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Leveraging limited information to understand ecological relationships of endangered Florida salt marsh vole

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We were able to substantially increase our knowledge of what is likely the least understood endangered terrestrial mammal in the United States, the Florida salt marsh vole (FSMV; *Microtus pennsylvanicus dukecampbelli*). We developed a predictive landscape model that estimated 264 ha of potential habitat for FSMVs. Evaluating our model, we found voles at 8 of the 36 sites sampled, yielding a model accuracy of 22% for a subspecies that previously was known from only 3 locations. Within areas of potential habitat, FSMVs selected patches of marsh vegetation > 0.49 ha with at least some (≥ 16.75% and ≤ 43.61%) smooth cordgrass (*Spartina alterniflora*) cover. Suggestive of a meta-population dynamic, FSMV activity decreased outside of patches of smooth cordgrass and saltgrass (*Distichlis spicata*) identified by the predictive landscape model. Our hierarchical approach to studying FSMVs allowed us to leverage a limited amount of data to ultimately produce important ecological information about an endangered species. This approach easily may be adapted to other mammals with similar information needs.

Key words: classification regression tree, distribution, meadow vole, remote sensing

We are in the midst of the planet's 6th major extinction event, with one-half of all mammal populations declining and many others threatened with extinction (Schipper et al. 2008; Ceballos et al. 2015). Mammals are a diverse and well-studied class, yet due to their often cryptic nature, we still are discovering new mammals and have large gaps in our understanding of many known mammalian species (Schipper et al. 2008; Ceballos and Ehrlich 2009). Even the most basic information about some species' ecology is completely missing (Foster and Vincent 2004). Currently, over 15% of mammals in the world do not have the basic information needed to assess their status or to provide sufficient information for conservation efforts (Schipper et al. 2008). This fundamental information on mammalian distributions, populations, and environmental associations are lacking not only in the developing world, but in nations with considerable resources and legislative mandates. In the United States, currently there are 62 terrestrial mammal species and subspecies listed as federally endangered (United State Fish and Wildlife Service [USFWS] 2016), but a number of those species, particularly rodents and bats (e.g., Yelm pocket gopher [*Thomomys mazama yelmensis*], Buena Vista Lake shrew [*Sorex ornatus relictus*], Florida bonneted bat [*Eumops floridanus*]), have only minimal ecological information to contribute to the development of conservation strategies. Possibly the least understood of all endangered mammals in the United States is the Florida salt marsh vole (FSMV; *Microtus pennsylvanicus dukecampbelli*); there is a lack of basic information on its distribution, population dynamics, and environmental associations.

The endangered FSMV is a slightly larger and genetically distinct subspecies of the common meadow vole (*Microtus pennsylvanicus*) with darker pelage and smaller ears (Woods et al. 1982, 1992). The meadow vole utilizes areas of dense grasslands with high soil moisture and its southern distribution is thought to be restricted by temperature (Martin 1968). FSMVs were discovered in the salt marshes around Cedar Key, Florida in 1979 (Woods et al. 1982). From fossil evidence, it was hypothesized that the once widespread meadow vole was isolated in Florida after the retreat of glaciers at the end of the Pleistocene (Martin 1968; Woods et al. 1982). Basic ecological information about FSMVs is limited due to very low capture success (Hotaling et al. 2010). Despite considerable trapping effort (11,123 trap nights—Hotaling et al. 2010) over the last 30 years, researchers working in 18 localities have captured only 43 individuals at 3 sites. From these limited captures, it was speculated that the FSMV was restricted to saltgrass

(*Distichlis spicata*) dominated tidal flats (Woods et al. 1982; Raabe and Gauron 2005). Like other efforts on rare animals, however, researchers trapped only in areas where they believed FSMVs occurred (McCleery et al. 2007). To date, there has not been a systematic approach to finding and understanding this endangered species.

Recent advances in remote sensing (including texture-based classification—see Johansen et al. 2007), machine learning (Olden et al. 2008), and passive capture technologies (O'Connell et al. 2010) have contributed to a broader toolbox for finding and understanding the ecology of rare and cryptic species. We used the FSMV as a model to understand how we can use limited data, technological innovations, and targeted field work to advance our ecological knowledge of a poorly understood mammal. Our goal for this study was to obtain basic information on the distribution and environmental associations of the elusive and endangered FSMV. Specifically our objectives were: 1) develop and test a landscape-scale model to determine the extent of potential FSMV habitat within the Big Bend salt marsh ecosystem, 2) refine our landscape model by determining the factors influencing vole occurrence at patch scale, and 3) test the assumption in the patch and landscape models that voles are restricted to specific vegetation communities within the salt marsh.

Materials and Methods

Study area.—Our study was conducted in the Big Bend salt marsh (Fig. 1), running over 250 km from the St. Marks River to south of the Waccasassa River on the west coast of Florida (Williams et al. 1999). This area is a low or no energy coastline (Tanner 1960), encompasses one of the last undeveloped watersheds in Florida (Bergquist et al. 2006), and is the only known habitat for FSMVs. The distribution of plants in the marsh can change abruptly due to elevation and flooding, creating a patchy matrix. In general, Big Bend salt marsh is dominated by black needlerush (*Juncus roemerianus*) and smooth cordgrass (*Spartina alterniflora*) in the lower reaches of the tidal zone and saltgrass in the high marsh that is less frequently inundated. There also are isolated patches of saltgrass interspersed with smaller or "dwarf" smooth cordgrass in the lower tidal zone by the water's edge. The extent of our search for potential FSMV habitat covered over 75 km of coastline from the mouth of the Suwannee River to 10 km south of the Waccasassa River (Fig. 1). Common mammals found in these salt marshes included raccoons (*Procyon lotor*), salt marsh mink (*Neovison vison halilimnetes*), cotton rats (*Sigmodon hispidus*), and rice rats (*Oryzomys palustris*).

Landscape-level habitat model.—We conducted exploratory trapping efforts in the salt marshes around Cedar Key, Florida, to find FSMVs. We used Sherman traps (Model LFATDG, Tallahassee, Florida) secured to a floating platform and baited with a mix of birdseed. We placed traps in transects of 8–15 traps with 10 m spacing at 5 separate sites in areas of thick vegetative cover similar to that commonly inhabited by northern populations of meadow voles. This trapping yielded 30 captures of FSMVs. All of our captures occurred in dwarf smooth cordgrass and saltgrass on the seaward edge of the marsh.

We identified 20 patches of dwarf smooth cordgrass and saltgrass in and around our FSMV captures and delineated them by walking around them with a handheld GPS (Garmin 72H GPS, Olathe, Kansas). We imported patch boundaries into ArcGIS 10.1 (ESRI, Redlands, California), converted them to polygons (training polygons), and overlaid them on digital imagery. We obtained digital RGB aerial photography of the Big Bend salt marsh (0.3 m resolution) from the state of Florida and mosaicked images in ERDAS Imagine (Intergraph, Huntsville, Alabama), creating 1 image from the mouth of the Suwannee River to the Waccasassa River. We used the distinctive digital textural and spectral signatures within our training polygons to classify the coastline based on spectral and texture characteristics with Feature Analyst (Overwatch Systems, Austin, Texas) for ArcGIS 10.1 (ESRI). Feature Analyst is an ArcGIS add-on that uses machine learning algorithms (neural networks and genetic algorithms) along with texture and spectral characteristics to classify user-defined categories of land cover. It integrates manual and task-specific automated approaches through an iterative cycle of automated modeling and correction by the

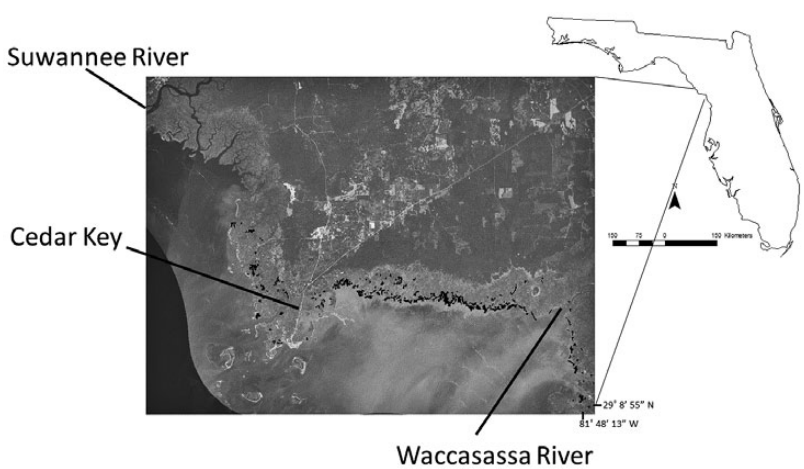

Fig. 1.—Model of potential Florida salt marsh vole (*Microtus pennsylvanicus dukecampbelli*) habitat patches (dark polygons) from spectral and texture characteristics of aerial imagery from the west coast of Florida.

user (Blundell and Opitz 2006). We deleted all polygons under 0.25 ha, considering them too small to be useable habitat.

Model evaluation.—To evaluate our landscape-level habitat model, we randomly selected 36 patches (continuous polygons of potential habitat) separated by at least 500 m and trapped them using floating camera traps (McCleery et al. 2014) to deal with daily tidal inundation. These cameras are highly effective for detecting and identifying FSMVs (McCleery et al. 2014). We placed cameras in a 4×5 grid with 20 m spacing (0.48 ha) and activated them for at least 7 days. We programmed the cameras to take a set of 3 pictures when triggered by movement, with a 1-min reset time. We baited each trap with sunflower seeds and chicken scratch. After each survey, we reviewed the photographs and recorded the presence/absence of voles at each camera trap. We conducted 4,900 nights of camera trapping from December 2012 to August 2013.

One potential shortcoming of this simplified approach to evaluating the model is that it did not account for the possibility that animals might go undetected, yielding false absences (MacKenzie et al. 2005). To determine the probability that our study design yielded false absences, we used an occupancy modeling approach where we counted each survey night as an independent survey to estimate the probability of detecting a FSMV if it was present on the camera trapping grid (Mackenzie et al. 2005). All research on live animals followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and was approved by the University of Florida Animal Research Committee, protocol ARC #016-12WEC.

Patch-level models.—In an effort to refine our model and further our understanding of FSMV's use of the environment, we examined factors influencing vole occurrence. We specifically looked at a suite of environmental variables that likely influenced the occurrence of FSMVs within habitat patches identified by the landscape-level habitat model.

We defined a patch as the contiguous polygons of potential habitat as identified by the landscape-level habitat model. Using ArcGIS, we quantified patch size and used it as a variable in our model, because of its relevance to meta-population dynamics, minimum viable populations, and population persistence in rodents. We also measured the distance from the edge of the patch to treeline to determine placement of the patch within the salt marsh and to quantify how far a vole would have to travel to dry ground during tidal inundation.

Given their sparse distribution, we believed that FSMVs might select particular vegetative composition and structure within the marsh. Within patches that we surveyed for FSMVs, we sampled the vegetation systemically at every other trap (n = 10 per site). We sampled five 1-m^2 plots around the traps, placing 1 plot next to the camera trap and the 4 additional plots 3 m away in each cardinal direction. Within each plot, we measured percent cover by species of the dominant vegetation. We also measured maximum vegetation height, maximum height of smooth cordgrass, and visual obstruction as measured from a Robel pole at a distance of 4 m.

CART modeling.—We utilized a machine learning Classification and Regression Tree (CART) model (Breiman et al. 1984) to understand factors influencing the occurrence of FSMVs within habitat patches identified by the landscape-level habitat model. We used CART modeling due to our limited understanding of environmental factors influencing occurrence of FSMVs. Additionally, CART models are easily interpreted and well suited for the discovery of patterns from systems with complex, often nonlinear relationships (De'ath and Fabricius 2000). Our CART model utilized a nonparametric, machine learning approach that partitioned data into previously defined classes (voles present or voles absent) by our environmental characteristics (vegetation cover and height, habitat patch size, distance to tree line, and visual obstruction) creating a branching decision tree to predict presence or absence of FSMVs (McCune et al. 2002). We created our CART model using Salford Predictive Modeler v 7.0. CART. We ran the model with the default settings that use the Gini index for splitting nodes, a minimum of 10 for parent node cases and 1 for terminal node cases, and 10-fold cross-validation runs. We used the cross-validation procedure to partition data into subsets to train and test the model. To determine the model's predictive ability, we used classification accuracy and the receiver operating characteristic (ROC), which effectively ranges from 0.5 to 1.0.

Gradient study.—A potential shortcoming of our models was that they assumed voles only occur in areas similar to the training polygons (area dominated by dwarf smooth cordgrass with seashore saltgrass). This assumption may lead to an underrepresentation of potential vole habitat. To test if voles used other vegetative communities, we conducted a gradient study to examine activity levels of voles. We established 4 transects on 4 patches (n = 16) with known vole occurrence identified from the landscape-level habitat model validation. Each transect consisted of 5 floating camera traps placed 20 m apart in a line running across an ecotone, from patches of dwarf smooth cordgrass and saltgrass into patches dominated by black needlerush. The transect started 40 m from the ecotone into the dwarf smooth cordgrass/saltgrass patches and ended 40 m into the black needlerush dominated community. Each transect had 2 cameras in each vegetation community and 1 camera at the ecotone. We used the same trapping protocol for the validation of the landscape-level habitat model, baiting camera traps and surveying for 7 nights. We recorded the number of independent sighting of FSMVs as an index of activity at each point along the transects. We calculated activity levels as the number of occurrences spaced 15 min apart; after identifying a FSMV in a picture, we did not record another occurrence until after 15 min. To determine how vole activity changed across the ecotone, we tested the potential hypotheses: 1) activity did not change (*Null*), 2) activity was different in both communities and on the ecotone (*Edge*), 3) activity changed continuously across the gradient (*Gradient*), or 4) activity in the dwarf smooth cordgrass and saltgrass and on the ecotone was different than in the black needlerush (*Edge and Cordgrass*). To test these hypotheses, we generated 4 models of vole activity as a function of the vegetative community. Using a generalized linear mixed model with the glmmADMB package in R 3.2.3 (R Development Core Team 2011), we fit vole activity to a negative binomial distribution and used patch as a random effect. We selected the most parsimonious model based on Akaike Information Criteria corrected for small sample size (AICc) and examined the beta estimates of the best models to determine if their 95% confidence interval (*CI*) included 0.

Results

Examining ~ 13,000 ha of salt marsh, the landscape-level habitat model estimated 264 ha of potential habitat within our study area. The average patch size of potential habitat was 0.68 ha. Most of these patches were located on the seaward side of the saltmarsh, often extending right up to open water (Fig. 1). The majority of potential habitat identified was south of the town of Cedar Key. We did identify habitat to the north of Cedar Key but not within 4 km of the mouth of the Suwannee River (Fig. 1). Evaluating our model, we found voles at 8 of the 36 sites sampled, yielding a model accuracy of 22%. From our occupancy model, assuming constant detection, we estimating the probability of detecting a FSMV during 1 of the 7 surveys to be relatively high (detection = 0.65, 95% *CI* = 0.51–0.77). With a less that 0.07% probability of missing a FSMV during our 7 day of surveys, it was unlikely that we would record any false absences.

Patch-level models.—We surveyed environmental features on 30 patches of potential habitat. We were unable to sample vegetation on 6 patches of the 36 patches sampled for FSMVs due to tides and accessibility constraints. The patches sampled averaged 0.84 ha (range 0.25–3.2 ha). Dominant vegetation consisted of saltgrass ($\bar{X}$ = 61%, range 18–88%), smooth cordgrass ($\bar{X}$ = 31%, range 9–66%), and black needlerush ($\bar{X}$ = 18%, range 0–44%). The optimal tree from our CART model included 4 nodes based on patch areas and the percent cover of smooth cordgrass, with respective variable importance scores of 100 and 93. The model predicted that within potential habitat, FSMVs would be found in patches > 0.49 ha with average smooth cordgrass cover ≥ 16.75% and ≤ 43.61% (Fig. 2). The model had a classification accuracy of 0.83 and ROC of 0.78, suggesting fair to good predictive accuracy of the model.

Gradient study.—We found that the model combining activity on the edge of the patch with activity in dwarf smooth cordgrass and saltgrass (*Edge and Cordgrass*) provided the most parsimonious model with a delta AICc value 1.1 points higher than the gradient and null models (Table 1). Using the black needlerush community as a reference category, the beta estimate for the edge and dwarf smooth cordgrass and saltgrass areas was positive and its 95% *CI* did not contain 0 (β = 0.85, 95% *CI* = 0.07–1.63), suggesting a clear difference between the categories. The average number of independent detections on cameras on the edge and in the dwarf smooth cordgrass and saltgrass was 10.2 (95% *CI* = 5.5–14.9) and in black needlerush was 4.5 (95% *CI* = 1.2–6.8). Evaluating the gradient model, the 95% *CI* of the beta estimate for the continuous variable of distance along the ecotone included 0 (β = 0.013, 95% *CI* = −0.01 to 0.03), suggesting it was not a relevant predictor of vole activity.

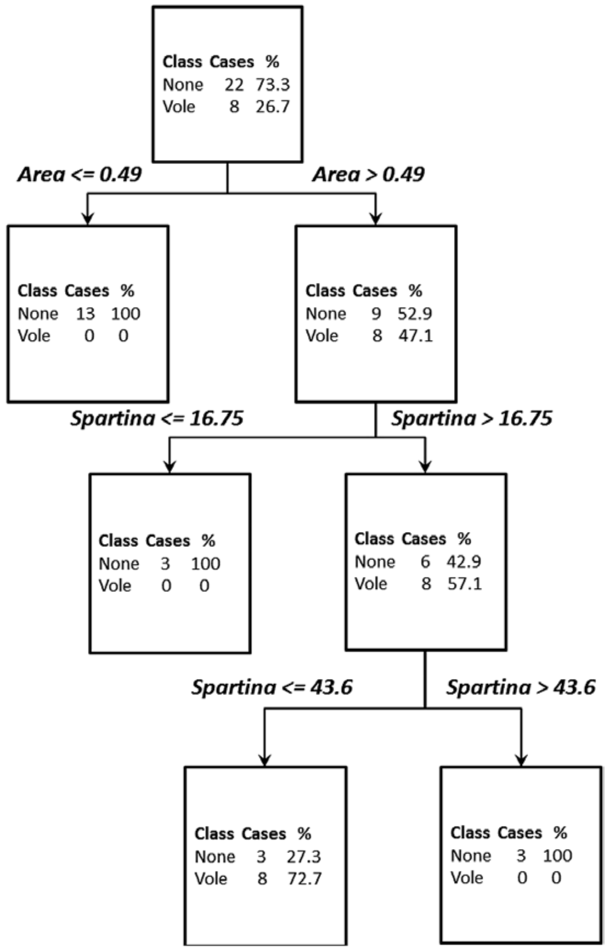

Fig. 2.—Classification and Regression Tree models for Florida salt marsh voles (*Microtus pennsylvanicus dukecampbelli*) within potential habitat identified by the landscape model (Fig. 1) on the west coast of Florida. Tree nodes classify observations into the number sites with voles (Vole) and the number of sites where no voles were detected (None). The model indicates that voles were found in patch sizes > 0.49 ha (Area) and with a percent cover of smooth cordgrass (*Spartina*, *Spartina alterniflora*) between 16.75% and 43.61%.

Discussion

Northern populations of meadow voles appear to move readily in and out of salt marshes (Howell 1984), but FSMVs have never been found outside of the Big Bend salt marsh. This vast wetland is difficult to actively sample for rodents, but by focusing on a 75 km strip of coastline, we created a landscape model that narrowed the area of potential habitat down to 264 ha. With 22% predictive accuracy, this landscape-level habitat model certainly can be improved; however, with only 3 known locations prior to this study, this model will greatly enhance efforts to find, research, and conserve FSMVs.

Considering the limited area identified by our landscape-level habitat model (Fig. 1), it may be possible to extend the model north and south of our study area to find more potential FSMV habitat. Our visual and field inspections, however, suggest dwarf smooth cordgrass and saltgrass communities

Table 1.—A comparison of models to explain Florida salt mash vole (*Microtus pennsylvanicus dukecampbelli*) activity in different vegetation communities on the west coast of Florida from August to September 2013. Four models are compared: 1) *Null*, 2) activity differences in both communities (dwarf smooth cordgrass/saltgrass and black needlerush) and on ecotone (*Edge*), 3) activity changed continuously across the gradient (*Gradient*), and 4) activity in the dwarf smooth cordgrass/saltgrass combined with the ecotone and activity in the black needlerush (*Edge and Cordgrass*). Models are compared on 5 parameters: (K), −2 log likelihoods (−2lnL), Akaike Information Criterion corrected for small sample size (AICc), change in AICc (ΔAICc), and AICc weights for models of vole activity.

Model	K	−2lnL	AICc	ΔAICc	AICc weights
Edge and Cordgrass	5	216.555	443.9	0	0.404246
Gradient	5	217.083	445.0	1.1	0.23323
Null	4	218.256	445.0	1.1	0.230618
Edge	6	216.477	446.1	2.2	0.131906

occurred rarely outside our study area. Our landscape model did not identify FSMV habitat at the northern extent of our study area that borders the Suwannee River (Fig. 1). This may be due to changes in vegetation composition from the influx of freshwater from the Suwannee River or because the energy of the coastline changes from "zero" to low tidal energy (Tanner 1960). To the south of our study area, mangroves become more frequent at the seaward edge of the marsh, decreasing the area of open marsh available to FSMVs. Our texture-based model was very specific to the dwarf smooth cordgrass and saltgrass communities and is unlikely to identify areas with different structural composition. Future sampling efforts to the north and south of our study area should identify and trap for FSMVs in thick vegetation with saltgrass to establish the presence or absence of FSMV in different vegetation communities.

Within patches of potential habitat (Fig. 1), FSMVs appeared to be selective. FSMVs selected the larger patches (> 0.49 ha) that only accounted for 35% of the potential habitat patches identified in the landscape model (Fig. 2). This may be the minimum area necessary for viable FSMV populations. Densities for FSMV populations have not been estimated but are likely considerably less (Hotaling et al. 2010; Austin et al. 2014) than the 70 individuals per hectare documented for meadow voles in saltmarshes in Virginia (Bloch and Rose 2005). Larger patches also may be advantageous for higher rates of colonization and lower localized extinction within a meta-population dynamic (Hanski 1994). Preliminary molecular analysis suggests genetic separation among subpopulations, indicative of a meta-population (Austin et al. 2014).

As with previous research conducted on FSMVs, we found they were associated with saltgrass (Woods et al. 1982; Hotaling et al. 2010). However, instead of finding that FSMVs avoided lower and wetter areas with smooth cordgrass (Woods et al. 1982), we only found voles in patches of habitat with at least some (16.75–43.61%) dwarf smooth cordgrass. These areas were most common in the lower elevations of the salt marsh and frequently were inundated with tides. In northern salt marshes, the diet of meadow voles is dominated by saltgrass (*Distichlis* sp.) and cordgrass (*Spartina* sp.—Howell 1984), but the advantage of this unique mix of species for FSMVs is unclear. FSMVs may be inhabiting these areas because of the height of the vegetation. The lower regions of the salt marsh where this combination of plants occurs have consistently taller and thicker vegetation than the higher and drier regions of the marsh where saltgrass occurs without smooth cordgrass (Montague and Wiegert 1990). Meadow voles have been shown to occur in higher densities and have higher survival in thick tall grass in both salt marsh (Adler and Wilson 1989; Bloch and Rose 2005) and prairie vegetation (Peles and Barrett 1996). We hypothesize that the taller/thicker vegetation at lower elevations may provide shelter and favorable building materials, allowing voles to create their network of tunnels in the vegetation (Madison 1980). The wetter environment at lower elevations additionally may help buffer FSMVs from potentially hotter and drier conditions at higher elevations in the marsh. Meadow voles have shown the ability to reduce water loss by creating humid microclimates under mats of grass (Howell 1984). We suggest that previous descriptions of FSMV habitat at higher elevations in the marsh (with shorter saltgrass) may represent marginal habitat that voles use only when population densities are high in areas with thicker cover (Adler and Wilson 1989). This might explain the low numbers and ephemeral nature of FSMV populations in these areas (Hotaling et al. 2010).

We found that vole activity within the marsh decreased to low levels outside of patches of dwarf smooth cordgrass and saltgrass vegetation. FSMVs low level usage of areas of black needlerush might increase the overall extent of FSMV occurrence, but it has been suggested that black needlerush stems are a marginal food source for voles (Woods et al. 1982). Accordingly, it will be necessary to determine if FSMVs can persist without access to dwarf smooth cordgrass and saltgrass and if the voles using needlerush vegetation show reduced fitness, suggestive of an ecological sink.

Using a suite of modern technologies (i.e., remote sensing, camera trapping, machine learning) and targeted field work, we were able to drastically increase our knowledge of what is most likely the least understood endangered terrestrial mammal in the United States. Using spectral and texture characteristics from aerial imagery, we were able to use limited data to generate a map of potential habitat patches. Within these potential habitats, we used passive camera traps to validate our model, study patch habitat occupancy, and test our assumptions. Only recently have camera traps been used to study rodents; they have a number of advantages including reduced trapping related deaths, reduced effort in difficult environments, and multiple nightly detections at each trap (McCleery et al. 2014). Finally, we used a machine learning approach that allowed us to detect nonlinear patterns of patch characteristics from sparse data.

Our ongoing conservation crisis necessitates that researchers and managers rapidly obtain information on many of the planet's cryptic and poorly understand mammals. We believe our hierarchical approach to studying FSMVs may be adapted to other species with similar information needs. This approach transformed limited data into necessary information on distribution and environmental relationships that are needed for conservation. Now that we have some basic information about FSMVs, we can begin to address questions that ultimately will help ensure the persistence of this endangered species, such as: 1) what limits the activity of FSMVs in black needlerush, 2) how much movement is there among patches of dwarf smooth cordgrass and saltgrass vegetation, 3) are there management actions that can enhance or create vegetation communities used by FSMVs, and 4) how do voles persist in the marsh after storm surges and tidal events?

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