CHARACTERIZATION OF TEXAS TORTOISE (*GOPHERUS BERLANDIERI*) HOME RANGES, HABITAT USE, AND LANDSCAPE-SCALE HABITAT CONNECTIVITY IN CAMERON COUNTY, TEXAS

by

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LIST OF ABBREVIATIONS

Abbreviation	Description
LRGV	Lower Rio Grande Valley
LANWR	Laguna Atascosa National Wildlife Refuge
KDE	Kernel Density Estimate
MCP	Minimum Convex Polygons
PABNHP	Palo Alto Battlefield National Historical Park
NLCD	National Landcover Database
WSS	Web Soil Survey
MRLC	Multi-Resolution Land Characteristics
NRCS-USDA	National Resources Conservation Service – United States Department of Agriculture
TIGER	Topographically Integrated Geographic Encoding and Referencing
NPS	National Parks Service
USFWS	United States Fish and Wildlife Service
TPWD	Texas Parks and Wildlife Department
TNC	The Nature Conservancy
CF	Cameron Silty Clay, Saline

I. INTRODUCTION

Anthropogenic conversion of natural landscapes threatens many species, especially those that live in restricted geographic areas. Taxa such as *Gopherus* tortoises including *G. agassizii* in the American Southwest and *G. flavomarginatus* in the Bolson de Mapimi region of Central Mexico face high risks across their ranges where preferred habitat is rapidly converting from natural landcover to anthropogenically influenced land. The specifics of how tortoises use their environment and what landcover constitutes habitat within their living area or home range is beneficial towards developing conservation efforts for the genus *Gopherus*.

The potential for animals such as *Gopherus* tortoises to move between patches of preferred habitat is vital to maintaining healthy populations via processes like genetic diversity, reduced mortality during dispersal, and reduced likelihood of local extinction due to catastrophic events. While dispersal of these animals is infrequent, it can be useful to examine the landscape as a conduit for potential connectivity of populations and study the variable permeability of different landcover types. This potential connectivity can be combined with habitat use behaviors to study the actualized or realized connectivity of the landscape, where the probability of successful dispersals can be calculated.

Ecology of the Texas Tortoise

The Texas Tortoise (*Gopherus berlandieri*) is the smallest and least studied *Gopherus* tortoise (Figure 1). There is evidence of differential habitat use between coastal populations in south Texas (Kazmaier et al., 2001; Carlson et al., 2018) and populations farther north and west (Kazmaier et al., 2001). Studies in coastal portions of the Texas

Tortoises' range such as Cameron County indicate that tortoises are typically encountered on or near *lomas*, low-relief ridges filled with mesquital Tamaulipan thornscrub (Carlson et al., 2018). Understanding habitat associations of *G. berlandieri* is of particular interest due to their relatively small home ranges: the largest recorded home range on record is 2.38 ha, and the longest known movement is 1.6 km (Rose and Judd, 1975; Judd and Rose, 2000). Thus, depending on the amount of fine-scale heterogeneity (or lack thereof) in the landscape, a given tortoise could potentially spend its entire life within one habitat type.

G. berlandieri ranges roughly south of a line from Del Rio to San Antonio and from San Antonio to Rockport in the United States, with Mexican populations in the states of Coahuila, Nuevo Leon, and Tamaulipas (Figure 2). Populations in Texas can be separated based on genetics; a weak north-south genetic division lies approximately along the southern border of Duval County (Fujii and Forstner, 2011). Genetic differentiation among *G. berlandieri* populations at a fine-scale (e.g., over an extent of 10-30 km) has not been studied, although presumably populations in highly fragmented landscapes such as the Lower Rio Grande Valley (LRGV) could be somewhat genetically isolated from one another.

The typical home range of *G. berlandieri* individuals is estimated to be approximately 2.38 ha for males, and no more than 1.40 ha for females (Rose and Judd, 1975). A coastal population in Cameron County at Laguna Atascosa National Wildlife Refuge (LANWR, Figure 2) has an estimated home range of 0.47 ha for males and 0.34 ha for females (Rose and Judd, 2014). Despite these small home ranges, tortoises at LANWR have been observed making movements of up to 1.2 km and a single tortoise has been observed 1.6 km away from its previous location (Judd and Rose, 2000).

In the Texas portion of their range, *G. berlandieri* individuals generally live in environments with Tamaulipan thorn scrub vegetation. *G. berlandieri* prefers cactus, especially prickly pear (*Opuntia spp.*) as forage, and avoids forbs, grasses, and woody vegetation (Scalise, 2011). Habitat conversion from Tamaulipan scrubland to urban or agricultural land may exclude tortoises, although there is some evidence that certain grazing or pasture management practices may not be detrimental to some *G. berlandieri* populations (Kazmaier et al., 2001).

Gopherus berlandieri was listed as a state-level threatened species by the Texas Parks and Wildlife Department in 1981 due to declining habitat and increased capture of individuals for the pet trade. The species is listed as “least concern” by the International Union for the Conservation of Nature, although the last assessment was almost 25 years ago in 1996. The population of *G. berlandieri* in Mexico is poorly understood and the regions in which they live are experiencing rapid urban development. Conversion of natural habitat into agricultural development including ranching is common in northern Mexico; such anthropogenic land conversion could be negatively affecting the species although this has not been studied.

Animal Home Range and Habitat Use

A species’ use of its environment can be examined through its home range, or the part of the environment that it uses on a regular basis (Burt, 1943). Home ranges can be constructed from animal locations recorded over some finite amount of time. In delineating a home range and estimating its area, locations representing occasional forays into the surrounding environment or areas that are not frequently visited (Vander Wal and Rodgers, 2012) can be excluded in an objective way. Home ranges based on all recorded locations likely include areas of infrequent usage, especially in species that have a definite core area that is used frequently and thoroughly (Borger et al., 2006). A large sample size of locations is needed to accurately construct a given home range (Seaman et al., 1999). A home range that represents only 50% of all recorded locations of an animal may therefore more accurately represent areas of high use, or "core" areas whereas a home range based on 95% of recorded locations is larger and more inclusive and might include areas that the animal enters into only occasionally. Commonly, home ranges are calculated as Kernel Density Estimates (KDEs), which use statistical formulas to generate home ranges with relatively low error (Seaman et al., 1999) or as Minimum Convex Polygons (MCPs), which draw a shape around a percentage of points that minimizes the number of lines drawn by not allowing three points to form a concave line (Nilsen et al., 2008). Landcover types that individuals include in home ranges can be characterized as the species habitat. The habitat then presumably includes all the needs of the individual such as forage/prey resource, shelter or refugia, and has a set of abiotic or biotic factors that the species is adapted to and can tolerate.

How tortoises use their landscape and associated habitat is of great importance due to their typically low mobility. Large-bodied tortoise species such as *Centrochelys sulcata* tend to be highly correlated with their preferred habitat, dry riverbeds called *kori* in sub-Saharan Africa (Petrozzi et al., 2017). A similar pattern of strong habitat associations is seen in *Gopherus spp.* such as *Gopherus flavomarginatus* associated with Chihuahuan halophytic grasslands (Bercerra-Lopez et al., 2017); *Gopherus agassizii* associated with dry desert washes (Nussear and Tuberville, 2014; Nafus et al., 2017); and *Gopherus polyphemus* associated with longleaf pine forests in the American Southeast (Auffenberg and Franz, 1982).

Habitat Connectivity Within a Landscape

The loss of available habitat is among the leading causes of declines in species populations as well as declines in general biodiversity (Horvath et al., 2019). On a landscape or regional scale, habitat is characterized as fragmented if it exists in spatially discrete patches that are embedded in an otherwise inhospitable matrix of non-habitat (Saunders et al., 1991). For example, patches of desert vegetation surrounded by agricultural land represent habitat fragmentation if the species (e.g., tortoises, lizards) that depend on the vegetative patches cannot generally use or disperse through the agricultural land. Habitat connectivity is a characteristic describing the permeability of the landscape between two distinct habitat patches – that is, the ability of the matrix to facilitate movement of a given organism between two distinct areas of preferred habitat. The ability of the matrix to facilitate movement is based on the permeability of the various landcover types (within the matrix) to movement of a given animal. These landcover types may be relatively easy to move through – i.e., an open agricultural field may be permeable to tortoise movement – but may not provide suitable resources to promote permanent occupancy of the area, or animals may prefer to associate with other landcover types that are more consistent with species habitat. Connectivity is therefore a characteristic of the landscape connecting distinct patches of preferred habitat via the permeability of the intervening matrix for a species.

Habitat connectivity allows for dispersal between distinct patches of preferred habitat. Dispersal promotes gene flow and prevents inbreeding, maintaining genetic diversity at a population and metapopulation level. Genetically diverse populations of sufficient size have greater resistance to the genetically homogenizing effects of bottlenecks and inbreeding, providing a sufficiently large gene pool in which advantageous alleles can persist and allow the species to adapt to environmental changes.

By definition of habitat fragmentation, the intervening matrix between patches of preferred habitat consists of landcover types that resist the presence or movement of individuals between the patches. Natural geographic barriers such as rivers and anthropogenic barriers such as urban development or roads can impede movement or increase mortality rates, eroding habitat connectivity across a landscape. Roads are a known barrier to *Gopherus* tortoise movement and can depress population density in the American Southwest (Boarman and Sazaki, 2006; Nafus et al., 2013). For slow-moving organisms such as *Gopherus* tortoises, even railways can hinder dispersal and be a cause of mortality (Rautsaw et al., 2018). The various abiotic stressors between any two patches of preferred habitat can therefore influence the degree to which the patches are effectively connected. In addition to geographic barriers, stressors can manifest simply as natural mortality agents. Tortoises can be killed within the intervening matrix by predators (especially juveniles) or succumb to various diseases. *Mycoplasma agassizii*, a bacterium known to cause upper respiratory infections in a variety of tortoises, was recently documented in *Gopherus berlandieri* (Guthrie et al., 2013). Thus, these stressors or mortality agents can negatively affect tortoise populations in addition to the overall negative effect from habitat fragmentation.

Residential development may transform a relatively continuous landscape of preferred habitat into highly isolated and fragmented patches of habitat embedded into a human-populated matrix. Anthropogenically modified matrix could be very resistant to the presence and movement of tortoises, further decreasing the connectivity of remaining habitat patches. Anthropogenic alteration of habitat, such as the removal of shrubs, often eliminates microhabitat necessary for tortoises to thermoregulate or seek shelter from predators as seen in the Moorish tortoise (*testudo graeca soussensis*) (Lagarde et al., 2012). Hermann's tortoise (*Testudo hermanni*) have a lower population density in highly fragmented landscapes, particularly in urbanized or arable land including vineyards (Couturier et al., 2014). High human density associated with urban development near tortoise populations increased predation on *Gopherus agassizii* by subsidized predators on urban edges near Fort Irwin, California (Esque et al., 2010). The composition of intervening matrix between preferred habitat patches can directly impact the behavior of individual organisms attempting to move or disperse between patches (Romero et al., 2009). If geographic barriers are encountered, individuals may react with behaviors like "fence-running" similar to observed behaviors in reptiles near physical man-made barriers. Individuals may become trapped in or by the barrier with eventual mortality or be immediately killed by the barrier itself, such as an individual crossing a heavily trafficked roadway. Individuals could also be trapped in a location for an extended period of time resulting in decreased fitness or death.

The response of an individual to characteristics of a landscape matrix combine to form a total resistance of the matrix to an organism's movement (Moran-Ordonez et al., 2015). Matrices with high resistance to movement will tend to prevent dispersal, thus effectively fragmenting habitat and isolating populations. Conversely, an intervening matrix with low resistance to movement will tend to easily allow individual dispersal and facilitate connectivity among populations. Maintaining connectivity between fragmented populations is highly important; in general, one migrant per generation into a population is sufficient to maintain genetic diversity and prevent inbreeding depression (Mills and Allendorf, 1995). Modeling connectivity among habitat patches is thus essentially a way to identify the "paths of least resistance" that could be used by dispersing individuals.

Another possibility is that the intervening matrix of a given landscape has suitably low resistance and a sufficient amount of resources to sustain activities by an individual such as foraging, nesting, and other activities indicative of an organism residing in their preferred habitat (Gascon et al., 1999). These activities are consistent with behaviors typically associated with residency in a given area instead of dispersal behaviors. In this situation, the matrix could be considered to consist of landcover types that can function as non-preferred habitat despite these parcels not being as effective in supporting individuals as the preferred habitat that exists in the fragments of the most preferred habitat type. Individuals who have home ranges comprised partially or wholly within the intervening matrix between patches of preferred habitat may not be able to exploit resources as effectively as those who have home ranges entirely within patches of preferred habitat. Nonetheless, individuals that are encountered within the matrix are not necessarily dispersing. In these situations, modeling habitat connectivity may be worthwhile in revealing how much of a given landscape is of potential use and available to be occupied by the species, whether dispersing or not.

Habitat connectivity modeling can be used to hypothesize habitat corridors across a broad landscape. These models integrate resource selection, habitat suitability, and organism behavior to calculate least-cost paths as a way of identifying corridors connecting areas of suitable habitat (Wilson and Willis, 1975; Chetkiewicz et al., 2006). One approach to habitat connectivity modeling is to consider a landscape as an electrical circuit board where the paths traversed by individuals are analogous to current flow. In this analogy, landcover types (e.g. *lomas*, salt prairie grasslands, agricultural fields) or features (e.g., highways, rivers, fences) on a landscape have different resistance values, and hence "electrical circuits" or habitat corridors are that are likely to be used are the lowest-resistance paths between two disparate points in any direction. This modeling approach can be used to determine omni-directional connectivity across a range (Gray et al., 2019) or to determine how anthropogenic factors like land use or climate change may affect connectivity over time (Dilts et al., 2016).

Objectives of the Study

The objectives of my study were to (1) characterize habitat use of *G. berlandieri* individuals at a study site in Cameron County, Texas. I used GPS loggers to track tortoises and comprehensively analyzed habitat use within delineated home ranges. I determined whether *G. berlandieri* uses *loma* versus non-*loma* habitat selectively. If tortoises use habitat non-selectively – that is, using both salt prairie and *loma* habitat types at rates proportional to availability in contrast to prior findings – then further research into precise habitat use behavior such as thermoregulation via use of refugia or foraging patterns in each habitat is warranted. (2) Map the potential connectivity of *G. berlandieri* habitat among *lomas* to characterize of potential dispersal across the landscape. I aim to discover if the landscape across Cameron County would provide differential facilitative movement of *G. berlandieri* based on the proportional amounts of different landcover types that vary in their resistance to tortoise movement.

II. METHODS

Study Site – Palo Alto Battlefield National Historical Park

Previous studies in Cameron County, Texas have characterized local populations as associating strongly with *lomas* at both Palo Alto Battlefield National Historical Park (PABNHP) and LANWR (Bury and Smith, 1986; Carlson et al., 2018). PABNHP covers 13.58 km^2 of mixed *loma*, scrub, and salt prairie grasslands. *Lomas* are low relief ridges, also known as clay dunes, that are characterized by slightly higher elevation (0.3 – 1 m difference) than surrounding areas. Further, *lomas* typically consist of Tamaulipan thorn scrub vegetation whereas the slightly lower surrounding areas have grassy vegetation typical of salt prairies (Carlson et al., 2018). A typical *loma* is shown in Figure 3.

Lomas in PABNHP vary in vegetation composition due to historical land use prior to the parks formation. Many *lomas* retain native Tamaulipan thorn scrub vegetation consisting of small trees and perennial shrubs such as honey mesquite (*Prosopis glandulosa*), spiny hackberry (*Celtis pallida*), cat-claw acacia (*Senegalia greggii*), colima (*Zanthoxylum fagara*), huisache (*Vachellia farnesiana*), brasil (*Condalia hookerii*), Spanish dagger (*Yucca teculeana*), pencil cactus (*Opuntia leptocaulis*) and Engelmann's prickly pear (*Opuntia engelmannii*) (Carlson et al., 2018). Prior to the establishment of the park, some *lomas* were cleared for cattle grazing and have since regrown into lower diversity mesquital scrub, with *P. glandulosa* trees and a grassy understory including invasive Guineagrass (*Urochloa maxima*) (Carlson et al., 2018). Salt prairie grasses sometimes occur in the understory of mesquite trees on these *lomas*. Additionally, the soil in *lomas* tends to be less saline than the surrounding coastal plains and drains better than surrounding soils (Carlson et al., 2018). Previous studies in LANWR revealed that tortoise occurrence was well correlated with higher elevations, leading the authors to suggest that *lomas* (being approximately 0.3-1 m higher elevation than surrounding areas) provide refuge from tidal surges during tropical storm events (Bury and Smith, 1986).

Salt prairies compose much of the natural intervening matrix between *lomas* in the LRGV, particularly near the coast and Rio Grande River. Salt prairies are mostly flat, with very deep and poorly draining soils. Soils also tend to be highly saline and may become saturated from rainfall or occasional storm surges. Salt prairies are typically dominated by Gulf cordgrass (*Spartina spartinae*). Other abundant species include little bluestem (*Schizachyrium scopartum*), bushy bluestem (*Andropogon glomeratus*), and marshhay cordgrass (*Spartina patens*). Other grasses such as saltgrass *(Distichlis spicata*) are common in lower lying, wetter areas. Forbs are uncommon. Shrubby species may also be present, especially *P. glandulosa* and exotic salt cedar (*Tamarix spp.*) (Carlson et al., 2018).

PABNHP has a known population of at least 200 tortoises, many of whom are individually marked and monitored during annual surveys intended to find and verify survival of each individual (Carlson et al., 2018). The park is bordered by major highways to the south and west, a flood canal to the north, and is open to scrubland on private property along the eastern boundary. Tortoise fencing was recently installed along the western edge of the park in an attempt to limit mortality that could occur when tortoises exist the park and attempt to cross the highway (Carlson et al., 2018). LANWR has a population of tortoises, although no census or estimate of *G. berlandieri* in the refuge has been undertaken (Bury and Smith, 1986).

Modeling Tortoise Habitat Connectivity

I constructed maps in ArcGIS Pro (ESRI Software) of Cameron County that identify and highlight *lomas*. *Lomas* are differentiated from other shrub or scrubland landcover types by their soil – typically *lomas* have well drained clay and clay loam soils (Carlson et al., 2018). I used the 2016 National Landcover Database (NLCD) as a landcover base layer at a 30 x 30 m pixel resolution and the Web Soil Survey (WSS) as a soil base layer at a 10 x 10 m pixel resolution. The NLCD is provided by the Multi-Resolution Land Characteristics (MRLC) consortium and the WSS is provided by the Natural Resources Conservation Service – United States Department of Agriculture (NRCS-USDA). Both soil data and landcover data were coarsened to 90 x 90 m pixel resolution to accommodate connectivity modeling calculations via Circuitscape (see below). During this process, 90 x 90 m pixels were assigned landcover or soil values based on the composition of the 9 (NLCD) or 81 (WSS) pixels present at the finer resolution.

Criteria to classify a given 90 x 90 m pixel as *loma* are given in Table 1. A given pixel was considered to be *loma* if it consisted of shrub/scrubland landcover (NLCD class 52) and had a soil type that roughly matched known *loma* soils having high clay content, slight salinity, and being well drained (e.g., soil similar to Cameron County soil type Cameron silty clay [CF] in the WSS). I selected other *loma* candidate soils by comparing Cameron County soil characteristics to soil type CF. Pixels that satisfied both criteria were placed into a raster using the extract by attribute feature in ArcMAP. Non-*loma* shrub/scrublands were then separated from *lomas*.

I overlaid road data from the Topographically Integrated Geographic Encoding and Referencing (TIGER) database (U.S. Census Bureau) at a 90 x 90 m resolution on the landcover map. Pixels of the road layer were snapped to the landcover map to ensure an overlay function properly compared pixels in the same physical space. TIGER data files included all levels of road classification.

Circuitscape modeling software (Anantharaman et al., 2020) was used to build habitat connectivity models. Circuitscape models the landscape as an electrical grid where each individual pixel has a resistance to electrical "flow" which represents abstracted animal movement. Circuitscape performs habitat connectivity simulations by running an electrical current between pairs of nodes. During a Circuitscape simulation, I designated nodes of a certain landcover characteristic and the program ran simulations for every possible pair of nodes before aggregating all simulations into a cumulative map.

I constructed and analyzed three resistance maps: a low resistance, medium resistance, and high resistance scenario. Each 90 x 90 m pixel in a map was then assigned a resistance value based on the given resistance of the landcover and roads within the pixel. Resistance values were assigned by ordinally ranking how resistant each landcover or road type would presumably be to a dispersing *G. berlandieri* individual. The lowest resistance value of 1 was assigned to *lomas*, scrublands and herbaceous grasslands, and the highest resistance value for each resistance category was assigned to primary roads such as multilane highways. All resistance values are listed in Table 1. Many pixels contained both landcover information from the NLCD and road information from TIGER. In these situations, the higher of the two resistances was assigned to the pixel.

For the Circuitscape simulations, I placed focal nodes at the centroid of each *loma* at PABNHP where each *loma* was represented as a polygon in ArcGIS. The *loma* polygons also included some pixels bordering actual *loma* and surrounding salt prairie grasslands. I assumed these small areas to be appropriate because field observations revealed that tortoises were often encountered on the edges of *lomas*. These focal nodes represented areas of probable *G. berlandieri* occurrence in that they were placed in the center of habitat patches (*lomas*).

I also obtained GIS polygons of all public or privately managed conservation land in Cameron County to represent protected areas. This set of protected natural areas included polygons from the National Parks Service (NPS), United States Fish and Wildlife Service (USFWS), Texas Parks and Wildlife Department (TPWD), and The Nature Conservancy (TNC). As with PABNHP, I placed a node in each polygon representing *loma* habitat within each of the protected areas following the methods above.

My analysis included 151 focal nodes and resulting in 11,325 unique pairs of focal nodes. Circuitscape modeling focused exclusively on Cameron County as it has undergone rapid urbanization in recent decades and PABNHP and LANWR, both known to have substantial and well-studied *G. berlandieri* populations, exist within this large county.

In all three Circuitscape models, all focal nodes were paired with all other nodes to simulate electrical current flowing between nodes or dispersing hypothetical tortoises movement among *lomas*. That is, for every pair of nodes, one node was assigned as the ground and the other as the start point. One amp of current was “injected” into the starting node and the electricity (that is, the hypothetical tortoises dispersing) took the path of least resistance to the ground node. For each pair of nodes, Circuitscape builds a current map displaying this path. All current maps are then aggregated to form a cumulative map of current flow, which in the context of my study, is a county-wide habitat connectivity map for *G. berlandieri*.

For each model (low, medium, and high resistance), an integerized raster map was constructed of both the resistance maps and Circuitscape maps of cumulative current flow. Each integerized raster map aggregated landcover types of identical resistance into a broad resistance category. For example, *loma*, shrub/scrub, and herbaceous grasslands were assigned the same resistance value (Table 1) and thus I treated all three landcover types as a single resistance category.

Analyzing Circuitscape Maps

I analyzed the potential connectivity of Cameron County, Texas via analysis of expected and observed current pass-through of different landcover types. Expected current pass-through was calculated using permeability values and proportion of a resistance category within Cameron County. Permeability of a given resistance category was calculated as the greatest resistance category value (among all categories for a given model) divided by the resistance value for the given resistance category. The general formula for permeability can be expressed as:

$$P_i = R_j / R_i$$

where P is permeability, R is the resistance value, i is a given category, and j is the maximum resistance value in a given resistance scenario. Permeability indicates the *relative* ease with which electrical current (or a dispersing organism) could enter into a particular pixel having a given resistance value. Permeability ranges from 1 (the lowest possible permeability which occurs when $R_j = R_i$) to a value representing the resistance of the least resistance category scaled to the resistance of the most resistant category. For example, secondary roads in the medium resistance map have a permeability of 1.25, (maximum resistance (150)/resistance of secondary roads (125)). The number of pixels in each category was divided by the total number of pixels in the landscape to obtain the proportional representation of each resistance category (L_i) in the landscape. The value for proportional representation was then multiplied by the permeability value of the category:

$$D_i = L_i \times P_i.$$

The products of proportional representation and permeability for each category were then summed over all categories (ΣD) and used to obtain the *expected* amount of current (as a proportion of total current) passing through the landcover types composing each resistance category. The equation for expected amount of current pass-through for a resistance category can be expressed as:

$$E_{pass-through} = D_i / \Sigma D$$

For example, with a proportional representation of 0.00078 and a permeability of 1.2., the expected pass-through for secondary roads in the medium resistance map was approximately 7.43×10^{-9}. This is a very low value due to secondary roads being a relatively minor component (as a proportion of overall cover) of the landscape and also due to the relatively high resistance value (low permeability) assigned to secondary roads.

To obtain the *observed* frequency of current pass-through for each resistance category, I first projected the maps of cumulative current produced by Circuitscape into

ArcGIS. For a given map and resistance category, I calculated the observed current pass-through as:

$$O_{pass-through} = \Sigma C_i / \Sigma C_{total}$$

Where the sum of current pass-through for a given resistance category (ΣC_i) is divided by the total amount of current pass-through for the entire map (ΣC_{total}).

I then performed a χ^2 test to determine if observed current pass-through was significantly different than what would be expected based on permeability and proportional representation of a given resistance category across the landscape. In this context, a significantly large χ^2 value would indicate that for some of the landcover types the amount of current pass-through is either less than or greater than expected based on permeability and proportional representation. In such cases, the spatial arrangement of the landcover types might be influencing current pass-through. A non-significant or significantly small χ^2 value would indicate that current pass-through is as expected based simply on permeability and proportional amount of the landcover type in the landscape. In the context of my study, current pass-through is meant to represent hypothetical dispersing tortoises, so interpretation of Circuitscape results is sometimes put in those terms.

Tortoise Surveying and Tracking

Recent studies of *G. berlandieri* within the LRGV have relied on surveys exclusively focused on *lomas* in order to reliably locate tortoises and obtain sufficient data for estimating survival and population size (Carlson et al., 2018). Therefore, the extent at which *G. berlandieri* individuals occupy salt prairies or surrounding landcover types instead of *lomas* is poorly understood. I surveyed for tortoises within the landscape of PABNHP from 9 March 2020 to 12 March 2020 with a survey team of seven to ten people. We surveyed the intra-*loma* matrix as well as the interface between the *lomas* and salt prairie, preferentially searching within the salt prairie. Surveys took place twice daily, with two three-hour sessions between the hours of 0800-1100 and 1500-1800. The survey team was spaced approximately 3 meters apart and walked transects from the Visitor's Center at PABNHP to *lomas* of interest described below.

I encountered tortoises near two *lomas*, one along the southern boundary of the park identified as NPS survey unit 1 ("Southside") and one along the western boundary of the park near a maintenance shed identified as NPS survey unit 3 ("Maintenance"). I surveyed several other areas of interest within the park such as a scrubland patch approximately halfway between the Visitor's Center and NPS survey unit 1, the edge of a *loma* along the southernmost portion of the park's western boundary, and a scrubland patch of mixed grasses, yuccas and cactus located off of the visitors walking trail between the historic Mexican and American battle lines (Figure 4).

I encountered ten tortoises during the March survey period. Eight tortoises were located near NPS Survey Unit 1 (three males, five females) and two were located near NPS Survey Unit 3 (two females). Eight individuals (two males, six females) were outfitted with a radio transmitter and GPS logger. Radio transmitters consisted of Holohil RI-2B and PD-2 models, while the GPS loggers were i-gotU GT-120 USB GPS Travel Loggers. The GPS loggers were situated in a metal sled machined by the United States Geological Service (USGS) Western Ecology Research Station designed for use on *Gopherus agassizii* and *Gopherus morafkai* individuals in the western United States. Two tortoises (one male, one female) in NPS Survey Unit 1 were outfitted with only radio transmitters due to their small size. All equipment was attached using epoxy putty (JB Weld Quiksteel) to the carapace of an individual. Antennae of radio transmitters were wrapped in heat shrink tubing and secured to the costal scute adjacent to the transmitter using epoxy putty and clear silicone gel. GPS loggers (i-gotU model GT-120) were placed into metal sleds and secured using clear silicone gel (GE Kitchen & Bath Caulk GE284). The cumulative total of attached equipment did not exceed 7% of body weight of each individual tortoise.

I conducted monthly surveys after the March survey to relocate tortoises and replace GPS loggers, as battery life for the units was typically 4-6 weeks. Due to the COVID-19 pandemic and closure of PABNHP by the National Parks Service, surveys were not possible in April or May. I relocated tortoises monthly from June until August. I located two novel tortoises opportunistically as tagged tortoises were relocated: two tortoises were relocated in June near Survey Unit 1 with other, novel tortoises that were tagged with radio transmitters and GPS loggers. Tortoise 1 was located with Tortoise 11, a male; and Tortoise 6 was located with Tortoise 12, a female. This brought the total study population to six males and seven females. As time allowed, I surveyed between the American and Mexican battle lines among the shrub/scrub and salt prairie mixture for additional tortoises. In June, I located Tortoise 13 – a large male - approximately fifteen meters from the end of the visitor trail near the American battle line. This brought the total study population to six males and seven females. When I relocated tortoises, I removed the installed GPS logger using a knife and replaced it with a fresh GPS logger and re-secured the unit using clear silicone gel. Tortoises 3 and 7 were not outfitted with

GPS loggers and their locations were recorded as single points when encountered. Thus, I excluded Tortoises 3 and 7 from further statistical analysis due to the small amount of locality accumulated for them.

I programmed the GPS loggers to record a GPS point location every hour continuously using the proprietary software associated with the GPS logger units, @Trip (igotU). After I retrieved a GPS logger unit from a tortoise in the field, @Trip software was used to import the data points from the prior month in both .csv and .gpx file types. I trimmed the .csv files to only include the time period when a logger was actually on a given individual tortoise. Individual monthly data files were combined into a master GPS track for each individual tortoise. I visualized data files in ArcMAP against the landcover map built for habitat connectivity that includes *loma* habitat.

Statistical Analysis of Habitat Use

Data files for each individual tortoise were visualized in ArcMAP (ESRI) on top of the 30 x 30 m landcover map that includes *loma* habitat. I constructed three possible home ranges for each tortoise: a 100% minimum convex polygon (MCP) drawn using the Minimum Bounding Geometry tool in ArcGIS Pro (ESRI); a 95% Kernel Density Estimate range calculated using the *adeHabitatHR* (Calenge, 2020) and *sp* (Pebesma et al., 2020) packages in R (R Core Team) using the RStudio platform; and a 50% Kernel Density calculated using the *adeHabitatHR* and *sp* packages in RStudio. I transformed the 95% and 50% KDE ranges into shapefiles using the *GISTools* (Brunsdon and Chen, 2015) and *rgdal* (Bivand et al., 2020) packages in RStudio. For each home range, I placed a 100 m buffer around the boundaries of the range to represent possible area of use by a tortoise. If a tortoise's home range or buffered home range extended beyond the southern boundary of the park, I clipped the corresponding polygon using the park boundaries as areas outside the park are inaccessible due to tortoise proof fencing installed by the National Parks Service.

I performed a χ^2 analysis for each individual tortoise across all three home range sizes, as well as for all tortoises within a home range type. I calculated expected land use by extracting 30 x 30 m landcover pixels using the buffered home range as a mask and calculating proportions of *loma* versus non-*loma*. Observed land use was calculated in a similar manner using the unbuffered home range. Tortoise 13 was excluded from all χ^2 calculations as no *loma* was in any buffered home range and thus would cause a zero in the denominator. At the 50% KDE Range, Tortoises 9 and 12 home ranges were smaller than a single pixel and thus no pixels were able to be extracted. They were also excluded from the analysis at that scale.

III. RESULTS

Habitat Connectivity

Within Cameron County, proportions of the landcover types range from <0.0001 to 0.4456 when combined into resistance categories for modeling habitat connectivity using Circuitscape. Resistance categories were constructed from landcover types or roads that shared similar resistance values within a scenario. These proportions combined with specified permeability values were used to obtain the expected current (or tortoise) pass-through for pixels of each resistance category (Tables 2 – 4). Observed and expected circuit pass-through frequencies differed for some natural landcover resistance categories across all three resistance scenarios. For example, the category of *loma*/shrub/scrub/herbaceous grassland was expected to constitute at least 0.86 of current pass through in each resistance scenario (Tables 2 – 4), but only constituted at most 0.577 of current pass through (high resistance scenario, Table 4). Similar patterns can be seen for emergent herbaceous wetlands; expected current pass-through between 0.0193 – 0.0198 and observed current pass-through substantially higher between 0.2217 – 0.2719; and woody wetlands with expected current pass-through 0.0023 in all resistance scenarios and observed current pass-through between 0.0410 – 0.0447. Despite these fairly pronounced differences between observed and expected pass-through values for some resistance categories (landcover types), the χ^2 values for the medium and high-resistance scenarios were significantly small indicating a significant match between expected and observed frequencies of current pass-through in the resistance categories taken as a collective group (medium: $\chi^2 = 3.21$, left-tail $p = 0.045$; high: $\chi^2 = 3.24$, left-tail $p =$

0.046). The low-resistance scenario did not reveal a significant match between observed and expected pass-through values (χ^2 = 4.23, left-tail p = 0.25) nor a significant difference (right-tail p = 0.75).

Habitat Use in Tortoise Home Ranges

A total of 15,596 GPS locations were recorded across all 11 tagged tortoises (Table 5) between March and August 2020. GPS locations per tortoise range from 536 - 2300. Several tortoises are not represented continuously due to either GPS logger death before retrieval or GPS logger loss within the field. Tortoise 1 and 10 lost GPS loggers between the March survey event and the June survey event. Tortoises 9, 12 and 13 lost both their GPS loggers and attachment sleds between the July and August survey events. Home range size ranges from 0.33 - 3.35 ha (100% MCP), 0.22 - 6.53 ha (95% KDE), and 0.06 - 1.53 ha. The mean home range size is 1.46 ha ± 0.25 (100% MCP), 1.42 ha ± 0.54 (95% KDE), and 0.32 ha ± 0.13 (50% KDE).

No individual tortoise displayed significantly non-random habitat use when comparing *loma* and non-*loma* landcover (Tables 6-8). Tortoises tended to use *loma* and non-*loma* habitat (e.g., salt prairie grasslands) at frequencies that were not significantly different from the expected frequencies based on availability of each habitat type in the home range and 100 m buffer. The population-level analysis based on all eleven tortoises revealed significantly small χ^2 values for the 100% MCP home ranges (p=0.002) indicating that observed and expected frequencies were *significantly similar* to one another (Table 6). The population-level χ^2 value for the 95% KDE home ranges was also small and marginally significant (p=0.06). For the 50% KDE home ranges, the χ^2 value was non-significant ($p=0.67$).

IV. DISCUSSION

Gopherus berlandieri individuals within PABNHP appear to use both *loma* and non-*loma* landcover to an extent roughly equal to the availability of each landcover type within the home range and immediate vicinity. They do not selectively inhabit *loma* during spring and summer months. Potential connectivity among protected areas in Cameron County exists over an intervening matrix of landcover types that likely have varying but unknown resistance to tortoise movement. The connectivity of habitat patches (specifically, *loma* and scrub-dominated fragments) is relatively unaffected by the spatial arrangement of different landcover types in the matrix within medium- and high-resistance scenarios. Instead, connectivity in these resistance scenarios is as expected based on proportional representation and the specified resistance values (i.e., permeabilities) of the landcover types within Cameron County. However, this is a result from simultaneously examining all the landcover types (resistance categories) together, as in applying a χ^2 test. When considered individually, some natural landcover types differed in observed and expected current pass-through frequencies across all resistance scenarios (e.g., “habitat” resistance category of *loma*/shrublands/herbaceous grasslands, woody wetlands, emergent wetlands), possibly due to the spatial distribution of these landcover types within Cameron County and the location of protected natural areas within the county.

Habitat Use Within Home Ranges

G. berlandieri individuals indiscriminately use both *loma* and non-*loma* habitat within PABNHP whether home range is defined as the 100% MCP or the 95% KDE, or as a core represented by the 50% KDE. The χ^2 tests for each individual tortoise and each of the three home range delineations were always non-significant indicating each tortoise uses the two landcover types at frequencies that are not significantly different from what is expected based on availability of *loma* and non-*loma* within the respective home range and surrounding vicinity. Results from the χ^2 tests applied collectively to the entire group of ten tortoises is even more revealing. Those results are strong indicators of non-preferential habitat use during the time frame of the study. There were 15,060 unique GPS points included within each analysis (100% MCP and 95% KDE) and the χ^2 values for each test were significantly small ($p = 0.002$ and 0.060, respectively) indicating that as a group, the tortoises use *loma* and non-*loma* habitat at rates almost exactly equal to availability of these cover types. Although the p-value for the 95% KDE is slightly above the traditional threshold of significance ($\alpha = 0.05$), this value is interpreted as significant in that tortoises located in the field were often located along the edge of *lomas* and the resolution of landcover pixels (30 x 30 m) is relatively coarse in relation to *G. berlandieri* home range size.

This finding runs counter to the established paradigm that *G. berlandieri* populations along the Gulf Coast associate very strongly with *loma* and similar elevated scrubland (Rose and Judd; 1975; Bury and Smith, 1986; Carlson et al., 2018). This may be due to several factors: for example, the search effort required to find a tortoise is extremely high, and detectability may be much higher on *lomas*, particularly those that are relatively devoid of a thick vegetative understory. Early survey events conducted by the National Parks Service at PABNHP found between zero and four tortoises per survey per *loma*, and found zero tortoises after 40 hours of search effort within the salt prairie leading to the conclusion that *G. berlandieri* is primarily confined to *lomas* (Carlson et al., 2018). Surveys by the Gulf Coast Inventory Monitoring Network between Fall 2016 and Spring 2018 at PABNHP found 0.69 tortoises per hour of person-effort on *lomas*, where tortoises are presumably the densest (Carlson et al., 2018). This may bias conclusions as to where tortoises will occur within a landscape that includes *lomas* as well as other landcover types that might also be suitable habitat.

Tortoise home range size on or near *lomas* also appears to be smaller than home ranges in non-*loma* habitat. This is evident when comparing home ranges of Tortoises 2, 4, 6 and 11 who have home ranges on *lomas* to Tortoise 13 (Figure 5); the latter has a home range that does not include any *loma* habitat (Figure 6).

The home range of Tortoise 13 may be reflective of a more typical inland *G. berlandieri* home range, which are up to 70 times larger in the Chapparal Wildlife Management Area (inland) than at LANWR on the coast (Kazmaier et al., 2000). While Tortoise 13 is the only representation of *G. berlandieri* that does not inhabit *loma* at any home range size within this study, the vegetative community within the coastal vs. inland habitat associations of *G. berlandieri* may provide different density of suitable forage such as *Opuntia* cactus or herbaceous grasses and forbs (Rose and Judd, 2014). However, any interpretation of suitability of a given landcover as tortoise habitat necessitates further research into *G. berlandieri* dietary ecology, shelter requirements, and other factors such as predation, thermal cover, or microhabitat resistance to physical movement. Lastly, prior studies in Cameron County have largely focused on LANWR, which is located closer to the coast than PABNHP, and therefore may be more susceptible to catastrophic events such as flooding or storm surge (Rose and Judd, 1975; Bury and Smith, 1986; Briggs, 2016). Thus, the observed pattern of more tortoise sightings at higher elevations at LANWR may be accounted for due to these geographical differences within the landscape (Bury and Smith, 1986).

Habitat Connectivity

The habitat connectivity simulation demonstrates that, when simulated at a county-wide scale, a hypothetical *G. berlandieri* individual would not necessarily always follow corridors of the least resistant landcover types within medium- and high-resistance scenarios. Circuitscape modeling and the χ^2 tests revealed that current (as a proxy for hypothetical dispersing tortoises) tends to pass through landcover types at rates that are expected based on the relative permeability and proportional representation of the landcover types across the entire landscape. For medium- and high-resistance scenarios there was a significant, although not exact, match between observed and expected frequencies as indicated by statistically significant left-tail p-values from the χ^2 tests. For the low resistance scenario, observed and expected frequencies did not significantly match each other, but they also were not significantly different. These results are somewhat expected; non-resistant landcover types such as natural scrubland, grassland, and wetlands dominate much of the landscape particularly in eastern Cameron County, and thus might provide relatively permeable landcover for dispersing tortoises between relatively resistant and infrequent barriers such as primary roads. Agricultural lands also compose a substantial amount of cover in Cameron County and these lands also might be somewhat permeable to tortoise movement, at least in comparison to urbanized areas or highly trafficked roads. That is, all three resistance scenarios provided output that seems realistic with regard to potential habitat connectivity, although the extent to which the output represents realized habitat connectivity is unknown without further knowledge of tortoise long-distance dispersal.

The observed and expected pass-through frequencies for a given landcover type (resistance category) are relatively similar among the three resistance scenarios that were modeled (compare Tables 2 – 4) except for one landcover type. Observed pass-through frequency for emergent herbaceous wetlands in the low scenario was 0.2719 while only 0.2217 and 0.2231 for the medium and high scenarios respectively. All three scenarios had expected values of about 0.02. Thus, these differences led to a slightly higher χ^2 value for the low-resistance scenario.

Wetlands, comprised of two resistance categories (Table 1), had substantially greater observed current pass-through than expected across all three resistance scenarios. Woody and especially emergent herbaceous wetlands are much more common in the coastal portions of the county (Figure 7). Many of the protected land parcels (and therefore the focal nodes used in Circuitscape simulations) such as PABNHP and LANWR lie in the eastern and southern portions of Cameron County (Figure 8). Hence, current (and presumably tortoises) flowed through the wetlands more so than expected based on their relatively low proportional representation in all of Cameron County. Also, both types of wetland were modeled to have relatively low resistance in all three scenarios (Table 1). A point of clarification is in order: the classification “wetland” in either Emergent Wetlands or Woody Wetlands in the NLCD covers much of PABNHP. From observations in the field, these "wetland" areas tend to be relatively dry for the majority of the year and rarely have standing water of even a few centimeters, perhaps only after a major hurricane or prolonged heavy rainfall. Thus, the low resistance of wetland landcover types for current pass-through (and thus, hypothetical dispersing tortoises) is assigned under the assumption that these conditions are similar across Cameron County.

For the most common landcover type (or resistance category) consisting of *loma*/scrub/grassland, the expected current pass-through (approximately 0.87) was substantially greater than the observed pass-through (0.5 – 0.58). This result held across all three resistance scenarios. Given that *loma*/scrub/grassland is considered as tortoise habitat and was modeled as the least- resistant, most-permeable landcover type, this result is a bit surprising. The relatively high permeability of *loma*/scrub/grassland could have inflated the expected current pass-through in each resistance scenario. In all resistance scenarios, this combined landcover type was assigned a resistance value that resulted in a permeability that was five times greater than the next-most permeable landcover type (agricultural land). In addition, *loma*/scrub/grassland had relatively high proportional representation (0.45). These factors led to a high expected rate of current pass-through that could not be realized (in the observed pass-through) because much of this landcover type is in the western and northern portions of Cameron County away from PABNHP, LANWR, and other protected natural areas (that again served as the nodes in Circuitscape modeling).

It is worth noting several limitations of Circuitscape with regard to conducting a habitat connectivity analysis. First, the actual simulation is removed from the physiological limits and abilities of an organism. Within the current literature, there is no condition which will result in a "failure" for current running between two focal nodes. The impossibility to say a pairwise simulation "fails" is true even if the two nodes are separated by long distances or extremely resistant matrix which would be difficult for a dispersing individual to overcome. The inability to predict the probability of failure within Circuitscape is exacerbated by the presence of highly resistant landcover types such as roads, which likely represent impassable or otherwise extremely resistant barriers to various *Gopherus* species. (Gilson and Bateman, 2015; Peaden et al., 2017). Repeated road fatalities along PABNHP's southern boundary – near the *loma* where many tortoises in this study were located – was cited as a reason for installation of tortoise-proof fencing along that side of the park (Carlson et al., 2018). The possibility that a single tortoise could pass from a *loma* in PABNHP to a *loma* in northern LANWR is incredibly low given even a single primary road between the two parks, much less multiple local and secondary roads as well as obstacles not represented in landcover and road data such as fences, railroad tracks, curbs, and steep ditches. Hypothetically, such dispersal is not impossible as displacement distances of >1 km have been documented for *G. berlandieri* individuals (Carlson et al., 2018) and single-event movements of > 60 m have been recorded in Cameron County (Rose and Judd, 1975).

The conclusions from the habitat use analysis intersect with the construction of potential connectivity through Circuitscape when considering how *G. berlandieri* individuals would potentially travel among *lomas* and other habitat patches across Cameron County. For slow-moving and long-lived species such as *G. berlandieri*, a dispersing individual may become a resident in the intervening matrix if the dispersal takes place over a significant period of time. A tortoise that behaves in this way could be considered to be exhibiting prolonged dispersal, continually moving throughout the intervening matrix over a period of one or more years which necessitates that the matrix have enough resources (i.e., forage, refugia) to support an individual for the time it is dispersing. This pattern may be seen in *G. berlandieri*'s congeneric *G. agassizii*, which will display both much longer distance dispersals and daily displacement distances than does *G. berlandieri*. Given that this prolonged dispersal behavior is found in *G. agassizii*, it is likely that *G. berlandieri* exhibits similar behavior, and the intervening matrix between two given *lomas* would also need to be of sufficient quality to support a dispersing individual.

Conclusion

G. berlandieri is an extremely understudied species when compared to congenerics such as *G. polyphemus*, *G. agassizii*, *G. morafkai* or *G. flavomarginatus*. As urbanization and expansion of agricultural lands continue to cause habitat loss in portions of the species range such as the LRGV it is vital to provide a baseline for future research and conservation efforts. This study contributes to this baseline: the conclusion that tortoises do not favor *loma* over non-*loma* during the time frame of this study and the county-wide assessment of potential habitat connectivity provide an opportunity to further research aspects of *G. berlandieri* habitat use, selection, and movement patterns. The underlying cause of non-selective use of both *loma* and non-*loma* habitat can be explored through studies such as a comprehensive dietary analysis, further GPS tracking through colder fall and winter months as thermal shelter becomes more important (Rose and Judd, 1975), and similar studies at varied sites such as LANWR, Southmost Nature Preserve, or Resaca de las Palmas State Park within Cameron County or inland sites such as the Chaparral WMA.

Many aspects of *G. berlandieri* ecology are still unknown, as is much of their population status throughout their range not only in Texas but in northeastern Mexico. The conclusions presented in this thesis therefore should be seen not only as additional knowledge about the species habitat use and potential for habitat connectivity in Cameron County, but as a piece of the puzzle in the ecology of the species as a whole. *G. berlandieri* has relatively well studied congenerics in *G. polyphemus, G. flavomarginatus*, and the desert tortoise complex of *G. agassizii*, *G. morafkai*, and *G. evgoodei*, all of which face significant challenges with the continued conversion of their natural habitat for anthropogenic use. *G. evgoodei*, *G. agassizii*, and *G. polyphemus* are listed as Vulnerable by the IUCN, and *G. flavomarginatus* is listed as Critically Endangered. Additionally, both *G. agassizii* and *G. polyphemus* are listed as Threatened by the United States Fish and Wildlife Service. The conservation threats the various members of *Gopherus* face apply to *G. berlandieri*: habitat conversion and the erection of major obstacles to movement such as roads. As more intensive research and conservation effort is applied to *Gopherus spp.*, it is important that *G. berlandieri* be included lest the species becomes at serious risk of endangerment.

V. TABLES AND FIGURES

Table 1. Resistance values for low, medium, and high resistance scenarios modeled in Circuitscape.

Pixel Type	Source	Low Resist.	Med. Resist.	High Resist.
Developed Open Space	NLCD	20	30	50
Developed Low Intensity	NLCD	40	50	100
Developed Medium Intensity	NLCD	50	75	150
Developed High Intensity	NLCD	75	100	200
Barren Land	NLCD	5	5	5
Deciduous Forest	NLCD	5	5	5
Evergreen Forest	NLCD	5	5	5
Mixed Forest	NLCD	5	5	5
Non-*Loma* Shrub/Scrub	NLCD	1	1	1
Loma	NLCD, WSS	1	1	1
Herbaceous Grasslands	NLCD	1	1	1
Pasture/Hays	NLCD	5	5	5
Cultivated Crops	NLCD	5	5	5
Woody Wetlands	NLCD	15	15	15
Emergent Herbaceous Wetlands	NLCD	10	10	10
Secondary Road	TIGER	90	125	300
Minor Road	TIGER	50	75	225
Service Drive	TIGER	20	30	40
Private Road	TIGER	10	20	30
Ramp	TIGER	50	90	120
Primary Road	TIGER	100	150	400
Alley	TIGER	10	10	10
Vehicular Trail (4WD)	TIGER	5	5	5
Parking Lot Road	TIGER	20	20	20
Walkway/Pedestrian Trail	TIGER	5	5	5
Bike Path/Trail	TIGER	10	10	10

Table 2. Results of the χ^2 tests for each resistance category in the low-resistance scenario modeled in Circuitscape. For each category, table shows proportional representation (*L*) of the landcover types in Cameron County and permeability (*P*) as derived from specified resistance values for the landcover types of the category. Observed pass-through is the amount or frequency of current (hypothetical tortoise passage) observed to pass through pixels of the given resistance category. Expected pass-through is the amount of current expected based on *L* and *P* of the resistance category (see text for further details). Over all categories, χ^2 = 4.23 and left-tailed p-value = 0.25.

Resistance Category	*L*	*P*	Observed pass-through	Expected pass-through
Loma, Shrub/Scrub, Herbaceous Grasslands	0.4456	100	0.5026	0.8662
Agricultural Land	0.2711	20	0.1594	0.1054
Emergent Herbaceous Wetlands	0.1018	10	0.2719	0.0198
Woody Wetlands	0.0174	6.67	0.0447	0.0023
Developed Open Space	0.0027	5	0.0005	0.0002
Urban and suburban development, including minor roads	0.1527	2	0.0192	0.0036
Secondary Road	0.0077	1.1	0.0016	0.0002
Primary Road	0.0010	1	< 0.0001	<0.0001

Table 3. Results of the χ^2 tests for each resistance category in the medium-resistance scenario modeled in Circuitscape. For each category, table shows proportional representation (*L*) of the landcover types in Cameron County and permeability (*P*) as derived from specified resistance values for the landcover types of the category. Observed pass-through is the amount or frequency of current (hypothetical tortoise passage) observed to pass through pixels of the given resistance category. Expected pass-through is the amount of current expected based on *L* and *P* of the resistance category (see text for further details). Over all categories, χ^2 = 3.21 and left-tailed p-value = 0.045.

Resistance Category	*L*	*P*	Observed pass-through	Expected pass-through
Loma, Shrub/Scrub, Herbaceous Grasslands	0.4452	150	0.5472	0.8681
Agricultural Land	0.2711	30	0.1532	0.1057
Emergent Herbaceous Wetlands	0.0991	15	0.2217	0.0193
Woody Wetlands	0.0174	10	0.0427	0.0023
Private Road	0.0030	7.5	0.0007	0.0003
Developed Open Space	0.0027	5	0.0006	0.0001
Urban and suburban development, including minor roads	0.1522	2	0.0315	0.0039
Ramp	0.0005	1.6	<0.0001	<0.0001
Secondary Road	0.0077	1.2	0.0022	0.0001
Primary Road	0.0010	1	< 0.0001	<0.0001

Table 4. Results of the χ^2 tests for each resistance category in the high-resistance scenario modeled in Circuitscape. For each category, table shows proportional representation (*L*) of the landcover types in Cameron County and permeability (*P*) as derived from specified resistance values for the landcover types of the category. Observed pass-through is the amount or frequency of current (hypothetical tortoise passage) observed to pass through pixels of the given resistance category. Expected pass-through is the amount of current expected based on *L* and *P* of the resistance category (see text for further details). Over all categories, $\chi^2 = 3.24$ and left-tailed p-value = 0.046.

Resistance Category	*L*	*P*	Observed pass-through	Expected pass-through
Loma, Shrub/Scrub, Herbaceous Grasslands	0.4452	400	0.5770	0.8706
Agricultural Land	0.2711	80	0.1357	0.1060
Emergent Herbaceous Wetlands	0.0991	40	0.2231	0.0194
Woody Wetlands	0.0174	26.6	0.0410	0.0023
Private Road	0.0030	13.3	0.0006	0.0002
Service Road	0.0027	10	0.0006	0.0001
Ramp	0.0005	3.3	<0.0001	<0.0001
Urban and suburban development, including minor roads	0.1522	1.7	0.0201	0.0013
Secondary Road	0.0077	1.3	0.0017	<0.0001
Primary Road	0.0010	1	< 0.0001	<0.0001

Table 5. Number of GPS locations per tortoise, date tagged and home range sizes under 100% MCP, 95% KDE and 50% KDE conditions.

Tortoise	Date Tagged	# of GPS locations	Home range (ha)		
			100% MCP	95% KDE	50% KDE
1	10 Mar	1345	1.14	0.88	0.21
2	10 Mar	1945	1.95	1.20	0.16
4	11 Mar	2300	1.58	1.00	0.30
5	11 Mar	1970	1.64	1.00	0.14
6	11 Mar	1386	1.66	1.84	0.42
8	11 Mar	1835	0.82	0.40	0.10
9	12 Mar	1057	0.50	0.23	0.04
10	12 Mar	1382	1.26	0.53	0.13
11	22 Jun	1279	1.82	1.75	0.47
12	22 Jun	576	0.33	0.22	0.06
13	23 Jun	536	3.35	6.53	1.53

Table 6. Habitat use within the 100% MCP home ranges for ten Texas tortoises (*Gopherus berlandieri*) at Palo Alto Battlefield National Historical Park. Habitat was categorized as either loma or non-loma; the latter is primarily salt prairie or grassland (see text for details). Non-significant p-value indicates that observed frequency of use of the two habitat types did not statistically differ from frequencies of use based on relative availability.

Tortoise	Loma		Non-loma		χ^2	P-value
	Observed	Expected	Observed	Expected		
1	0.308	0.205	0.692	0.795	0.06	0.20
2	0.429	0.215	0.571	0.785	0.27	0.40
4	0.706	0.546	0.294	0.454	0.10	0.25
5	0.824	0.657	0.176	0.343	0.12	0.27
6	0.667	0.514	0.333	0.486	0.09	0.24
8	0.300	0.186	0.700	0.814	0.09	0.23
9	0.000	0.143	1.000	0.857	0.17	0.32
10	0.133	0.097	0.867	0.903	0.02	0.10
11	0.238	0.147	0.762	0.853	0.07	0.20
12	1.000	0.721	0.000	0.279	0.39	0.47
All	------	------	------	------	1.372	0.0020

Table 7. Habitat use within the 95% KDE home ranges for ten Texas tortoises (*Gopherus berlandieri*) at Palo Alto Battlefield National Historical Park. Habitat was categorized as either loma or non-loma; the latter is primarily salt prairie or grassland (see text for details). Non-significant p-value indicates that observed frequency of use of the two habitat types did not statistically differ from frequencies of use based on relative availability.

Tortoise	Loma		Non-loma		χ^2	P-value
	Observed	Expected	Observed	Expected		
1	0.400	0.189	0.600	0.811	0.29	0.41
2	0.467	0.230	0.533	0.770	0.32	0.43
4	0.800	0.536	0.200	0.464	0.28	0.40
5	0.889	0.663	0.111	0.337	0.23	0.37
6	0.667	0.474	0.333	0.526	0.15	0.30
8	0.750	0.213	0.250	0.787	1.72	0.81
9	0.000	0.133	1.000	0.867	0.15	0.31
10	0.000	0.099	1.000	0.901	0.11	0.26
11	0.200	0.163	0.800	0.837	0.01	0.08
12	0.500	0.730	0.500	0.270	0.27	0.40
All	------	------	------	------	3.528	0.0604

Table 8. Habitat use within the 50% KDE home ranges for ten Texas tortoises (*Gopherus berlandieri*) at Palo Alto Battlefield National Historical Park. Habitat was categorized as either loma or non-loma; the latter is primarily salt prairie or grassland (see text for details). Non-significant p-value indicates that observed frequency of use of the two habitat types did not statistically differ from frequencies of use based on relative availability.

Tortoise	Loma		Non-loma		χ^2	P-value
	Observed	Expected	Observed	Expected		
1	1.000	0.240	0.000	0.760	3.17	0.07
2	0.000	0.243	1.000	0.757	0.32	0.57
4	0.750	0.358	0.250	0.642	0.67	0.41
5	1.000	0.796	0.000	0.204	0.26	0.61
6	0.667	0.540	0.333	0.460	0.07	0.80
8	1.000	0.237	0.000	0.763	3.22	0.07
9	------	------	------	------	------	------
10	0.000	0.091	1.000	0.909	0.10	0.75
11	0.000	0.182	1.000	0.818	0.22	0.64
12	------	------	------	------	------	------
All	------	------	------	------	8.02	0.67

Figure 1. Photo of a Texas tortoise (*Gopherus berlandieri*) in Cameron County, Texas.

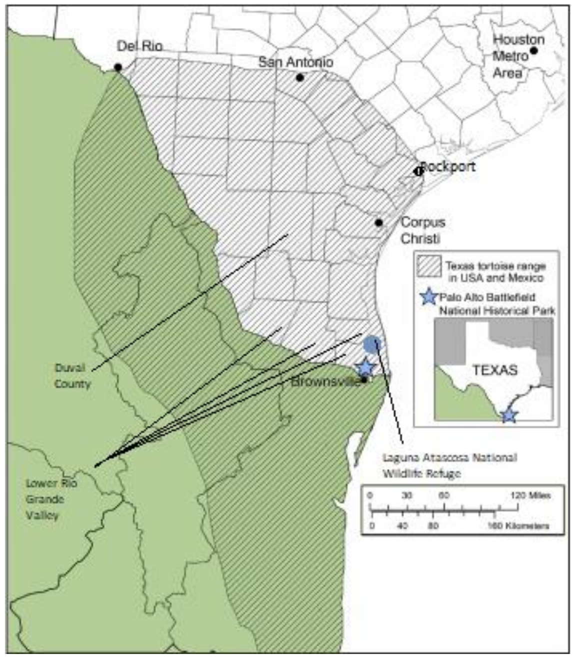

Figure 2: The geographic range of *Gopherus berlandieri*. Major metropolitan centers are marked, as well as Duval County which acts as a rough divider between genetically different populations to the north and those to the south including one at Palo Alto National Battlefield Historical Park, the focal population for this study. Map adapted from Carlson et al. (2018).

Figure 3. Typical *loma* habitat in Palo Alto Battlefield National Historical Park near Brownsville, Texas in September 2020.

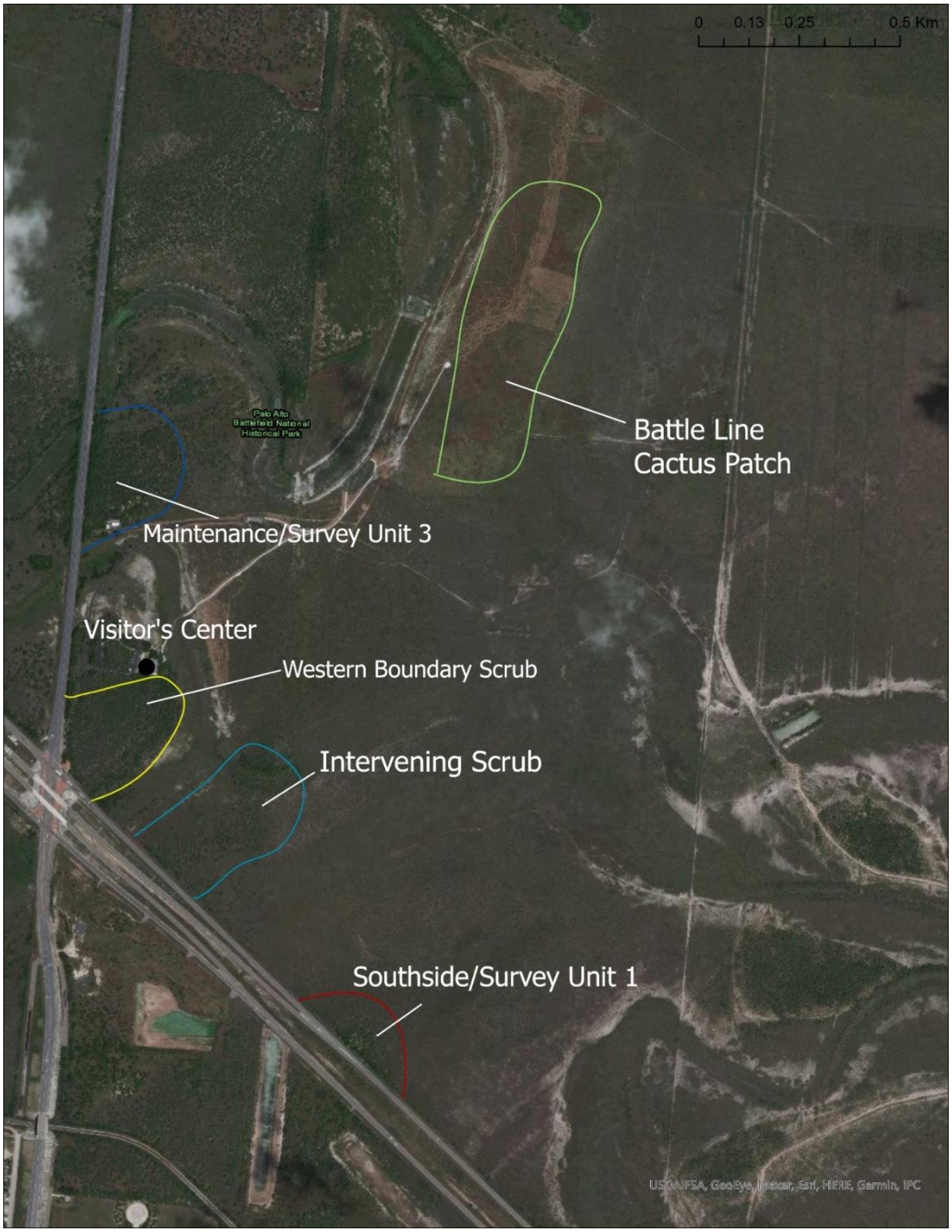

Figure 4. A map of units surveyed for tortoises in Palo Alto Battlefield National Historical Park.

Figure 5: Ninety-five percent KDE home ranges for Tortoises 2, 4, 6, 11 and 13 at Palo Alto Battlefield National Historical Park.

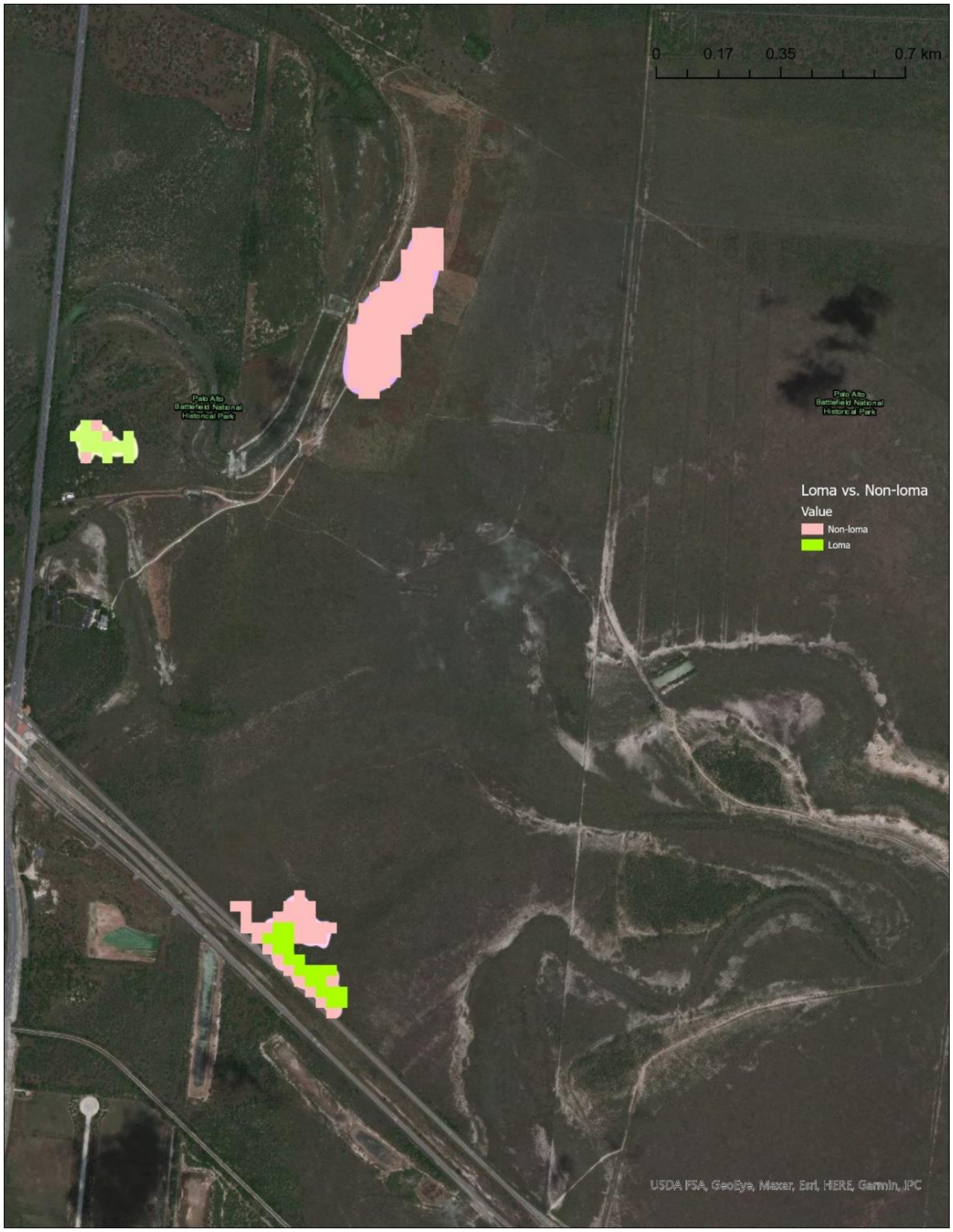

Figure 6: *Loma* vs. non-*loma* occurrence within selected tortoise 95% KDE home ranges at Palo Alto Battlefield National Historical Park. Tortoises 2, 6 and 11 overlap on the southern portion of the park. Exact proportions of *loma* and non-*loma* for individual tortoises may be found in Table 7.

Figure 7: A satellite imagery map of Cameron County, Texas. Note that wetlands tend to be more common in the eastern portion of the county near Laguna Atascosa National Wildlife Refuge and agricultural land tends to be more common in the western portions of the county.

Figure 8: Protected natural areas in Cameron County with focal node polygons (black).

Palo Alto Battlefield National Historical Park is highlighted in green.

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