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LizLand: A geomorphic approach to lizard habitat modeling in the Mojave Desert

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Abstract

The macro-habitat preferences of three conspicuous and widely distributed species of lizards (*Aspidoscelis tigris*, *Callisaurus draconoides*, and *Uta stansburiana*) were examined across four geomorphic landforms (sandy wash, rocky wash, alluvial plain, and alluvial deposit) in the southern Mojave Desert, California. All three species were non-randomly distributed across the four geomorphic landforms. The goal of this study was to develop less ecologically generalized habitat models (LizLand) than the vegetation-based wildlife–habitat relationship models in the California Gap Analysis Program (CA-GAP). Conceptually, LizLand is a geomorphological approach to habitat modeling in arid environments. Specifically, LizLand is a series of spatially explicit habitat models that define and predict habitat for *A. tigris*, *C. draconoides*, and *U. stansburiana* in Joshua Tree National Park and the Marine Air Ground Task Force Training Command, Marine Corp Air Ground Combat Center. LizLand models resulted in higher resolution habitat models with minimal reduction in model accuracy. These models more accurately captured the complexity of the Mojave Desert ecosystem and offered greater ecological resolution in identifying habitat in contrast to the CA-GAP models.

Keywords: Mojave Desert; Geomorphic landforms; Habitat model; *Aspidoscelis tigris*; *Callisaurus draconoides*; *Uta stansburiana*

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1. Introduction

Reptiles and amphibians have often been excluded from consideration in habitat evaluation and management (Clawson et al., 1984) although they comprise 30% of the North American native terrestrial vertebrates (Bury et al., 1980), and 19% of California's desert terrestrial vertebrates (Cornett, 1987). Exceptions include species listed under federal or state endangered species acts such as *Gopherus agassizii* (Anderson et al., 2000; Aycrigg et al., 2004) and *Uma inornata* (Barrows, 1997). In addition, while general habitat requirements are known for many reptiles and amphibians, little quantitative work has been done to evaluate habitat quality or suitability (Baltosser and Best, 1990), especially in arid environments. Exceptions include the desert riparian island study by Szaro and Belfit (1986), the Chihuahuan Desert ''natural'' versus herbicide modified landscape study by Peterson and Whitford (1987), and the undisturbed/disturbed mesquite study by Germano and Hungerford (1981).

In general, research on lizards in the arid South-west has focused primarily on comparative, demographic, and life history studies. When lizard habitat or space niche dimension has been investigated, the focus has been on micro-habitat niche requirements (Pianka, 1975, 1986, 1993). For example, much of Pianka's (1966, 1967, 1973, 1986), and Pianka and Parker (1975), as well as others (Waldschmidt, 1980; Waldschmidt and Tracy, 1983; James, 1994), has advocated using indices of spatial heterogeneity to predict and/or describe habitat for desert reptiles. The focus has been primarily on vegetation structure and sun and shade space, not vegetation composition or geomorphic landforms. More recent attempts have centered on vegetation structure, density and volume, substrate size, and density of rodent burrows (Smith et al., 1987; Baltosser and Best, 1990; Shenbrot et al., 1991; Martin and Lopez, 1998). Vegetation composition has been shown to be important in controlling the distribution of some desert reptiles, especially at the local and/or micro-habitat levels. For example, within the southern portions of its range *Xantusia vigilis* has been closely associated with Joshua trees and other *Yucca* sp. (Pianka, 1986). However, at higher elevations in the Mojave Desert, *X. vigilis* has been shown to exploit small rock micro-habitats (Morafka and Banta, 1972).

Aspidoscelis tigris is a habitat generalist occurring in many different vegetation, soil, and geomorphic habitats in the Great Basin, Mojave, and Sonoran deserts. This active, widely foraging species (Mitchell, 1979; Anderson, 1993) prefers open habitat (Vitt and Ohmart, 1977b). A ''frequent mover,'' *A. tigris* spends little time in one place. It rarely flees far when threatened (Anderson, 1993), usually running to the nearest bush where it begins foraging again almost immediately. *A. tigris* spends the majority of its time foraging by digging and rummaging through detritus (Peterson and Whitford, 1987; Anderson, 1993).

Callisaurus draconoides is a speedy, sit-and-wait insectivorous predator that prefers open, unbroken terrain (Pianka, 1986; Bulova, 1994). When approached, *C. draconoides* curls its tail over its hindquarters and back exposing a bold black and white zebra pattern underneath, and wiggles its tail from side to side (Pianka and Vitt, 2003). If approached further, it resorts to extreme speed estimated at up to 20–30 km/h, and long zigzag runs (Dial, 1986; Hasson et al., 1989). *C. draconoides* does not avoid rocks (Pianka and Parker, 1972; Tanner and Krogh, 1975; Vitt and Ohmart, 1977a; Stebbins, 2003), though rocky environments may not always provide ideal conditions.

Uta stansburiana is a sit-and-wait, insectivorous predator that prefers very broken, spatially heterogeneous terrain. This species is most often associated with rocks, but is also found in sandy and gravelly soils, and often in sandy washes with scattered rocks and/or bushes (Stebbins, 2003). The ecology and life history of *U. stansburiana* is well known (Miller and Stebbins, 1964; Pianka, 1966, 1967, 1986; Tinkle, 1967; Parker and Pianka, 1975; Peterson and Whitford, 1987; Svensson and Sinervo, 2004).

The state-of-the-art in Mojave Desert, California, habitat modeling has been the combined work of the California portion (CA-GAP) (Davis et al., 1998) of the US Geological Survey National GAP Program (Scott et al., 1993) and the California Wildlife Habitat Relationships System (CWHR) (Mayer and Laudenslayer, 1988). The GAP and CWHR programs were built upon one of the most successful and widely used means of defining species habitat relationships: the categorization of the landscape into land cover classes based upon vegetation composition. The science of wildlife–habitat relationships was developed (and continues) with the use of birds as model species and vegetation as the habitat predictor (Merriam, 1890; Adams, 1908; Lack, 1933; Svardson, 1949; Hilden, 1965; Verner et al., 1986; George and McEwen, 1992; Kellner et al., 1992; Scott et al., 1993; Morrison et al., 1998; Scott et al., 2002). Though many other factors have been included more recently in modeling efforts, vegetation, because of its historical usage, universal availability, and success with many species, has remained the primary variable used to predict animal habitat.

GAP is a biodiversity assessment and inventory tool that employs a "coarse" vegetation filter of community inventory and protection (Davis et al., 1998). This method is hypothesized to protect 85–90% of the species, leaving the remaining 10–15% for "fine" filter approaches (Jenkins, 1985; Noss, 1987). Because vegetation is sparse to non-existent across much of California's Mojave Desert, the "coarse" vegetation filter approach of GAP is not likely to work for this ecosystem. Just as a "fine" filter approach is necessary for some species, it is also necessary for ecosystems that are unusual, rare, or in which vegetation is sparse to non-existent.

Geomorphic landforms provide alternative correlates for predicting habitat, especially in arid lands where they capture the unique complexity of the ecosystem. Geomorphic landforms define the ranges of vertebrate species (Forman and Godron, 1986). They affect abiotic conditions, the flow of organisms, propagules, energy and material, and the frequency and spatial pattern of disturbance regimes, as well as constraining the very geomorphic processes that create them (Swanson et al., 1988; McAuliffe, 1994). The term "geomorphic habitats" refers to cliffs, caves, talus, lava flows, sand dunes, and playas formed by geomorphic processes in both south-eastern Oregon's Great Basin (Maser et al., 1979b) and the Blue Mountains of Oregon and Washington (Maser et al., 1979a). Within all ecosystems, geomorphic landforms and processes affect the spatial and temporal distribution of plants (Schulz and Whitney, 1986; Yeaton and Manzanares, 1986; McAuliffe, 1994; Wondzell et al., 1996; Garcia-Pichel and Belnap, 2001) and animals (Brown, 1973; Brown and Lieberman, 1973; Hoover et al., 1977; Mackay et al., 1986; Shenbrot et al., 1999; Shepherd and Kelt, 1999). Species shift geomorphic habitat preferences or retreat to micro-habitats on a daily or seasonal basis in order to seek shelter from seasonal conditions, especially the high spatial–temporal variability, unpredictability, intensity, and duration of precipitation in arid environments (Reynolds et al., 1999; Whitford, 2002).

Extensive work exists on the ecology, basic habitat, and life history requirements of *A. tigris*, *C. draconoides*, and *U. stansburiana*. However, other than GAP, no efforts include the development of spatially explicit habitat models. The GAP program in general and CA-GAP specifically, present "ecologically generalized" habitat models, or models with low ecological resolution. For example, field guides show the greatest degree of ecological generalization; they depict the outline of a species' range. The interpretation is clear; the species will only be found in appropriate habitats within the range. Habitat models that rely on vegetation have less ecological generalization. These models work well in many environments. However, in the Mojave Desert where vegetation is sparse to non-existent, vegetation may serve as a poor indicator of habitat. In contrast, demographic and population viability studies have the greatest amount of ecological resolution. These studies predict and compare the probability of extinction under different options for habitat protection (Boyce, 1992; Beissinger and Westphal, 1998; Groom and Pascual, 1998). However, these models can be expensive and difficult to develop, are not always available, and the results often vary.

Habitat models and their expression in maps, such as CA-GAP, are designed to aid conservation management decisions. The basic assumption is that habitat is a necessary (if not always sufficient) condition for preservation of any species. As such, we propose that models based upon geomorphology would have greater ecological resolution than vegetation-based CA-GAP models in the Mojave Desert. This study focuses on the development of geomorphology-based habitat models for *A. tigris*, *C. draconoides*, and *U. stansburiana*, because in the Mojave Desert we believe them to be less ecologically generalized than CA-GAP models.

2. Materials and methods

2.1. Study site

Walking transects were located in Joshua Tree National Park (JOTR) and the Marine Air Ground Task Force Training Command, Marine Corps Air Ground Combat Center (MCAGCC), both in the southern Mojave Desert, California. Joshua Tree National Park transects were located in Pinto Basin in the eastern half of the park. Transects located in MCAGCC fell within four southeastward trending unnamed basins, herein referred to as Emerson Lake, Sand Hill, Quackenbush, and Lavic Lake after their respective training areas.

General transect locations and their geomorphic classification are shown in Fig. 1. Pinto Basin has a relatively low elevation (300–600 m) and is a sandy, fairly level basin that drains to the south-east between the Eagle and Coxcomb mountains. The north-east, lower sub-basin is dominated by Mojave creosote bush scrub, and the south-west, upper sub-basin by Mojave mixed woody and succulent scrub (Sawyer and Keeler-Wolf, 1995). Each MCAGCC basin is dominated by Mojave creosote bush scrub (Sawyer and Keeler-Wolf, 1995). Emerson Lake and Sand Hill have sandy, gently sloping, low rolling terrain and elevation averages 750 m. Quackenbush is more steeply sloped and dominated by alluvial deposits. Average elevation is 830 m. Lavic Lake has gently sloping, rocky, alluvial deposits made of mostly basalt. Average elevation is 700 m.

2.2. Lizard surveys

A stratified, random sample design was used to survey for *A. tigris*, *C. draconoides*, and *U. stansburiana*. Sampling locations were designated within two patch landforms: alluvial

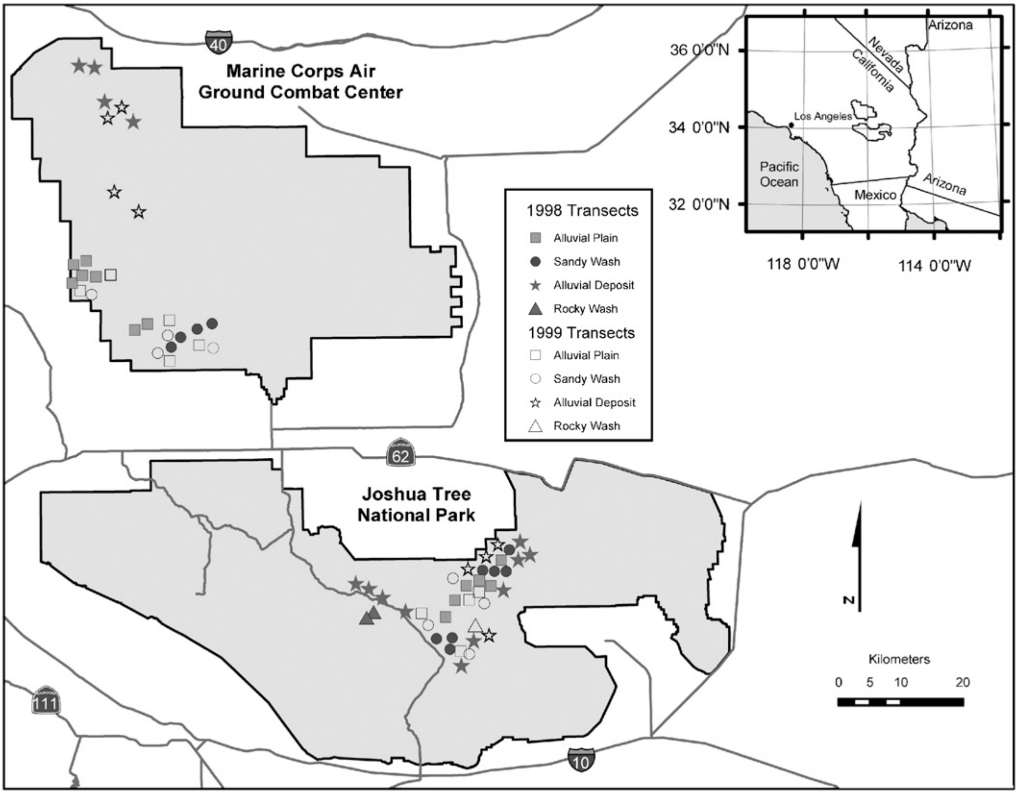


Fig. 1. Generalized transect locations within Joshua Tree National Park and the Marine Task Force Training Command, Marine Corps Air Ground Combat Center. Locations have been generalized for presentation purposes only using the principle of displacement to preserve their visibility and distinctiveness (Longley et al., 2001).

plains and alluvial deposits; and one fluvial landform: sandy washes (Fig. 2). Subsequent to the initial surveys, three sandy washes were reclassified as rocky. In addition, numerous lizard observations were made in rocky washes. Wash transects were restricted to large dry washes (>20 m width). This was consistent with the spatial resolution of GIS files used to generate the LizLand models. Alluvial plains were analogous to Peterson's (1981) "basin floor" minus washes, playas, sand dunes, and rocky outcrops. He broadly defined the basin floor as the area extending from the toeslope of a fan to the playa of a closed basin or to the central wash of an open basin. He further described it as a nearly level, graded surface built of sediment carried by sheet floods or large streams. Alluvial deposits were analogous to Peterson's (1981) "piedmont slope" minus washes, playas, sand dunes, and rocky outcrops. He broadly defined the piedmont slope as the area between the mountain front and the basin floor including alluvial fans and rock pediments.

Attempts were made to equalize the number of samples between alluvial plains, alluvial deposits, and sandy washes. However, logistical problems and military restrictions limited our ability to do so. Transects were walked in the spring and summer months of 1998 and 1999, from May to mid-July (Table 1). Transect start points were between 100 and 500 m from a road. Two-person teams walked all transects (1.5 km). Observers walked between

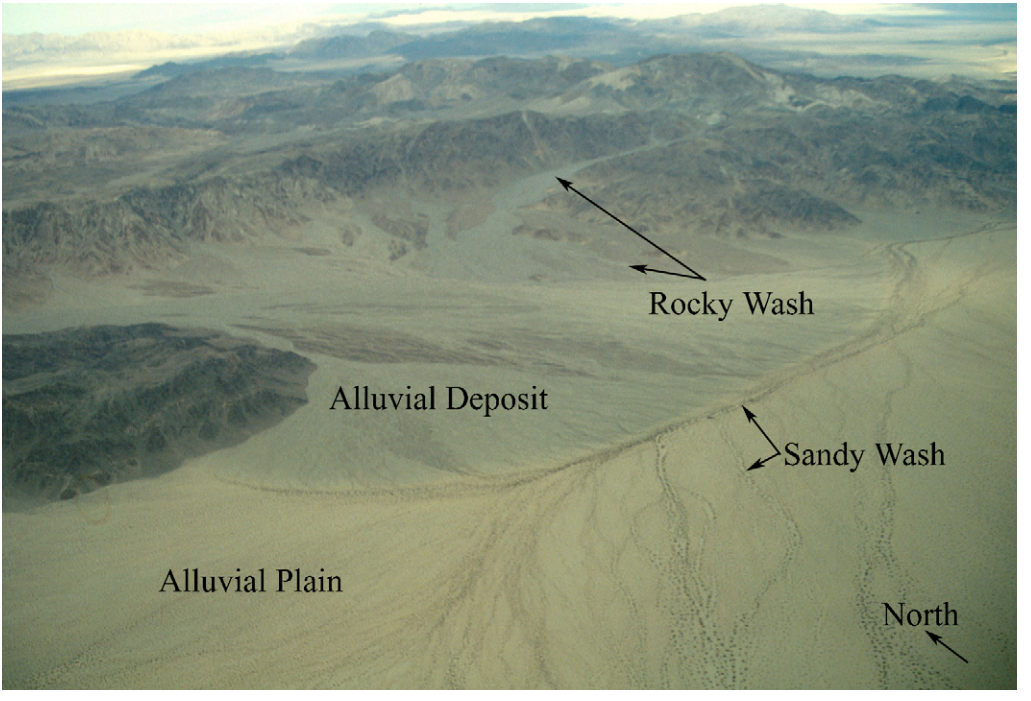


Fig. 2. Aerial view of Pinto Basin, Joshua Tree National Park with macro-habitat sampling classes labeled.

10 and 15 m apart, visually surveying the surrounding area. Lizards were counted once. If we suspected that a lizard had already been counted it was not included in the sample. The following information was recorded for each lizard: species, date, time (24 h), temperature (°C) (1 m above-ground in the shade), vegetation and substrate cover, geographic coordinates (Universal Transverse Mercator [UTM] easting and northing), observer, transect ID, and plot number. Adults and juveniles were not differentiated in the analyses as our focus on macro-over micro-habitat averaged any differences relative to daily activities of adults and juveniles over a large area (James, 1994).

Percent vegetation and substrate cover were estimated within a 1000 m^2 circular plot. Procedures for estimating percent cover followed guidelines established by the California Native Plant Society (www.cnps.org), Franklin et al. (2001), and Thomas et al. (2004). Percent vegetation cover consisted of shrub crown cover (>0.5 m height) and ground vegetation (<0.5 m height). Substrate cover was adopted from standard soil survey methods (US Department of Agriculture, 2003) and consisted of boulder (>600 m), stone (250–600 mm), cobble (75–250 mm), gravel (5–75 mm), pebble (2–5 mm), and sand (<2 mm). Because boulder, stone, cobble, and gravel were positively correlated within each landform, they were combined to create a single index of rockiness:

$$R_i = ([\text{boul}_i + 0.0001] \times [\text{ston}_i + 0.0001] \times [\text{cobb}_i + 0.0001] \times [\text{grav}_i + 0.0001])^{0.25},$$

where R_i is rockiness for the ith plot, and boul_i, ston_i, cobb_i, and grav_i are percent of that resource covering the ith plot. In order to negate the influence of 0% substrate cover for any one size class, 0.0001 was added to each value before calculating R_i.

Table 1
Transect sample details for Joshua Tree National Park (JOTR) and Marine Task Force Training Command, Marine Corps Air Ground Combat Center (MCAGCC)

Landform	Location	Date ddmmyy	Start time	Mean temp.	*Number of observations*		
					Asti	*Cadr*	*Utst*
Sandy wash	JOTR	300598	0800	30.9	9 (2)	1 (0)	3 (0)
		310598	1025	35.7	5 (0)	6 (0)	0 (0)
		090698	0755	27.5	9 (0)	9 (0)	8 (0)
		090698	1249	34.0	0 (0)	14 (0)	2 (0)
		080798	0723	33.9	4 ((0)	5 (0)	7 (0)
		080798	1034	37.5	5 (0)	6 (0)	0 (0)
		130798	0751	33.0	4 (0)	3 (0)	0 (0)
		070599	1232	32.9	2 (0)	7 (0)	0 (0)
		060699	0859	29.6	2 (0)	30 (0)	0 (0)
		080699	0746	31.7	3 (0)	2 (0)	1 (0)
		250699	0806	31.2	1 (0)	12 (0)	0 (0)
		Within total		31.7	44 (2)	95 (0)	21 (0)
	MCAGCC	020798	0721	29.7	2 (0)	9 (0)	0 (0)
		020798	1003	36.5	0 (0)	5 (0)	1 (0)
		030798	0726	29.3	1 (0)	3 (0)	0 (0)
		030798	1003	35.5	0 (0)	4 (0)	0 (0)
		170599	0918	27.1	2 (0)	16 (0)	0 (0)
		310599	1130	28.1	1 (0)	33 (0)	0 (0)
		230699	0808	31.3	2 (0)	44 (0)	1 (0)
		060799	0737	30.8	2 (0)	10 (0)	1 (0)
		Within total		30.3	10 (0)	124 (0)	3 (0)
		Between total		31.1	54 (2)	219 (0)	24 (0)
Alluvial plain	JOTR	310598	0832	28.5	6 (0)	0 (0)	0 (0)
		160698	0840	36.8	2 (0)	1 (3)	0 (0)
		170698	0854	30.7	1 (4)	1 (6)	0 (0)
		070798	0630	29.3	1 (0)	1 (1)	0 (0)
		120798	0651	32.3	6 (0)	6 (2)	0 (0)
		160798	0600	32.2	4 (1)	3 (5)	0 (0)
		070599	1117	30.2	2 (0)	2 (1)	0 (0)
		060699	0857	28.5	3 (0)	2 (3)	0 (0)
		080699	1107	30.3	0 (0)	3 (0)	0 (0)
		250699	0801	30.7	3 (1)	2 (1)	0 (0)
		Within total		31.2	28 (6)	21 (22)	0 (0)
	MCAGCC	250698	0639	27.0	3 (0)	0 (0)	0 (0)
		250698	0748	29.0	4 (0)	0 (2)	0 (0)
		260698	0826	29.9	7 (0)	0 (2)	0 (0)
		270698	0732	29.5	3 (1)	0 (2)	0 (0)
		280698	0640	28.6	7 (0)	0 (1)	0 (0)
		300698	0708	30.0	9 (0)	0 (0)	1 (0)
		010798	0720	28.3	15 (0)	0 (0)	0 (0)
		160599	1349	27.3	3 (0)	0 (0)	0 (0)
		170599	1105	29.0	0 (0)	3 (0)	0 (0)
		310599	1251	30.0	1 (0)	0 (2)	0 (0)
		230699	1013	33.1	2 (3)	0 (2)	1 (0)
		060799	0958	34.7	4 (1)	0 (6)	1 (0)
		Within total		30.1	58 (5)	3 (17)	3 (0)
		Between total		30.6	86 (11)	24 (39)	3 (0)

Table 1 (*continued*)

Landform	Location	Date ddmmyy	Start time	Mean temp.	*Number of observations*		
					Asti	*Cadr*	*Utst*
Alluvial deposit	JOTR	060298	0830	33.5	3 (2)	3 (2)	0 (0)
		060398	0815	27.7	3 (0)	7 (2)	1 (0)
		060698	0918	31.0	1 (0)	0 (0)	1 (0)
		060698	1115	32.5	0 (0)	0 (0)	2 (0)
		060798	0915	28.4	1 (1)	0 (0)	14 (1)
		060898	0938	32.5	5 (3)	1 (1)	0 (0)
		061398	0849	28.1	3 (4)	0 (2)	2 (1)
		061398	1047	29.8	0 (0)	0 (1)	0 (3)
		071598	0630	33.5	4 (1)	0 (0)	6 (2)
		071798	0553	32.1	4 (0)	1 (0)	2 (0)
		051099	1240	30.0	1 (4)	1 (0)	0 (1)
		052499	0923	29.3	1 (0)	6 (7)	0 (0)
		062999	0842	33.7	1 (2)	2 (1)	0 (0)
		070499	0821	32.8	4 (0)	3 (0)	9 (1)
		Within total		30.8	31 (17)	24 (16)	37 (9)
	MCAGCC	062098	0757	30.1	1 (3)	0 (4)	5 (1)
		062198	0803	26.9	1 (0)	0 (0)	6 (0)
		062298	0701	28.3	0 (2)	0 (2)	4 (6)
		062398	0705	29.2	1 (1)	0 (1)	13 (1)
		052299	1214	27.2	0 (0)	7 (0)	2 (0)
		052399	1114	26.3	0 (0)	2 (2)	8 (1)
		052899	1045	33.0	1 (1)	2 (3)	0 (0)
		052999	0927	28.4	2 (0)	0 (1)	10 (1)
		Within total		28.6	6 (7)	11 (13)	48 (10)
		Between total		29.9	37 (24)	35 (29)	85 (19)
Rocky wash	JOTR	071198	0637	34.7	0 (0)	6 (0)	10 (0)
		071198	1045	41.3	2 (0)	3 (0)	1 (0)
		062999	0720	32.2	4 (0)	6 (0)	0 (0)
		Within total		35.2	6 (0)	15 (0)	11 (0)
	MCAGCC	NA					
		Between total		35.2	6 (0)	15 (0)	11 (0)

Start time represents transect start time. Mean temp. is average temperature at time of observations. Numbers outside parentheses equal lizard transect observations, numbers within parentheses equal lizard landform observations. *Asti* = *Aspidoscelis tigris*, *Cadr* = *Callisaurus draconoides*, *Utst* = *Uta stansburiana*.

Lizard observations were maintained in a series of geospatial databases (see below). The transect observations data were analysed using Pearson's χ^2 and analysis of variance (ANOVA). Differences in vegetation and substrate cover estimates were evaluated using ANOVA. Games–Howell post hoc pairwise comparison was used to handle unequal sample sizes and heterogeneity in variance (Day and Quinn, 1989). The master landform observations data were used to calculate the overall proportional distribution of lizards across the four landforms, the mean temperature at time of sighting for each species, and Simpson's Reciprocal Index (Simpson, 1949) as a measure of macro-habitat niche breadth (Pianka, 1986). Statistical analyses were performed in SPSS 10.1 (SPSS Inc., 1999). The criterion for statistical significance was $p \leqslant 0.05$ for all tests.

2.3. LizLand model development

LizLand was composed of geomorphic landform and surface composition data (Mojave Desert Ecosystem Program (MDEP), 2000) and US Geological Survey (USGS) 1:100,000 digital line graph hydrology data (US Geological Survey, 1989). The MDEP data consisted of 32 geomorphic landforms and 24 surface-composition categories. We collapsed and reclassified these categories into 12 LizLand habitat classes based upon geomorphic landform, surface composition, and relative rockiness (Table 2). Relative rockiness was a subjective, micro-landform characterization derived from author-knowledge, fieldwork, and literature (Mabbutt, 1977; Cooke, 1993; Dokka, 1998). Assignment of the 12 LizLand habitat types to Suitable, Moderate, Marginal, or Unsuitable habitat for each species was based upon quantitative data (primary field work) and qualitative data (existing literature and expert opinion). Table 3 aligns equivalent LizLand and CA-GAP habitat classes.

Independent lizard observations from MCAGCC used to test the models were recorded to the nearest 1 m for data from Cutler et al. (1999) and the nearest 100 m for the data from Minnich et al. (1993) and Fromer et al. (1983). These independent lizard observations were assigned to alluvial plain, alluvial deposit, sandy wash, or rocky wash based upon study site descriptions and field notes. Species data were plotted in a GIS against the four LizLand habitat suitability classes and the equivalent CA-GAP classes. Model accuracy was calculated for two groups of collapsed habitat suitability classes: (1) "Habitat" (i.e. Suitable, Moderate, and Marginal) versus Unsuitable Habitat; and (2) Suitable Habitat versus all other categories (i.e. Moderate, Marginal and Unsuitable). Contingency tables of primary field data and independent data for each species were used to calculate LizLand percent model accuracy, and omission and commission errors. Due to the lack of independent observations, model validation statistics were not calculated for JOTR. All spatial analyses were conducted in ESRI™ Arc™ products.

3. Results

3.1. Lizard observations

We observed 775 individual lizards ($N = 247$ *A. tigris*; $N = 377$ *C. draconoides*; $N = 151$ *U. stansburiana*). Maintaining transect homogeneity (Jaeger, 1994) through alluvial plain and alluvial deposit was difficult because washes and roads were frequently encountered. In order to eliminate this bias when predicting the distribution and habitat preferences for each species of lizard, observations associated with roads were removed from the analyses. Observations associated with washes in alluvial plain and alluvial deposit transects were eliminated from the lizard "transect" database and stored in the "landform" database (see below). The transect database included only lizard observations that occurred within the sampled landform ($N = 183$ *A. tigris*; $N = 293$ *C. draconoides*; $N = 123$ *U. stansburiana*). The observations eliminated due to transect homogeneity violations were re-coded to either sandy or rocky wash and maintained within the lizard "landform" database ($N = 37$ *A. tigris*; $N = 68$ *C. draconoides*; $N = 19$ *U. stansburiana*). A "master landform" database was created by combining the transect and landform observations ($N = 220$ *A. tigris*; $N = 361$ *C. draconoides*; $N = 142$ *U. stansburiana*). This database captured the true landform location of all lizard observations. Lizards observed off the sampled transects

Table 2
Aggregated geomorphic and landform surface composition data (Mojave Desert Ecosystem Program, 2000) merged to create each LizLand habitat class

Geomorphic landform	Surface composition	LizLand class
Active alluvial plain	N/A	Sand and gravel[a]
Alluvial fan	Gabbroid, granitoid, gravel/sandstone, undifferentiated plutonic, undifferentiated metamorphic	
Bajada	Gabbroid, granitoid, gravel/sandstone, siltstone/mudstone/clayst, undifferentiated chemical, undifferentiated clastic, undifferentiated metamorphic, undifferentiated plutonic	
Bedrock plain	Granitoid, gravel/sandstone, siltstone/mudstone/clayst	
Lacustrine terrace, older alluvial plain, undifferentiated sediment	NA	
Alluvial fan	Basaltoid, dioritoid, dolostone, felsic metamorphic rock, limestone, marble metamorphic rock, undifferentiated volcanic rock, undifferentiated rock	Rocky[b]
Bajada	Aluminous metamorphic rock, andesitiod, basaltoid, decitoid, dioritoid, dolostone, felsic metamorphic rock, limestone, rhyolitoid, undifferentiated volcanic rock, undifferentiated rock	
Bedrock plain	Dioritoide, rhyolitoid, undifferentiated metamorphic	
Intramontaine alluvial plain, intramontaine undifferentiated, lava field, volcanic dome, volcanic tableland, volcano	NA	
Wash, fluvial floodplain, fluvial terrace	NA	Sandy Wash[a]
Older alluvial deposit	NA	Desert Pavement[b]
Erosional highland	NA	Erosional Highland[b]
Brachanoid dune, climbing/falling dune, coppice dune, linear dune, parabolic dune, star dune, undifferentiated dune fields	NA	Wind Blown Sand[c]
Playa	NA	Playa[d]
Reservoir	NA	Reservoir[e]
Unmapped	NA	Unmapped[e]
Canyon bottomland	NA	Rocky Wash[b]
Inselberg	NA	Inselberg[b]
Sand sheet	NA	Sand sheet[d]

Landform relative rockiness categories.
[a]Coarse to sandy.
[b]Rocky.
[c]Fine wind blown sand.
[d]Sands and clays.
[e]NA.

Table 3
Equivalent habitat classes for LizLand and CA-GAP

LizLand habitat class	CA-GAP habitat class
Suitable habitat	⩾50% High suitability
	⩾50% Medium or high suitability
Moderate habitat	⩾50% Low, medium or high suitability
Marginal habitat	<50% Low, medium or high suitability, but >0%
NA	Suitable habitat in wetland/riparian type only (no areal estimate)
Unsuitable habitat	No suitable habitat
NA	Unmapped

LizLand Unsuitable habitat may include areas of habitat below the spatial resolution of the LizLand input GIS data.

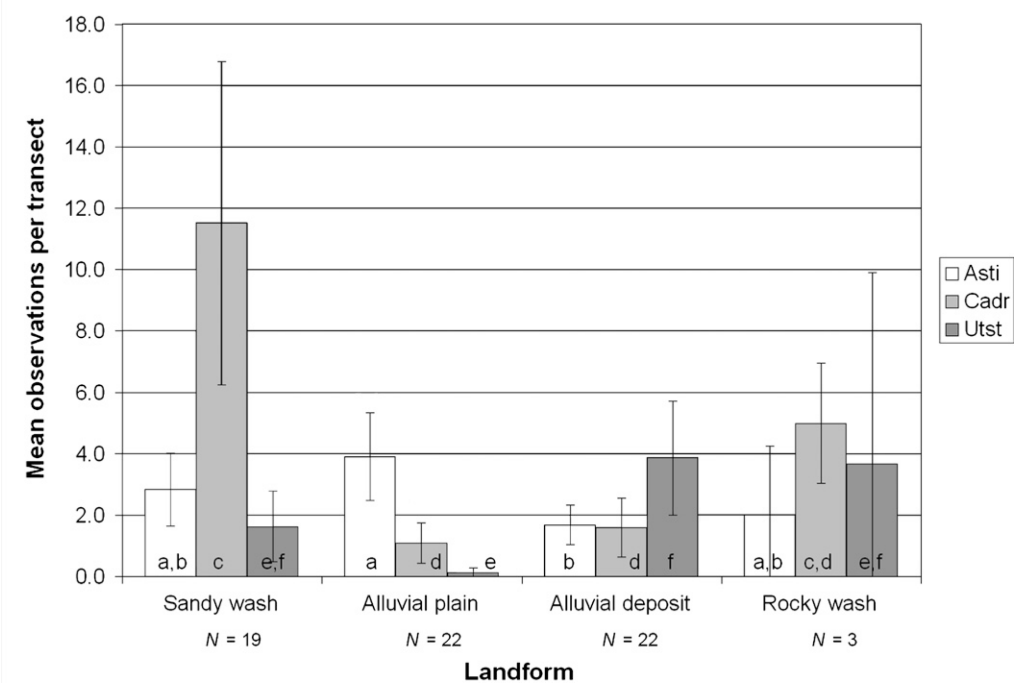


Fig. 3. Mean number of combined transect lizard observations. Bars represent the 95% confidence intervals. Within species, landforms with the same letter are not significantly different (analysis of variance, Games–Howell post hoc pairwise comparisons). Asti = *Aspidoscelis tigris*, Cadr = *Callisaurus draconoides*, and Utst = *Uta stansburiana.*

were maintained within the "off-transect" database ($N = 27$ *A. tigris*; $N = 16$ *C. draconoides*; $N = 9$ *U. stansburiana*). The "Global Positioning System" (GPS) database contained all lizard observations, both from the master landform and off-transect databases ($N = 247$ *A. tigris*; $N = 377$ *C. draconoides*; $N = 151$ *U. stansburiana*). The GPS and independent observations ($N = 736$ *A. tigris*; $N = 631$ *C. draconoides*; $N = 439$

U. stansburiana) (Fromer et al., 1983; Minnich et al., 1993; Cutler et al., 1999) were used to test the LizLand models.

Analysis of variance year and location comparisons indicated few statistical differences between the individual lizard transect observations across years (1998 and 1999) and location (JOTR and MCAGCC) by landform. As a result, transect observations from both year and location categories were combined for each unique lizard/landform combination (Fig. 3). Transects were walked within expected activity temperature and time periods for all three species. Average temperatures at observation time were warmer for *A. tigris* (mean = 30.8 °C, SD = 3.83 °C) and *U. stansburiana* (mean = 29.8 °C, SD = 3.52 °C), but not *C. draconoides* (mean = 31.2 °C, SD = 3.21 °C) than reported by Pianka (1965) at his Twentynine Palms study site located between JOTR and MCAGCC.

Pearson's χ^2 analysis of the transect data revealed that *A. tigris* (df = 3, $N = 183$; $p < 0.001$), *C. draconoides* (df = 3, $N = 293$; $p < 0.0001$), and *U. stansburiana* (df = 3, $N = 123$; $p < 0.0001$) were non-randomly distributed across landforms. Analysis of variance results for the landform data indicated that the mean number of *C. draconoides* and *U. stansburiana* were significantly different across landforms, but not so for *A. tigris*. However, subsequent Games–Howell post hoc pairwise comparisons indicated that the mean number of *A. tigris* within alluvial plains was significantly higher than any other landform (Fig. 3). Analysis of the master landform data revealed that 73% of all observations of *C. draconoides* were in sandy washes and 60% of all observations of *U. stansburiana* were in alluvial deposits (Fig. 4). For *A. tigris*, master landform data were

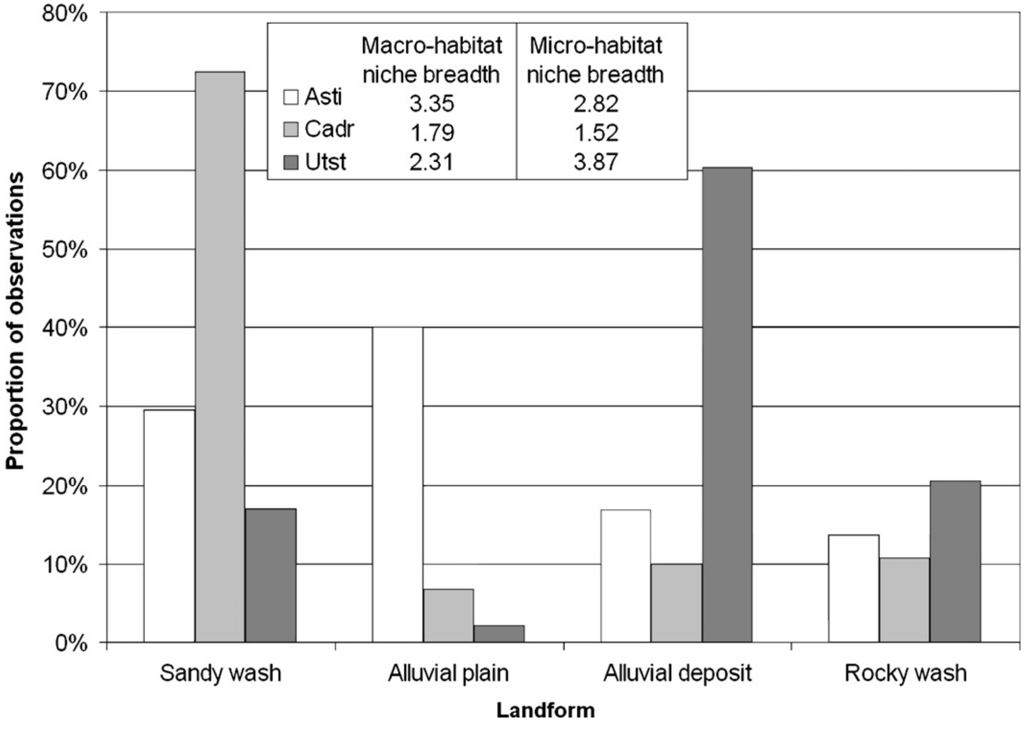


Fig. 4. Proportional distribution of lizard master landform observations. Micro-habitat niche breadths calculated by Pianka (1986). Asti = *Aspidoscelis tigris*, Cadr = *Callisaurus draconoides*, Utst = *Uta stansburiana.*

Table 4
Mean percent vegetation and substrate cover ANOVA statistics by landform (F-ratio, $df = 3$, $N = 775$, $*p \leqslant 0.001$)

Cover	F-ratio	Sandy wash ($N = 320$)	Alluvial plain ($N = 175$)	Alluvial deposit ($N = 246$)	Rocky wash ($N = 34$)
Total vegetation	9.01*	4.1 a	5.5 b	5.3 b	5.3 b
Shrub vegetation	38.1*	3.2 a	1.9 b	2.3 c	4.1 d
Ground vegetation	42.3*	1.3 a	4.1 b	3.1 b	1.2 a
Pebble	12.2*	29.0 a	22.0 b	20.0 b	22.0 b
Sand	85.5*	60.0 a	62.0 a	32.0 b	45.0 c
Rocky index	96.2*	0.27 a	0.16 a	2.0 b	3.1 c

Within the same row, means with the same letter are not significantly different (Games–Howell post hoc comparisons).

relatively evenly distributed between alluvial plains (40%) and sandy washes (30%), and though not as frequent, still roughly equally distributed between alluvial deposits (17%) and rocky washes (14%) (Fig. 4).

Macro-habitat niche breadths varied among the three species (Fig. 4). Analysis of variance results for vegetation and substrate varied among the four landforms (Table 4). Though not apparent from the statistics, vegetation was primarily restricted to the edges and banks of sandy and rocky washes with little to no shrub or ground cover within the channel itself. Shrubs were mostly evenly dispersed across alluvial plains and deposits with a majority of the ground cover concentrated under shrubs.

3.2. LizLand

The LizLand and CA-GAP general models for JOTR and MCAGCC are presented in Figs. 5 and 6, respectively. The specific LizLand and CA-GAP habitat models for *A. tigris*, *C. draconoides*, and *U. stansburiana* are presented in Figs. 7 and 8, respectively. Percent habitat type available for each species is summarized on each figure. Model validation results are presented in Table 5, along with the percentage of independent observations falling within each habitat suitability class.

4. Discussion

4.1. Aspidoscelis tigris

Macro-habitat niche breadth for *A. tigris* was the broadest of the three species (Fig. 4). Micro-habitat niche breadths for *A. tigris* were narrower than for *U. stansburiana*, but considerably broader than for *C. draconoides* (Pianka, 1986). In Australian desert lizards, neither dietary nor micro-habitat niche breadth correlated with macro-habitat niche breadth (Downey and Dickman, 1993; Pianka, 1996). Our data suggested a preference for sandy washes and alluvial plains over alluvial deposits and rocky washes. The former two were sandier, which facilitates digging, while the latter two were rockier (Table 4).

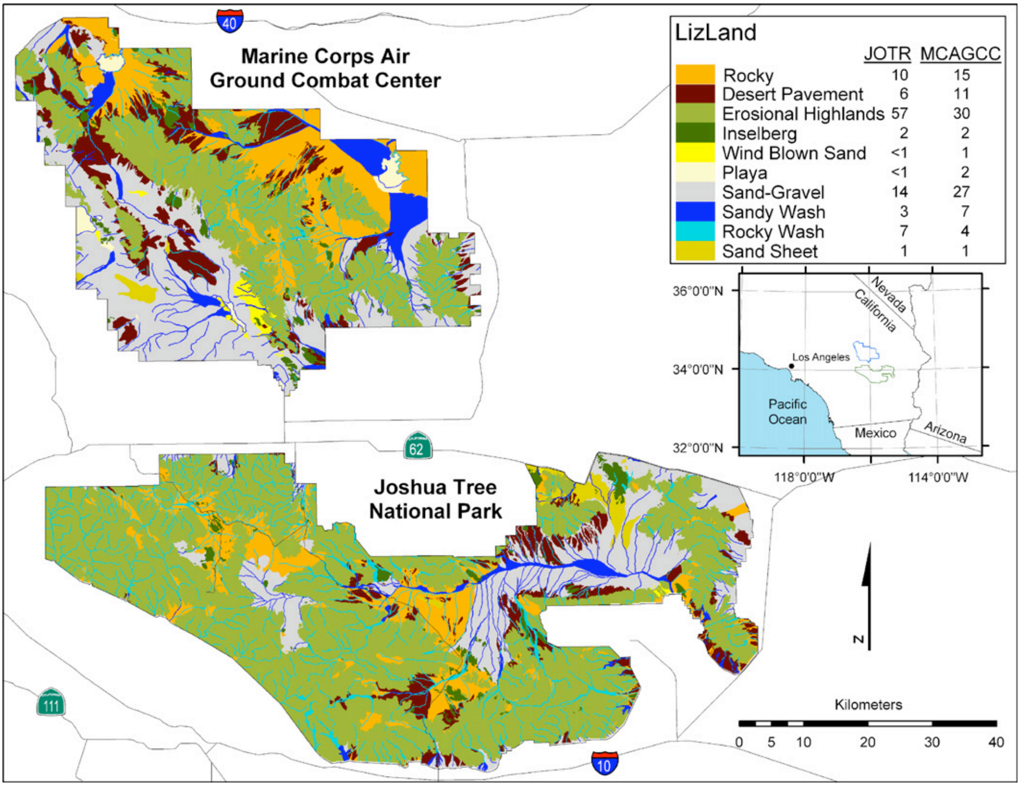


Fig. 5. General LizLand habitat model for Joshua Tree National Park (JOTR) and Marine Task Force Training Command, Marine Corps Air Ground Combat Center (MCAGCC). Numbers in the inset table represent percent of area in the designated category.

Lizland Suitable Habitat for *A. tigris* was restricted to Sand and Gravel, Sandy Wash, and Sand Sheet. Moderate Habitat was restricted to Rocky, Desert Pavement, Rocky Wash, Erosional Highlands, and Inselbergs. No Marginal Habitat was designated. Unsuitable Habitat was restricted to Wind Blown Sand, Playa, Reservoir, and Unmapped. In a one-to-one comparison with equivalent habitat categories, the top two CA-GAP classes constituted 97% of MCAGCC and contained 100% of the independent observations; the top LizLand category constituted 25% of MCAGCC and contained 88% of the independent observations. LizLand predicted 72% (97% minus 25%) less Suitable Habitat on MCAGCC than CA-GAP with only a 12% (100% minus 88%) loss in model accuracy. Likewise, the amount of Suitable Habitat for JOTR was reduced by 81% (99% minus 18%).

4.2. *Callisaurus draconoides*

Sandy and rocky washes in the Mojave Desert tend to have well defined, shrub-lined channels relatively clear of vegetation and debris. The rocky washes have very little ground cover and are generally sandy with very rocky banks. This ‘‘race track’’ like environment

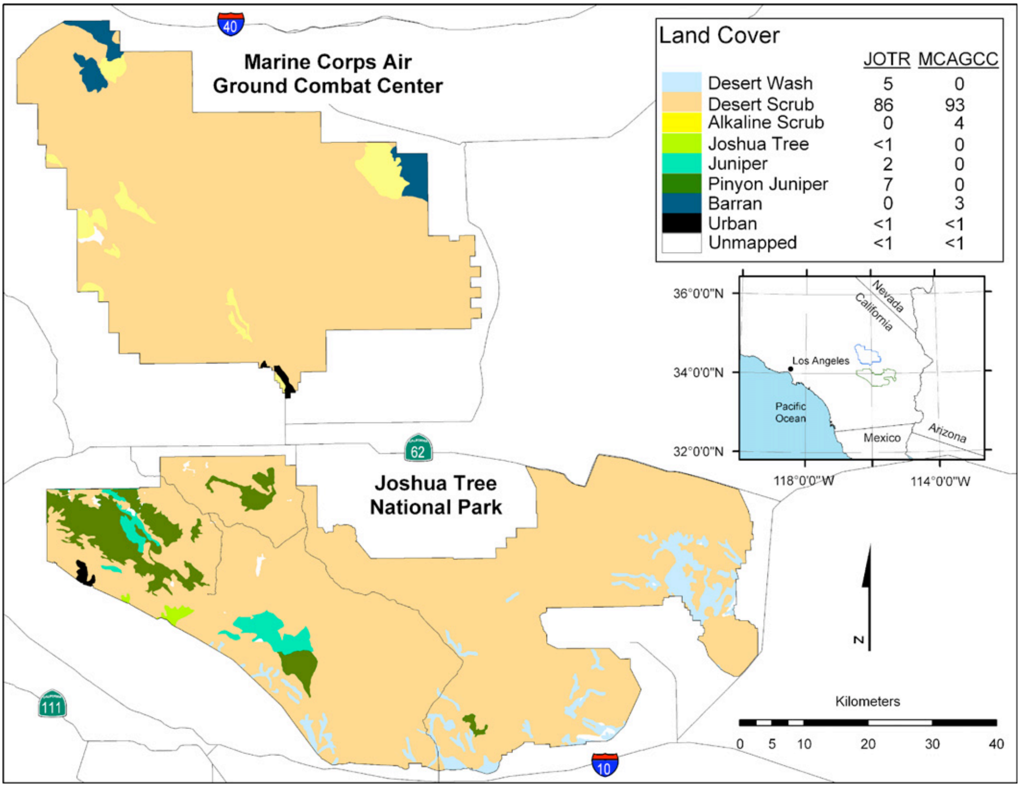


Fig. 6. General California GAP habitat models for Joshua Tree National Park (JOTR) and Marine Task Force Training Command, Marine Corps Air Ground Combat Center (MCAGCC). Numbers in the inset table represent percent of area in the designated category.

allows *C. draconoides* to move about easily. Alluvial plains and alluvial deposits both have high ground cover.

Of the four landforms sampled, the sandy washes had significantly less vegetation cover and were less rocky than most other landforms. Tanner and Krogh (1975) reported that alluvial plains had the highest abundance and tallest creosote bushes; under such conditions *C. draconoides* was expected to be less abundant. In this study, though we found that alluvial plains had the least amount of shrub cover and significantly more ground cover. The lowest number of *C. draconoides* occurred in alluvial plains. Vitt and Ohmart (1977a) found that *C. draconoides* was abundant in large sandy washes near and within the flood plains of the Colorado River. They reported it as substantially less abundant in surrounding alluvial plains. Others have reported low densities in similar habitats (Pianka, 1965; Pianka and Parker, 1972).

LizLand Suitable Habitat for *C. draconoides* was restricted to Sandy Wash. Moderate Habitat was restricted to Rocky Wash, Rocky, and Desert Pavement. Marginal Habitat was restricted to Sand and Gravel, and Sand Sheet. Unsuitable Habitat was restricted to Wind Blown Sand, Playa, Erosional Highlands, Inselbergs, Reservoir, and Unmapped.

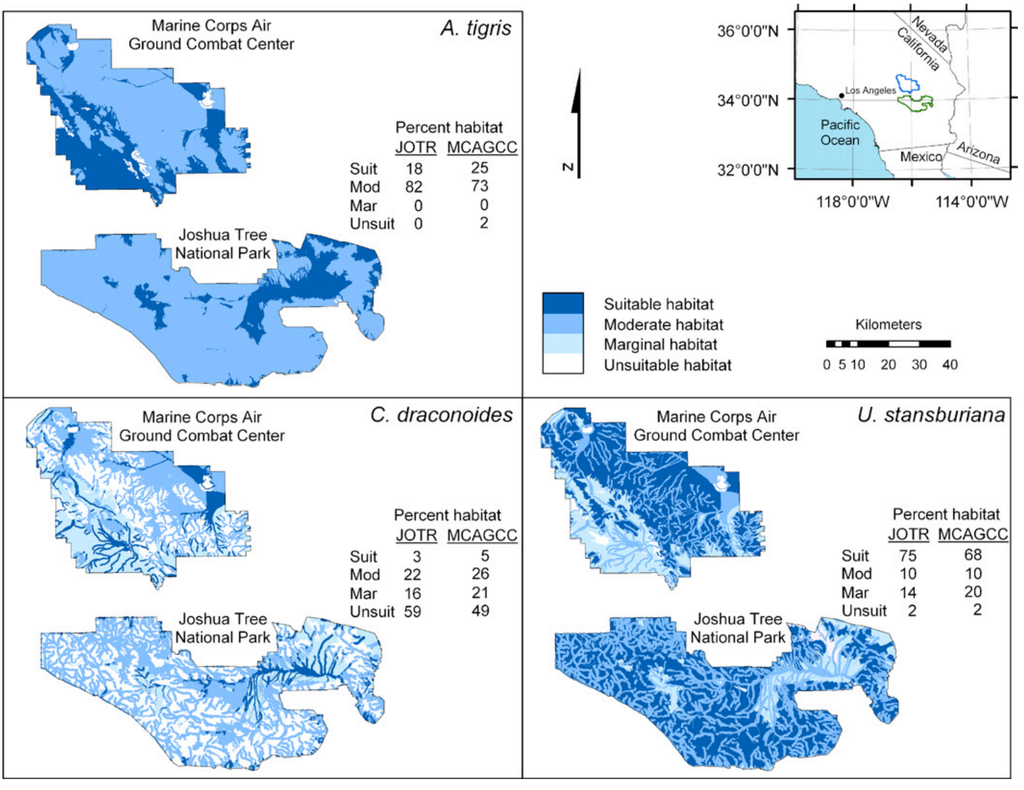


Fig. 7. LizLand habitat models for *Aspidoscelis tigris* (*A. tigris*), *Callisaurus draconoides* (*C. draconoides*), *Uta stansburiana* (*U. stansburiana*) in Joshua Tree National Park (JOTR) and Marine Task Force Training Command, Marine Corps Air Ground Combat Center (MCAGCC). Numbers in the inset tables represent percent area in each habitat category.

High commission error (41%) for differentiating Suitable Habitat from the rest indicated that LizLand tended to under-predict Suitable Habitat for *C. draconoides* (Table 5). For example, observations of *C. draconoides* fell primarily within actual sandy wash habitat (Fig. 9). However, few of those observations were contained within LizLand Sandy Wash. As a result, the suitable Sandy Wash habitat was under-represented, while the Marginal Sand and Gravel habitat was over-represented. The argument was the same when distinguishing rocky washes from surrounding Rocky, Erosional Highlands, or Inselbergs.

Just 2% of the independent observations fell within Suitable Habitat (i.e. Sandy Washes) on MCAGCC and 45% in Moderate Habitat. Despite shortfalls in identifying Suitable Habitat for *C. draconoides*, LizLand predicted less habitat (i.e. Suitable, Moderate and Marginal) for JOTR (42%) and MCAGCC (51%) compared to CA-GAP (99% JOTR; 100% MCAGCC) (Figs. 7 and 8). For LizLand, 79% of independent observations fell within "habitat" (i.e. Suitable, Moderate, or Marginal Habitat) on MCAGCC. As a result, LizLand predicted 49% (100% minus 51%) less "habitat" on MCAGCC than CA-GAP with a 21% (100% minus 79%) loss in model accuracy. For JOTR, the amount of "habitat" was reduced by 58% (99% minus 41%).

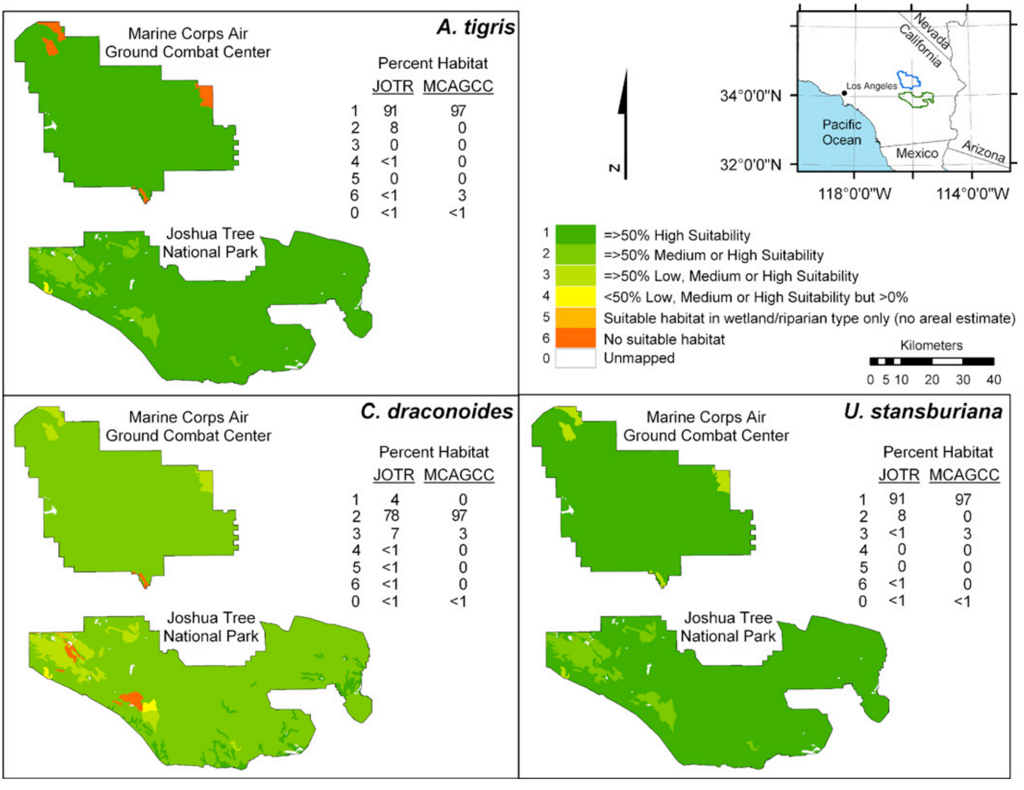


Fig. 8. California GAP habitat models for *Aspidoscelis tigris* (*A. tigris*), *Callisaurus draconoides* (*C. draconoides*), *Uta stansburiana* (*U. stansburiana*) in Joshua Tree National Park (JOTR) and Marine Task Force Training Command, Marine Corps Air Ground Combat Center (MCAGCC). Numbers in the inset tables represent percent area in each habitat category.

4.3. *Uta stansburiana*

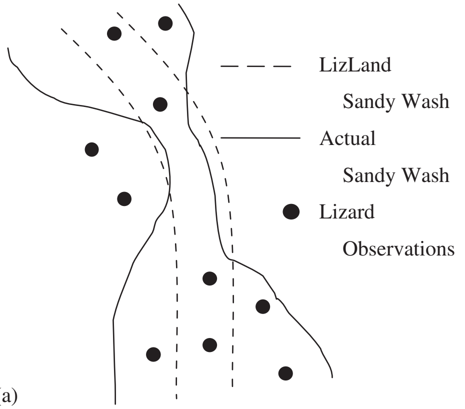
Individual *U. stansburiana* take cover immediately when threatened. Any number of conditions can provide cover: rocks, downed Joshua trees, shrubs, grasses, animal burrows, etc. (i.e. micro-topography). Therefore, one could argue that the greater the micro-topographic relief a landform provides, the more suitable it is for *U. stansburiana*. Plant volume diversity, though not directly linked to any one species, has been implicated as a measure of overall lizard species diversity in the North American flatland deserts (Pianka, 1966). Vegetation plays an important role in the distribution and abundance of *U. stansburiana* (Miller and Stebbins, 1964; Pianka, 1966, 1967, 1986, Tinkle, 1967; Peterson and Whitford, 1987). *U. stansburiana* thrives under both conditions of rockiness and complex vegetation structure and cover, both of which provide a high level of micro-topographic relief or spatial heterogeneity.

Our results indicated that *U. stansburiana* preferred the spatially heterogeneous alluvial deposits and rocky or sandy washes over sandy, homogeneous alluvial plains. Due to the relatively low vegetation cover and variability within our study area (Table 4), we were unable to speculate on preferences for complex vegetation structure or cover.

Table 5
Cross validation statistics for individual LizLand habitat models

Species	Habitat	Predicted group membership						% Correct	% Omission error	% Commission error
		Suitable	Moderate	Marginal	Unsuitable	Total				
Asti	Suitable	164 (88)	22 (12)	NA	0 (0)	186	Hab/Unsuit	100	0	0
	Moderate	30 (49)	31 (50)	NA	0 (0)	61	Suit/Rest	66	15	12
	Marginal	NA	NA	NA	NA	NA				
	Unsuitable	0 (0)	0 (0)	NA	0 (0)	0				
	Total	194	53	NA	0	247				
	MCAGCC independent observations	675 (88)	78 (10)	NA	12 (2)	765				
Cadr	Suitable	141 (59)	34 (14)	65 (27)	0 (0)	240	Hab/Unsuit	100	0	0
	Moderate	10 (13)	36 (45)	33 (42)	0 (0)	79	Suit/Rest	37	11	41
	Marginal	8 (14)	10 (17)	40 (69)	0 (0)	58				
	Unsuitable	0 (0)	0 (0)	0 (0)	0 (0)	0				
	Total	159	80	138	0	377				
	MCAGCC independent observations	10 (2)	298 (45)	208 (32)	137 (21)	653				
Utst	Suitable	57 (59)	4 (5)	35 (36)	0 (0)	96	Hab/Unsuit	100	0	0
	Moderate	9 (36)	11 (44)	5 (20)	0 (0)	25	Suit/Rest	38	25	41
	Marginal	10 (33)	12 (40)	8 (27)	0 (0)	30				
	Unsuitable	0 (0)	0 (0)	0 (0)	0 (0)	0				
	Total	76	27	48	0	151				
	MCAGCC independent observations	231 (51)	170 (38)	47 (10)	3 (1)	451				

Numbers outside parentheses represent observations. Numbers in parentheses represent percentages. *Asti* = *Aspidoscelis tigris*, *Cadr* = *Callisaurus draconoides*, *Utst* = *Uta stansburiana*, Hab/Unsuit = Habitat vs. Unsuitable habitat, Suit/Rest = Suitable habitat vs. remaining habitat categories.



(a)

	C. draconoides
Actual Habitat	80% Sandy Wash
	20% Sand/Gravel
LizLand Predicted	40% Sandy Wash
	60% Sand/Gravel

(b)

Fig. 9. Example scenario of lizard observations distributed across Sandy Wash and Sand/Gravel habitat: (a) under representation of *Callisaurus draconoides* preferred Sandy Wash habitat; and (b) habitat frequency table of hypothetical actual habitat and predicted LizLand habitat.

LizLand Suitable Habitat for *U. stansburiana* was restricted to Rocky, Desert Pavement, Erosional Highlands, and Inselbergs. Moderate Habitat was restricted to Sandy Wash and Rocky Wash. Marginal Habitat was restricted to Sand and Gravel. Unsuitable Habitat was restricted to Wind Blown Sand, Sand Sheets, Playa, Reservoir, and Unmapped. Omission and commissions errors were relatively high for *U. stansburiana*, indicating that LizLand omitted many areas that were suitable, and predicted many areas as suitable that were not (Table 5). LizLand predicted less Suitable Habitat (68% and 75%) than equivalent CA-GAP categories (97% and 99%) for MCAGCC and JOTR, respectively. While 51% of the MCAGCC independent observations fell within LizLand Suitable Habitat, 100% fell within equivalent CA-GAP categories. As a result, LizLand predicted 29% (97% minus 68%) less Suitable Habitat on MCAGCC with a 49% (100% minus 51%) loss in model accuracy. For JOTR the amount of predicted Suitable Habitat was reduced by 24% (99% minus 75%).

4.4. LizLand modeling error

Three types of error were present in this study: sampling, classification, and modeling. Sampling error included differential lizard detection probabilities in different geomorphic landforms, daily fluctuations in lizard activity, and observer-related detection variability. Differences in estimates of vegetation cover were minimal between the four landforms. Alluvial deposits and rocky washes were considerably more rocky than alluvial plains and sandy washes. However, we still saw significantly more *U. stansburiana* (Fig. 3), the most difficult to detect of the three species, in these rocky, uneven landforms. Transects were walked at times of appropriate temperature and time activity periods for each species, though this cannot compensate for natural daily fluctuations in lizard activity. In addition to the primary author, three additional observers were used to count lizards. The second error type, classification error, was discussed previously with regards to maintaining transect homogeneity.

Finally, modeling error was due to inaccurate representation of geomorphic landforms in the spatially explicit LizLand model. For *C. draconoides* and *U. stansburiana*, modeling error existed by either under-representing Suitable and Moderate Habitat (Fig. 9), or in the inability to distinguish between habitat categories. Minimum mapping units for both the geomorphic landform and surface composition and hydrology data sets limited the ability to detect washes less than 20 m wide. On-the-ground samples within alluvial plains were represented by the Sand and Gravel class in LizLand, and alluvial deposits by Rocky and Desert Pavement classes. Desert Pavement was easily identified using remote sensing and it was anticipated to be accurately represented in LizLand. Many clear cases of alluvial plains and/or alluvial deposits occurred within the sample area. However, even assignment on-the-ground between these two classes was difficult, let alone the more subjective use of remote sensing. The fuzzy nature of the boundaries between these two landforms introduced error.

5. Conclusions

Geomorphic landforms are good correlates of macro-habitat for *A. tigris*, *C. draconoides*, and *U. stansburiana*. Our data suggest a clear difference in on-the-ground habitat preferences for these three species. LizLand models more accurately capture the complexity of the Mojave Desert ecosystem and offer greater ecological resolution in identifying general habitat requirements in contrast to the CA-GAP models. Models with greater ecological resolution allow land managers to be more spatially specific in their decisions. This greater spatial specificity of land allocation means that habitat conservation goals are more likely to be met. As any land allocation imposes some cost, both economic and environmental, greater resolution can lead to more effective management.

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