	N	1.10	2.13	1.94	6.59	***
300	100	S	1.70	2.43	1.43	3.02	**
500	36	N	3.03	7.58	2.50	6.29	***
500	36	S	4.75	8.52	1.79	3.32	**
1000	9	N	12.11	60.77	5.02	8.03	***
1000	9	S	19.00	67.11	3.53	5.06	***
All Burrows ($N_n = 371, N_s = 555$)							
100	900	N	0.62	0.73	1.18	3.81	***
100	900	S	0.41	0.53	1.29	6.12	***
200	225	N	1.65	3.04	1.84	8.91	***
200	225	S	2.47	4.00	1.62	6.58	***
300	100	N	3.71	9.45	2.55	10.88	***
300	100	S	5.51	12.43	2.26	8.84	***
500	36	N	10.25	41.47	4.05	12.74	***
500	36	S	15.42	39.85	2.59	6.63	***
1000	9	N	41.00	372.2	9.08	16.16	***
1000	9	S	61.67	369.6	5.99	9.99	***

¹ * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

194.8 m at the south plot. Values of the Clark-Evans statistic for tortoises were nearly significant at the north plot ($p = 0.06$), suggesting an aggregated pattern, but not significant at the south plot. Nearest neighbor distances for active burrows and total burrows were significantly different from 1.0 at both the north and south plots. Again, the north plot showed a more aggregated pattern, as active burrows and

Table 2. Clark-Evans nearest neighbor statistics for tortoises and tortoise burrows at the north and south study plots. The parameter R represents the mean nearest neighbor distance (subscripts A = actual, E = expected). Values of R significantly different than unity ($p < 0.05$) are either clumped (< 1.00) or uniformly distributed (> 1.0).

Variate	Plot	N	r_A (m)	r_E (m)	R^1	Z	p
Tortoises	N	37	231.8	265.4	0.87	-1.34	0.06
Tortoises	S	61	194.8	203.1	0.96	-0.56	0.26
Active Burrows	N	111	125.0	149.0	0.84	-3.03	***
Active Burrows	S	171	110.2	118.5	0.93	-1.40	*
All burrows	N	371	67.8	79.4	0.85	-5.19	***
All burrows	S	555	58.4	64.9	0.90	-4.32	***

¹ $R = \text{actual } \bar{x} \text{ nearest neighbor distance} / \text{expected } \bar{x} \text{ nearest neighbor distance } (r_A / r_E)$

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

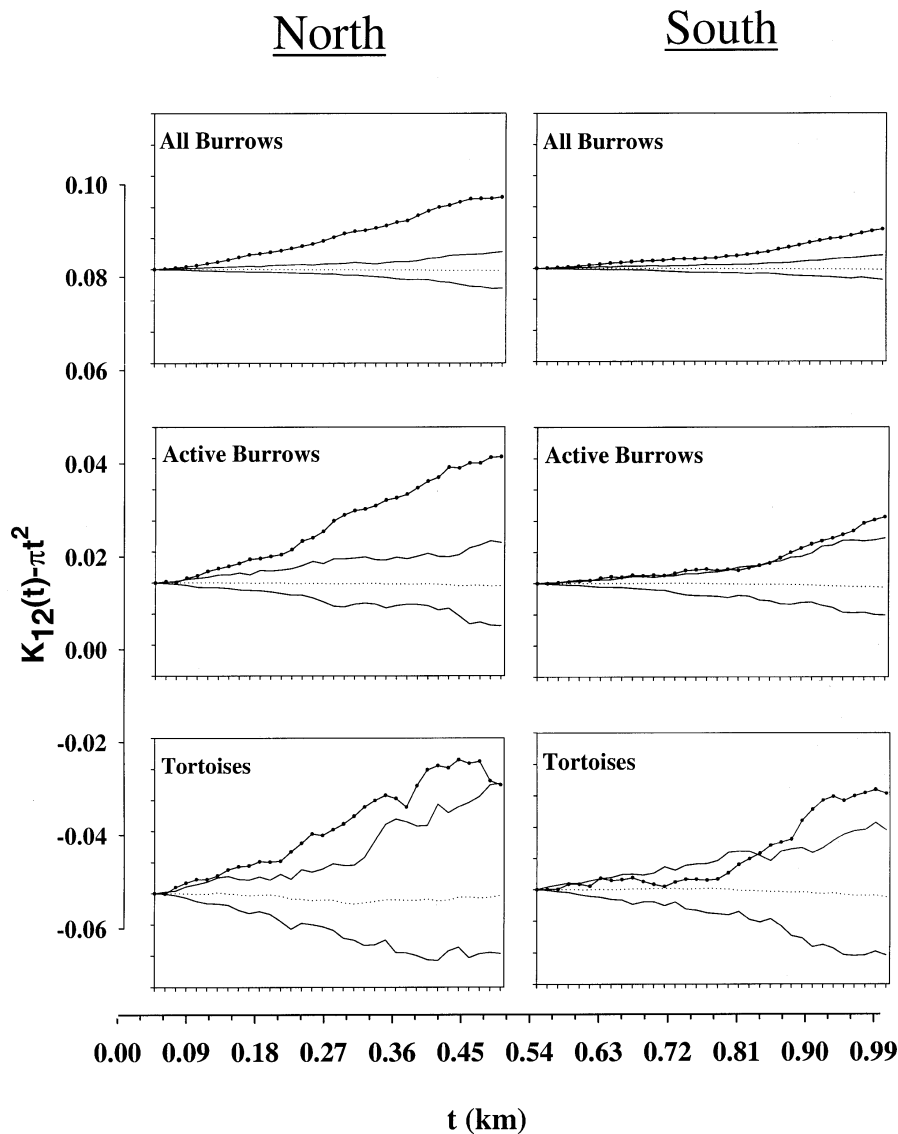


Figure 2. Graphs of Ripley's univariate $K(t)$ function versus distance (t) for (top) all burrows, (middle) active burrows, and (bottom) tortoises at two 9 km² study plots, Marine Corps Air Ground Combat Center, Twentynine Palms, California. Solid lines (confidence envelope) represent the maximum and minimum values and the dotted line represents the average value of the function derived from random data modeled with 99 Monte Carlo simulations. The line with diamonds represents the actual data. If this line lies outside of the confidence envelope, then the data differ from Complete Spatial Randomness at $p < 0.01$.

total burrows had nearest neighbor scores 16 and 17%, respectively, smaller than those expected from CSR.

Computation and graphical analysis of Ripley's univariate $K(t)$ function showed that desert tortoises, active burrows, and total burrows were aggregated and allowed a more detailed examination at the spatial scales where departure from CSR occurred. We conducted Ripley's $K(t)$ analyses using 150, 300, 600, and 900 m in steps of 10 m. For ease of presentation and conservation of space, we present graphs of $K(t)$ where distance = 900 m and do not present graphs of $G(y)$ and $F(x)$.

Ripley's function $K(t)$ for desert tortoises showed that tortoises were highly aggregated, especially as t increased past small values. At the north plot, $K(t)$ remained within the confidence envelope at small distances (ca. 1–50 m), suggesting CSR at this scale (Fig. 2). At distances greater than

60 m, $K(t)$ is beyond the upper limit of the confidence envelope, suggesting an aggregated pattern at all distances > 60 m. At the south plot, where abundance was 64% greater, spatial pattern conformed to CSR at longer distances than at the north (1–90 m), followed by a departure from CSR at distances > 90 m. However, the $K(t)$ curve re-enters the confidence envelope at intermediate values of t (300–625 m). We interpreted this to mean that tortoises at the south plot were randomly distributed at this range of distances. At all other distances up to 900 m, tortoises were aggregated. Analysis of the other two functions (graphs not presented) showed that at the north and south plots, the function $G(y)$ supported the trends apparent in $K(t)$, while $F(x)$ did not.

Our analysis using geospatial functions revealed that desert tortoise active burrows and total burrows also were

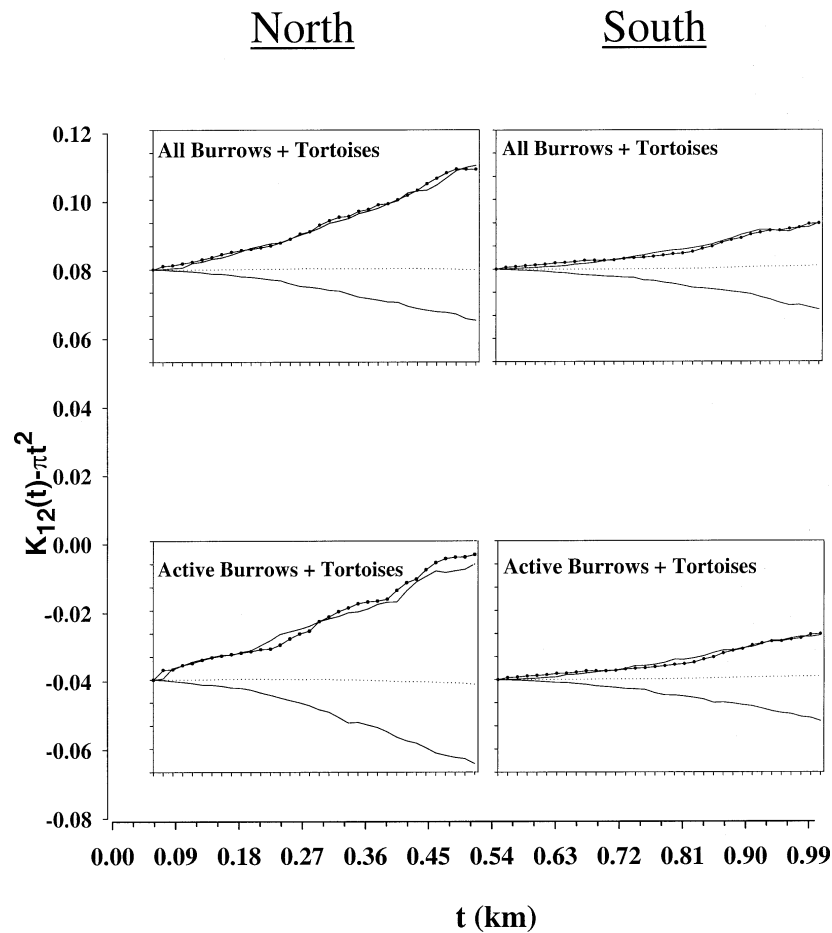


Figure 3. Graphs of Ripley's bivariate function $K_{12}(t)$ versus distance for (top) active burrows and tortoises and (bottom) total burrows and tortoises at two 9 km² study plots, Marine Corps Air Ground Combat Center, Twentynine Palms, California. Solid lines represent the maximum and minimum values and the dotted line represents the average value of the function from 99 Monte Carlo simulations. The line with diamonds represents the actual data. If this line lies outside of the confidence envelope, then the data differ from Complete Spatial Randomness at $p < 0.01$.

aggregated. Active burrows at the north plot exceeded the maximum value of the confidence envelope at distances > 60 m (Fig. 2). As with the analysis for tortoise locations, the south plot differed from the north in showing departure from CSR at intermediate and large distances, but not at small distances. The $K(t)$ function had values beyond the maximum limit of the Monte Carlo envelope at a range of distances from 146–346 m and 368–424 m, returned within the envelope from 425–800 m, and then exceeded the envelope again at distances greater than 848 m. Thus, active tortoise burrows were spatially aggregated at all distances greater than 60 m in the north plot, but were more erratic in the south plot, where they drifted into and out of CSR, especially when the function was evaluated at intermediate distances. Results for total burrows showed a consistent departure from CSR at both study plots at all distances > 30 m. These results were consistent with graphical analysis of function $G(y)$.

Association Between Tortoises and Burrows.—Ripley's $K_{12}(t)$ function detected significant spatial association between desert tortoises and both active and total burrows at both study plots (Fig. 3). The association between desert

tortoise and active burrow distributions was especially apparent at distances between 1–333 m at both study plots. At the upper limit of that range, the $K_{12}(t)$ function retreats into the confidence envelope at intermediate distances, but re-emerges again at distances > 788 m in the north and > 848 m in the south. Graphical analysis of the $G_{12}(y)$ function also supported a strong association at distances ≤ 200 m. We found similar results for the association between tortoises and total burrows, especially in the north plot. In the south plot there was a similar, strong association at short distances according to $K_{12}(t)$ and $G_{12}(y)$ (ca. 80 m), and then again at distances between 250–333 m.

We also documented an association between desert tortoises and their burrows using type II linear regression (Table 3). In order to increase sample size we pooled data from the north and south study plots. We found a strong positive association between desert tortoises and total burrows ($p < 0.05$, $r^2 = 0.80$) and also between desert tortoises and active burrows ($p < 0.01$, $r^2 = 0.88$) using 1000 m grid sizes. When we used grid sizes of 300 and 500 m, there still was a positive association, but the results were not significant for either active or total burrows ($p > 0.25$).

DISCUSSION

The analysis of spatial data, especially with geospatial functions, provides an important tool for placing autecological desert tortoise information into a conservation context. The spatial patterns of total and active desert tortoise burrows were decidedly aggregated, regardless of the algorithm used and these patterns were consistent across spatial scales ranging anywhere from 60 to 900 m for active burrows and 30 to 900 m for total burrows (Fig. 2). Desert tortoises, on the other hand, were clearly aggregated at the north plot, but results were inconsistent at the higher density south plot. We found a positive association between the density of desert tortoises and their burrows using both linear regression and Ripley's geospatial functions. Our regression analysis showed that 88% of the variance in desert tortoise density was explained by the density of active burrows (Table 3). Similarly, Ripley's $K_{12}(t)$ function (Fig. 3) and Diggle's $G_{12}(y)$ showed a strong association between both active and total burrows and desert tortoises, at multiple spatial scales. This information suggests that within a given spatial-temporal context (i.e., locality-year), desert tortoise burrows can be reliably used as surrogates for desert tortoise density and model population-level spatial structure.

Spatial Pattern. — Interpretations of spatial pattern, especially in a multi-scale context, provide insight into the underlying mechanisms responsible for the pattern (Levin, 1992). We propose that spatial aggregation in desert tortoises is expected for at least two fundamental reasons: habitat quality and social interactions. Habitat quality can be associated with several important features of individual fitness: quality and/or quantity of food resources, burrowing properties of soils, structure and density of shrubs, and availability and persistence of water puddles following rain events (see Medica et al., 1980; Nagy and Medica, 1986; Lovich and Daniels, 2000). Social interactions predominantly relate to finding mates, but complex social hierarchies cannot be ruled out and may be important for local population structure. Additionally, the spatial-temporal predictability of any or all of these resources would strongly reinforce site fidelity of individual desert tortoises.

Because individual desert tortoises use multiple burrows (at our study plots, desert tortoises used 2–11 burrows during a productive year and 1–6 during the following drought year [Duda et al., 1999]), the aggregation of indi-

vidual tortoises result in a clumping pattern of their burrows at a smaller spatial scale. Spatial aggregation of tortoises and their burrows may be evident because desert tortoises have relatively small home ranges relative to the spatial scales that we examined. At our study plots, desert tortoises possessed home ranges from 1–8 ha in both a drought year and a productive year (Duda et al., 1999). Assuming a perfectly square home range, this means that tortoises traveled in areas ranging from 100 m x 100 m to 283 m x 283 m. The majority of between-observation distances traveled by tortoises during these two years were 100 to 300 m. Also, 88% of the distances traveled by desert tortoises at the time of sampling (i.e., the drought year) were ≤ 200 m, a value falling within the range of average nearest neighbor distances for active burrows that we report here.

Home range dynamics, as described above, would clearly result in aggregated spatial patterns of both desert tortoises and their burrows. The home range of an individual tortoise, at least in studies of Mojave Desert populations (O'Connor et al., 1994; Duda et al., 1999; Freilich et al., 2000), is best viewed as a circumscribed network of burrows. During the peak activity season, a tortoise centers activities around a burrow, utilizing a local feeding neighborhood during favorable climatic conditions and sheltering during extremes. After a period of time, the tortoise will navigate to another burrow (perhaps repairing an old one or replacing a collapsed one), and center activities in that relatively small spatial area. The rate at which tortoises switch among different burrows during the activity season is dynamic, varying annually and seasonally according to climatic factors. On an annual basis, the number of burrows used and thus home range size varies and appears to be closely correlated to climatic conditions and food supply (Duda et al., 1999). Long-distance, single trip movements > 1 km by adults (non-dispersal) outside of the "typical" home range occur (Berry, 1986), but tortoises generally return to the neighborhood of the burrow network after a short period of time. Burrow switching patterns display high inter-individual variability (see below), yet Bulova (1994) documented significant differences between males and females in the intensity and timing of inter-burrow movement, apparently due to seasonal reproductive effects (Rostal et al., 1994). During the spring, females switched among burrows more frequently than males, probably searching for nest sites and then laying eggs. Use was similar between the sexes

Table 3. Slopes (b), intercepts (a), and summary statistics (r^2 , SE , p) of Type II regression analysis of desert tortoise abundance on active and total burrow abundance. Data in parentheses are standard deviations estimated by 10,000 bootstraps. Data are pooled from the north and south study plots.

Variable	Grid Size (m)	N	a	b	SE ¹	r ²	p
Active Burrows	100	200	0.02 (0.01)	0.34 (0.04)	1.19	0.45	> 0.25
	36	72	0.59 (0.17)	0.20 (0.06)	0.99	0.16	> 0.25
	9	18	-0.51 (0.13)	0.38 (0.04)	0.25	0.88	**
Total Burrows	100	200	-0.10 (0.02)	0.13 (0.02)	1.33	0.31	0.25
	36	72	0.20 (0.06)	0.09 (0.03)	0.99	0.18	> 0.25
	9	18	-2.10 (0.04)	0.15 (0.02)	0.32	0.80	*

¹ SE, calculated as $s_{y,x}/\bar{Y}$, is a unitless standard error of the regression (Zar, 1996).

² * $p < 0.05$ ** $p < 0.01$

during the summer, but during August and September, when courtship, cohabitation, and mating peak, male tortoises switched burrows more frequently, possibly to increase the number of encounters with females.

Habitat selection also helps to explain the aggregated pattern of desert tortoises and their burrows, although the factors most responsible for distribution patterns remain generalized. Over their entire geographic range, desert tortoises are known to occur in a wide range of habitat types, from rocky hillsides to alluvial flats and bajadas (Woodbury and Hardy, 1948; Bury et al., 1994; Germano et al., 1994). Recently, Andersen et al. (2000) published results from an intensive modeling effort based on Classification and Regression Tree Analysis, using remotely sensed imagery, GIS, supervised vegetation classifications, soil maps, and tortoise distribution and abundance data (represented by 73 variables held in 11 spatial data layers). They found that higher tortoise densities were related to southwest facing slopes with loamy soils and moderate cover of perennial vegetation. Baxter (1988), in a study of the spatial distribution of tortoises and burrows at Sand Hill, found that tortoises preferentially placed their burrows at the edge of vegetation types and washes. Thus, the selection of shelter sites by tortoises may be driven, in part, by soil type, exposure (affecting the thermal stability of the burrow), and food supply, which themselves may follow an aggregated pattern (Milne, 1997). Yet, the current distribution of any desert tortoise population is bound to be driven by factors that are difficult to parameterize, such as stochasticity and historic environmental conditions.

Finally, social factors help to explain the aggregated pattern of desert tortoise burrows and the strong association between tortoises and burrows. A comprehensive model of desert tortoise social structure is not available, but reproductive behavior and the availability of mates are paramount. In her review of the social structure of desert tortoises, Berry (1986) noted evidence of territorial behavior (especially for males), agonistic encounters, and dominance hierarchies. Yet, desert tortoises do not completely exclude conspecifics from their home range; rather, considerable home range overlap among multiple individuals is common (O'Connor et al., 1994). Other chelonians congregate during the mating season and disperse during other times (Brattstrom, 1974). Woodbury and Hardy (1948) noted that up to 20 desert tortoises shared a winter den in southwestern Utah that was outside of the normal home ranges of most individuals, although this behavior is uncommon, at least for tortoises of the Western Mojave Desert.

Our hypothesized factors driving the aggregated pattern of desert tortoises and their burrows, habitat selection and social interactions resulting in home range dynamics, are further supported by the strong site fidelity typically exhibited by desert tortoises. Freilich et al. (2000) surveyed the same study plot in Joshua Tree National Park for 6 consecutive years, documenting tenacious site fidelity in their population of desert tortoises. In addition to considerable overlap in 9 radio-tracked home ranges from one year to the next,

they found that 77% of tortoises recaptured during surveys after 1–4 yrs were found within 300 m of the original capture site, a distance within these tortoise's annual home range size. A strong level of site fidelity in the desert tortoise can be explained, again, through energetic considerations of living in a harsh climate. Because they are relatively slow moving and have small home ranges, it is more energetically efficient to reside in an area that produces reliable forage (under favorable growing conditions) and remain there, than to roam the desert in nomadic fashion. This strategy would seem to pay off especially well for females, who have to gain energy for reproduction and also provide (indirectly) an area of high resources for their progeny. Determining the factors most responsible for site fidelity in desert tortoises would be a major accomplishment, while solving the elusive problem of habitat selection.

Another factor selecting for site fidelity is the energetic investment that tortoises put into constructing their burrows. To our knowledge, there are no studies that have measured the energetic cost of burrow construction, but we can assume that it is non-trivial. It also seems reasonable to assume that the investment is considerably higher for deeper burrows, or dens, that serve as hibernacula during overwintering, yet tortoises are known to share these locations (Woodbury and Hardy, 1948; Bailey et al., 1995; Rautenstrauch et al., 1998). If indeed a non-trivial investment, tortoises should select soils for burrowing that maximize stability and longevity. Associating burrows with perennial vegetation, in addition to thermal benefits and reduced detectability by predators, provides structural stability via the rooting system. Because the distribution of soils (especially at scales similar to tortoise searching) is decidedly aggregated, the clumped patterns of burrows are again, in part, explained by this relationship. Additional research is needed to determine the soil characteristics (e.g., texture, content, and moisture) most responsible for burrow site selection and longevity.

The depth of tortoise burrows was variable and age dependent, but nearly 75% of burrows at Sand Hill were less than a meter deep. The detectability of desert tortoises resting in burrows, a matter of some debate, requires further attention. Our results suggest that ca. 90% of desert tortoise burrows at Sand Hill were ≤ 1.5 m deep, a depth that readily allows the use of light (reflected off mirrors) to illuminate the entire tunnel when looking for a tortoise. Moreover, the method of "tapping," where a retractable probe is placed into burrow and gently rapped against a tortoise's carapace (Medica et al., 1986), is a reliable method for determining the presence of tortoises concealed in burrows.

Conservation and Management Implications

The recovery plan for the desert tortoise requires statistically rigorous long-term monitoring that documents population trends (U.S. Fish and Wildlife Service, 1994). Determining the most efficient method for estimating abundance in desert tortoise populations has been a matter of some

controversy (Bury and Corn, 1994) because of the inherent difficulties in sampling tortoises (Turner et al., 1985; Krzysik and Woodman, 1991; Freilich et al., 2000). Recently, distance sampling (Buckland et al., 1993; Anderson et al., 2001) has been shown to be a robust method to estimate desert tortoise abundance, especially when compared with previous methods (U.S. Fish and Wildlife Service, 1998). Distance sampling is unburdened by the underlying spatial pattern of objects (Burnham et al., 1980). However, the strong positive association between tortoises and their burrows provides a strong argument for the further development of techniques that use active and total burrows in concert with desert tortoise density estimates for monitoring desert tortoise populations.

The use of desert tortoise burrows, and even tortoise scat, at a given locality and time frame shows promise for adjusting local tortoise densities at smaller nested spatial scales from actual tortoise density estimates and tortoise/sign ratios derived across larger spatial landscapes (Krzysik, 2002). The utility of this approach is highlighted when managers are faced with surveying low density areas or need better information about density patterns across the landscape. Ideally, 60–80 objects of interest are needed for robust density estimation using distance sampling, although 40 has been cited as a practical minimum (Burnham et al., 1980). Many tortoise populations have very low densities; in these areas, reaching sufficient sample sizes of individual desert tortoises may become prohibitive or even unlikely. However, our experience suggests that in some cases enough desert tortoise burrows would be available in these areas to provide robust estimates of burrow density. If enough of these areas were surveyed during a season, then the techniques outlined by Krzysik (2002) become tenable and would be an invaluable adjunct technique to the distance sampling of live tortoises.

Managers responsible for assessing and monitoring the desert tortoise should take advantage of the strong association between the density of tortoises and their burrows. During standard tortoise surveys, a biologist must examine each burrow carefully for an occupant. The time and effort required to obtain additional information on burrows, such as GPS, condition, vegetation association, and distance sampling metrics, is small when compared to the potential large return on that investment. For example, in our survey we found 98 desert tortoises during a 2 month period. The spatial data provided, were it to be used for a study of habitat selection, would be incomplete, because they represent a mere snapshot of a dynamic, moving tortoise population. Burrows, in contrast, are relatively static features on the landscape that play a major role in the life history of desert tortoises. Certainly, in this context, they would be more useful for studying certain aspects of habitat selection. Furthermore, as discussed above, the order of magnitude difference between desert tortoise and burrow density can be exploited when surveying low density areas, where minimal sample sizes for robust density estimates are unavailable for desert tortoises, but possible with burrows.

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