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Landscape Physiognomy Influences Abundance of the Lone Star Tick, *Amblyomma americanum* (Ixodida: Ixodidae), in Ozark Forests

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Abstract

The lone star tick, *Amblyomma americanum* Linnaeus (Ixodida: Ixodidae), is emerging as an important human disease vector in the United States. While some recent studies have modeled broad-scale (regional or county-level) distribution patterns of *A. americanum*, less is known about how local-scale habitat characteristics drive *A. americanum* abundance. Such local-scale information is vital to identify targets for tick population control measures within land management units. We investigated how habitat features predict host-seeking *A. americanum* adult and nymph abundance within a 12-ha oak-hickory forest plot in the Missouri Ozarks. We trapped ticks using CO_2-baited traps at 40 evenly spaced locations for three 24-h periods during the summer of 2015, and we measured biotic and abiotic variables surrounding each location. Of 2,008 *A. americanum* captured, 1,009 were nymphs, and 999 were adults. We observed spatial heterogeneity in local tick abundance (min = 0 ticks, max = 112 ticks, mean = 16.7 ticks per trap night). Using generalized linear mixed models, we found that both nymphs and adults had greater abundance in valleys as well as on northern-facing aspects. Moreover, nymph abundance was negatively related to temperature variance, while adult abundance had a negative relationship with elevation. These results demonstrate that managers in this region may be able to predict local tick abundance through simple physiognomic factors and use these parameters for targeted management action.

Key words: *Amblyomma americanum*, tick-borne disease, management, spatial epidemiology

The lone star tick, *Amblyomma americanum* Linnaeus (Ixodidae), is an important vector of multiple zoonotic pathogens (Dumler and Bakken 1995, Childs and Paddock 2003, Fritz 2009, Sonenshine and Roe 2013), and it has been implicated in the recent emergence of Heartland and Bourbon Viruses (McMullan et al. 2012, Savage et al. 2013) and a red meat anaphylaxis linked to the carbohydrate galactose-α-1,3-galactose (Commins et al. 2011). The recent range expansion of *A. americanum* and concomitant spread of associated pathogens has increased interest in identifying the key environmental factors that drive tick abundance and spatial distribution (Springer et al. 2015, Dahlgren et al. 2016).

The local abundance of disease vectors results from a complex suite of biotic and abiotic factors influencing each stage of their life cycle. Ultimately, hosts must be present for life cycle completion, so the spatial distributions of ticks must be within the distributional extent of viable hosts. Within overlapping ranges, tick abundance

is positively associated with host density for both *Ixodes scapularis* Say and *A. americanum* and can be affected indirectly by environmental factors influencing host populations (Rand et el. 2003, Williams et al. 2009, Allan et al. 2010, Williams and Ward 2010, Adalsteinsson et al. 2016, Noden and Dubie 2017). For example, a high ambient saturation deficit reduces survival and increases mortality in ixodid ticks (Stafford 1994, Rodgers et al. 2007), and *A. americanum* is susceptible to drying, evidenced by relatively higher rates of water loss at low humidity compared to its congeners (Needham and Teel 1991).

While measuring host density and monitoring microclimate may be useful for predicting tick abundance, these methods are often costly and time consuming; thus, determining cost-effective and simple correlates for tick abundance are of more immediate and practical utility for land managers who strive to reduce disease exposure for wildlife and human populations. Due to strong correlations with

surface conditions and microclimate, landscape physiognomy—specifically slope, aspect, and elevation—could be a viable proxy for tick abundance. Although the effects of landscape physiognomy on *A. americanum* have not been examined, studies of other ixodid tick species suggest that it can have important effects on abundance (Lane et al. 1985, Cadenas et al. 2007, Medlock et al. 2008, Gilbert 2010). Therefore, landscape physiognomic characteristics may similarly have utility in predicting *A. americanum* abundance.

Here, we investigate the relationship between host-seeking *A. americanum* abundance and environmental variables, including landscape physiognomy. We present models for local tick abundance using easily measured landscape variables in a Missouri oak-hickory forest and compare their relative predictive performance with ecological variables requiring more time-intensive measurement, including stem density and leaf litter.

Materials and Methods

Study Area

We conducted our survey in a 12-ha (460 × 260 m) section of the Tyson Research Center Plot, which is part of the Smithsonian Center for Tropical Forest Science-Forest Global Earth Observatory (CTFS-ForestGEO) Network (Anderson-Teixeira et al. 2015), located 40 km southwest of Saint Louis, Missouri (38°31′N, 90°33′W). The plot is a deciduous oak-hickory forest and contains local areas of understory dominated by common buckthorn (*Frangula caroliniana* Walter), spicebush (*Lindera benzoin* Linnaeus), and paw paw (*Asimina triloba* Linnaeus). The primary bedrock consists of shale limestone, limestone, cherty limestone, and chert formations, producing silty loams and silty clays (Zimmerman and Wagner 1979). The most commonly encountered tick species of the region is *A. americanum*, while *D. variabilis* and *I. scapularis* are present but less common (Kollars 2000). Aspect is highly correlated with several abiotic conditions likely to directly drive tick abundance, including a derived measure of soil quality, with low soil quality corresponding to drier, more acidic soils on south and west-facing slopes and high soil quality corresponding to wetter, less acidic soils typical of northeast-facing slopes (Spasojevic et al. 2014, LaManna et al. 2016).

Tick Sampling

To capture host-seeking ticks, we used CO_2-baited traps consisting of a 6-quart cooler attached to a 12 × 16 in. plywood base, on which we attached Shurtape Indoor/Outdoor double-sided carpet tape (Hickory, NC). Due to their active questing behavior (Schulze et al. 1997, Rynkiewicz and Clay 2014, Mays et al. 2016), this design is effective at capturing adult *A. americanum* to a distance of 5 m and nymph *A. americanum* to a distance of 3 m (Kensinger and Allan 2011). Forty traps were spaced 60 m apart in an even grid in the 12-ha plot. Each trap was baited with 1-kg dry ice between 09:00 and 11:00 and set out for 24 h. All locations were sampled on 22–23 June, 29–30 June, and 13–14 July 2015, for a total of 120 trap nights. These dates were chosen for their consistency of meteorological conditions, including similar temperature (mean daily temperature 23.3–30°C) and zero recorded precipitation. These sampling events coincided with peaks in abundance of the nymph and adult stages of *A. americanum* in Missouri (Kollars 2000, Sonenshine and Roe 2013). All nymph and adult ticks were removed from the tapes, preserved in 95% ethanol, and identified to life stage and species (Goddard and Layton 2006). Nymph and adult abundance at each trap was the total of the *A. americanum* nymphs and adults, respectively, collected on each of the three sample dates.

Environmental Variables

We quantified abiotic and biotic variables that have been shown to affect ixodid tick abundance, including leaf litter, woody stem counts, slope, aspect, elevation, temperature, and soil characteristics (Harlan and Foster 1990, Schulze et al. 2001, Cadenas et al. 2007, Rodgers et al. 2007, Medlock et al. 2008, Gilbert 2010, Burtis et al. 2016). In September 2015, we collected all of the leaf litter contained in a 0.02-m^2 plastic ring 1 m away from the trap in each cardinal direction, for a total of four samples per trap. We dried these samples at 55°C for 5 d and recorded the dry mass of each. The average of the four samples from each site was calculated and recorded as the leaf litter mass for each site.

We extracted available woody stem, slope, aspect, elevation, and temperature data from the Smithsonian ForestGEO database at or near each of our trap locations (Spasojevic et al. 2014) using Esri ArcGIS 10.3.1. We partitioned the aspect data into 60° 'bins' corresponding to six cardinal and primary intercardinal directions. These divisions are 330°–30°: North (N, *n* = 5 traps); 30°–90°: Northeast (NE, *n* = 12 traps); 90°–150°: Southeast (SE, *n* = 2 traps); 150°–210°: South (S, *n* = 2 traps); 210°–270°: Southwest (SW, *n* = 9 traps); 270°–330°: Northwest (NW, *n* = 10 traps). These divisions were chosen to best balance the ability to determine fine variation in abundance predicted by aspect and the usefulness to land managers attempting to determine if an area may have high tick abundance. The total number of free-standing woody stems >1-cm diameter at breast height (1.3 m) was determined within a 10-m radius of each trap, which is greater than the maximum effective range of the traps used (Kensinger and Allan 2011).

Mean temperature and temperature variance were calculated based on temperature data recorded every 2 h using iButton data loggers (Maxim Integrated, San Jose, CA) closest to each trap site. Because ixodid ticks may be susceptible to desiccation from suboptimal temperature and large daily temperature variation, we used daily mean temperature and daily temperature variance data from July to October 2014, collected at the same locations as the soil collection points in the plot (Spasojevic et al. 2014). This time period coincides with the peak larval abundance for the cohort of nymphs that was observed and the end of the questing season for nymphs and adults of the cohort of adults that was observed.

Statistical Analysis

We evaluated the effects of environmental variables (Table 1) on nymph and adult *A. americanum* counts separately using generalized linear mixed models with Poisson distribution in R v. 3.2.4

Table 1. Mean and standard deviation for all continuous variables evaluated to predict tick abundance

Variable	Mean	SD
Slope (°)	17.77	6.35
Elevation (m)	207.51	14.50
Stem count	53.68	43.85
Temperature variance (°C)	22.90	5.58
Temperature mean (°C)	21.54	0.70
Leaf litter (g)	10.84	6.86

Slope and elevation are calculated for each trap site from geographic LIDAR data (Spasojevic et al. 2014). Stem count is the number of stems larger than 1-cm diameter at breast height (Spasojevic et al. 2014) within a 10-m radius of the trap. Temperature variance and mean were collected from the iButton sensor located closest geographically to the trap site (Spasojevic et al. 2014). Leaf litter is the average dry mass of leaf litter collected from each trap site.

(R Core Team 2016), using package lme4 v. 1.1–12 (Bates et al. 2015). We developed two sets of models to predict nymph abundance and adult abundance based on a priori hypotheses on the effects of our predictor variables. Our response variables were tick counts at each trap at each sampling event, and we included sampling date as a random effect in all models. We centered and scaled all predictor variables prior to model building, and we assessed potential collinearity among all predictor variables; variables with correlation coefficients equal to or greater than 0.6 were not included in the same models. With package AICcmodavg v.2.1-1 (Mazerolle 2017), we compared models using Akaike's Information Criterion adjusted for small sample sizes (AICc) to determine the best model(s) (Akaike 1974, Anderson and Burnham 2002). We evaluated model fit for best models using measures of marginal and conditional R^2 developed for mixed-effects models (Nakagawa and Schielzeth 2013) using the package MuMIn (Barton 2017). These pseudo-R^2 measures allowed us to compare model fit in terms of fixed effects only (marginal) and the combination of fixed and random effects (conditional).

Results

Tick Sampling

We collected a total of 2,089 ticks in 120 trap nights: 1,009 *A. americanum* nymphs; 999 *A. americanum* adults; 1 *A. americanum* larva; 72 *D. variabilis* adults; and 8 *I. scapularis* larvae. Of the total, 1,259 (60.3%) ticks were collected on 23 June, 551 (26.4%) on 30 June, and 279 (13.3%) on 14 July (Fig. 1). This observed effect weights the overall tick abundance toward the 23 June sample date; therefore, we accounted for temporal variation in our models of abundance, by including collection date as a random effect within all models.

Linear Models

We assembled and compared 26 models to investigate factors individually and in combination that we predicted would affect tick abundance (Tables 2 and 3). The best model for nymph abundance was an additive model including aspect, slope, and temperature

Fig. 1. Mean abundance per trap of *A. americanum* nymphs and adults collected on three sample dates (23 June, 30 June, July 14; *N* = 40 traps).

variance (Table 4; $R^2_{GLMM(m)} = 0.28$; $R^2_{GLMM(c)} = 0.45$). Aspect predicts greater nymph abundance on north-facing slopes (7.55–16.1 nymphs per trap) compared to south-facing slopes (0.64–2.70 nymphs per trap; Fig. 2). Nymph abundance is predicted to decrease by 23.2–28.4% for each 5.5°C increase in temperature variance. Slope also has a strong negative effect on nymph abundance, which decreases by 26.4–31.3% for each 6.4° increase in slope.

The best model for adult abundance included aspect, elevation, and slope (Table 4; $R^2_{GLMM(m)} = 0.17$; $R^2_{GLMM(c)} = 0.49$). Aspect predicts greater adult abundance on northeast- and north-facing slopes (4.56–13.42 adults per trap) and lesser abundance on south-facing slopes (0.71–3.16 adults per trap). For each 14.5-m increase in elevation and 6.4° increase in slope, adult abundance is predicted to decrease by 11.7–17.5% and 9.7–25.3%, respectively.

Discussion

We found that physiognomic variables have utility for predicting *A. americanum* abundance. Specifically, aspect, elevation, slope, and temperature variation influence spatial heterogeneity in *A. americanum* abundance for both nymph and adult life stages. Models that included aspect and slope were ranked higher than those with biological variables (i.e., stem density and leaf litter). Temperature variance was important for nymphs, whereas elevation was included in the best model for adults. Together, these results suggest that adult and nymph abundance may relate somewhat differently to environmental variables at this spatial scale (Tables 2 and 3).

Slope and aspect were useful for predicting both nymph and adult *A. americanum* abundance. North through southeast-facing areas with more gradual slopes were correlated with greater tick abundance relative to south and southwest-facing slopes for both life stages (Fig. 2). Since aspect is correlated with soil quality in this forest (Spasojevic et al. 2014, LaManna et al. 2016), *A. americanum* nymphs and adults may be responding to changes in the soil and/or host populations that directly or indirectly affect tick survival (Wilson et al. 1984, 1985; Pound et al. 1996; Stafford et al. 2003; Allan et al. 2010).

Temperature variance of the previous questing season was an important predictor of nymph, but not adult abundance. Larvae, which would become nymphs during the season we conducted the study, may be more strongly affected by fluctuations in temperature than nymphs or adults (Yoder and Spielman 1992, Stafford 1994). Large fluctuations in temperature may indicate that the area has a high level of direct sunlight during the day, and thus the saturation deficit at the surface may increase (Hoch et al. 1971).

Elevation was predictive of adult, but not nymph abundance; more adults were collected in valleys than on ridges. While elevation has been shown to have a negative effect on *I. ricinus* in European mountain ranges (Cadenas et al. 2007, Gilbert 2010), the elevation change in our study site (184–234 m) is much less substantial than in the larger mountain systems (620–900 m for Cadenas et al. 2007, 40–380 m for Gilbert et al. 2010). Valleys in our study area have a high density of understory species such as *L. benzoin* and *L. maackii* (Spasojevic et al. 2014); however, stem count did not contribute to either of the best models.

While our models explained ~50% of the variation in *A. amblyomma* abundance, the remainder of variation was unexplained by either physiognomy or biological variables that were included in more complex models. Some ecological factors (e.g., stem density and leaf litter) that have been important tick abundance predictors in different systems or spatial scales may not have been sufficiently
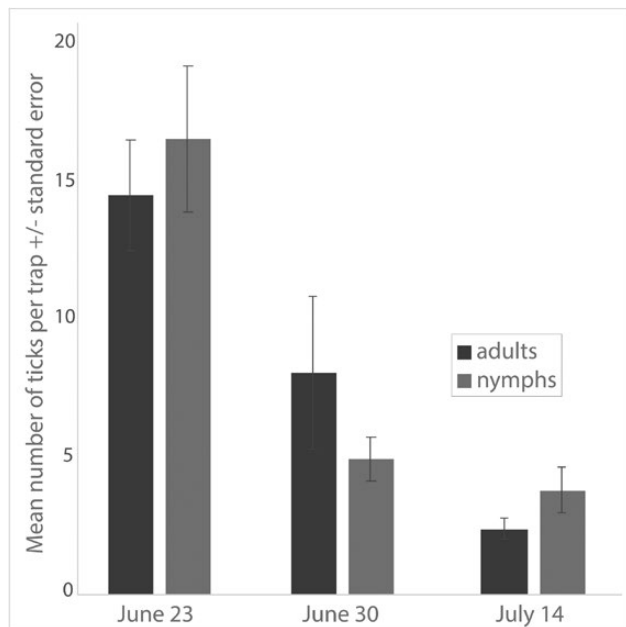
Table 2. AICc table for all 27 nymph abundance models tested

Model terms	K	Delta AICc	AICc weight	LL
Aspect + slope + temp variance	9	0	1	−540.16
Aspect + litter + temp variance	9	40.54	0	−560.43
Aspect + slope + litter	9	47.95	0	−564.14
Aspect + elevation + slope	9	62.77	0	−571.55
Aspect + litter + elevation	9	71.25	0	−575.79
Aspect + litter + stem	9	79.5	0	−579.90
Aspect + litter	8	97.68	0	−590.04
Aspect + elevation + temp variance	9	99.75	0	−625.45
Litter + stem + temp variance	5	162.32	0	−625.88
Litter + temp mean + temp variance	5	162.79	0	−626.11
Litter + temp variance	4	178.67	0	−635.14
Aspect + elevation + stem	9	185.06	0	−632.69
Aspect	7	192.61	0	−638.78
Stem + temp variance	4	221.3	0	−656.46
Temp mean + temp variance	4	223.32	0	−657.47
Temp variance	3	223.79	0	−658.77
Litter + slope + elevation	5	240.97	0	−655.20
Litter + slope	4	271.62	0	−681.62
Litter + elevation	4	273.24	0	−682.43
Litter + temp mean	4	278.74	0	−685.17
Slope + elevation	4	284	0	−687.81
Slope	3	294.59	0	−694.17
Elevation	3	364.6	0	−729.18
Temp mean	3	366.04	0	−729.90
Stem + temp mean	4	367.92	0	−729.77
Null	2	369.04	0	−732.80
Stem	3	370.04	0	−732.09

K indicates the number of parameters, and LL is the log-likelihood.

Table 3. AICc table for all 27 adult abundance models tested. K indicates the number of parameters, and LL is the log-likelihood

Model terms	K	Delta AICc	AICc weight	LL
Aspect + elevation + slope	9	0	0.95	−658.46
Aspect + litter + stem	9	6.32	0.04	−661.63
Aspect + elevation + stem	9	10.07	0.01	−663.50
Aspect + slope + temp variance	9	18.26	0	−667.60
Aspect + slope + litter	9	21.94	0	−669.44
Aspect + litter +elevation	9	23.9	0	−370.41
Aspect + elevation + temp variance	9	25.99	0	−671.46
Stem + temp mean	4	37.79	0	−683.01
Stem	3	44.35	0	−687.36
Stem + temp variance	4	45.83	0	−687.02
Litter + stem + temp variance	5	46.58	0	−686.31
Aspect + litter + temp variance	9	52.9	0	−684.92
Slope + elevation	4	53.74	0	−690.98
Litter + slope + elevation	5	55.7	0	−690.87
Aspect + litter	8	56.17	0	−687.72
Aspect	7	57.18	0	−689.38
Temp mean	3	58.79	0	−694.58
Litter + temp mean	4	59.22	0	−693.72
Temp mean + temp variance	4	60.07	0	−694.15
Litter + temp mean + temp variance	5	60.38	0	−693.21
Elevation	3	72.71	0	−701.54
Litter + elevation	4	72.98	0	−700.60
Litter + slope	4	103.8	0	−716.01
Slope	3	113.09	0	−721.73
Null	2	131.25	0	−731.86
Temp variance	3	131.64	0	−731.00
Litter + temp variance	4	133.00	0	−730.61

variable to influence tick abundance in our study area. Moreover, the influence of collection date (see conditional vs. marginal R^2_{GLMM}) underscores the complexity of tick life history and demonstrates the importance of characterizing phenological patterns at local scales. Regardless, that easily collected landscape characteristics were predictive of a substantial amount of variance in *A. americanum*

Table 4. Model summaries for the best models for nymphs (above) and adults (below)

		Coefficient estimate	SE	Z-value	P-value
Nymph	Intercept	2.399	0.378	6.339	<0.001
	NE aspect	−0.646	0.096	−6.716	<0.001
	SE aspect	−0.294	0.149	−1.967	0.049
	S aspect	−2.128	0.346	−6.144	<0.001
	SW aspect	−1.245	0.120	−10.367	<0.001
	NW aspect	−0.412	0.095	−4.340	<0.001
	Slope	−0.341	0.034	−9.879	<0.001
	Temp variance	−0.299	0.035	−8.628	<0.001
Adult	Intercept	1.996	0.441	4.523	<0.001
	NE aspect	0.061	0.099	0.618	0.537
	SE aspect	−0.509	0.196	−2.604	0.009
	S aspect	−1.590	0.305	−5.204	<0.001
	SW aspect	−0.134	0.108	−1.236	0.216
	NW aspect	−0.348	0.116	−2.998	0.003
	Elevation	−0.158	0.034	−4.621	<0.001
	Slope	−0.197	0.095	−5.678	<0.001

For each, the Intercept term corresponds with the North aspect and the estimates for each of the aspect values following are in relation to the intercept.
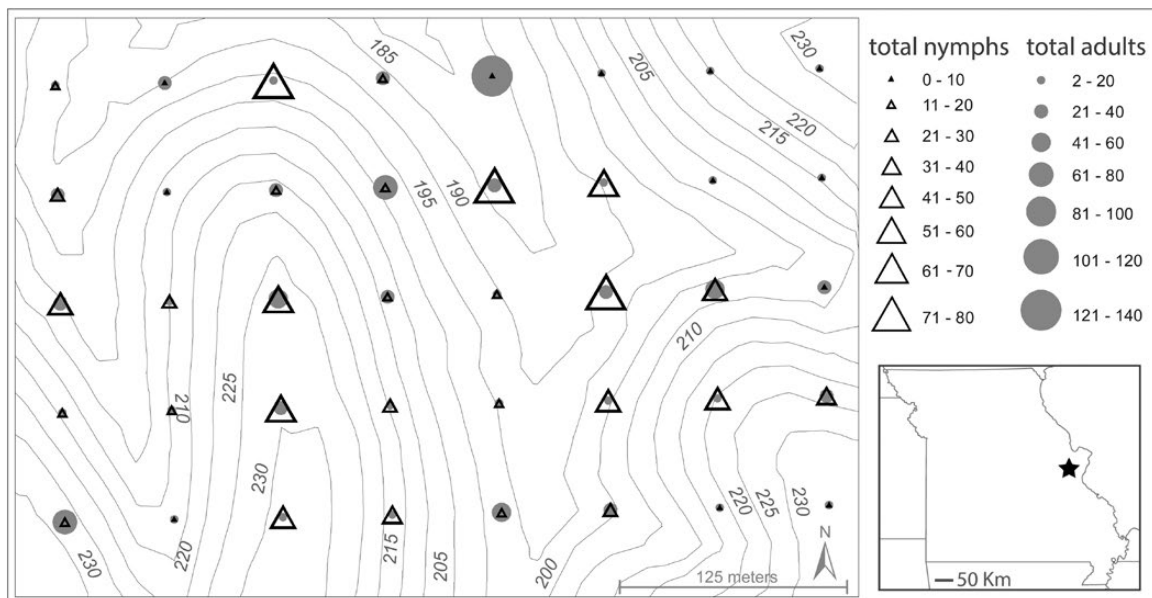
Fig. 2. Distribution of *A. americanum* (total nymphs and adults across three sample dates) captured at forty traps relative to landscape physiognomy. Contours are labeled with elevation (m). Star within inset at lower right shows location of study area, the Tyson Research Center (TRC) ForestGEO Plot, which is part of the Smithsonian Institution Center for Tropical Forest Sciences (CTFS) Forest Global Earth Observatories network, located 40 km southwest of Saint Louis, Missouri (38°31′N, 90°33′W).

abundance in our study system is encouraging for land management purposes.

Conclusion and Future Directions

Our results indicate that simplified physiognomic variables have potential to help predict *A. americanum* abundance in forest habitats. While it is generally not feasible to alter slope, aspect, or elevation, biotic variables may be more easily manipulated for management purposes. Within our 12-ha study site, tick abundance was spatially heterogenous; however, this local-scale variation is often not quantified in studies of ticks over larger spatial extents. Studies on the effect of potential control measures—such as fire or acaricide treatments—may find results confounded by physiognomic effects, which may explain a substantial portion of observed variation. Therefore, we propose that when estimating tick abundance, slope and aspect should be considered in experimental designs, particularly in the Ozarks *A. americanum* system. Variation in ixodid ticks' physiology and behavior may drive distinct spatial patterns (Sonenshine and Roe 2013). Thus, validation of these models in other systems is necessary to determine their broad applicability. Nevertheless, establishing the spatial pattern of a vector species at a scale relevant for management action is an essential first step in managing disease risk to humans.

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