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A Status and Distribution of the Florida Scrub Lizard (*Sceloporus woodi*)

Kevin M. Enge[1,3], Brett Tornwall[1,2], and Brittany Bankovich[1]

[1]*Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 1105 Southwest Williston Road, Gainesville, Florida 32601, USA*
[2]*Children's Oncology Group and Department of Biostatistics, Colleges of Medicine, Public Health and Health Professions, University of Florida, 6011 Northwest 1st Place, Gainesville, Florida 32607, USA*
[3]*Corresponding author, e-mail: Kevin.Enge@myfwc.com*

Abstract.—**To document the current distribution of the Florida Scrub Lizard (*Sceloporus woodi*), the lead author walked 541 km of barren, sandy areas April-November 2016–2017 searching for lizards, replicating methodology he used during a 1986 survey. We detected *S. woodi* in 52.0% of 402 interior ridge sites in six counties, 24.1% of 224 Atlantic coast sites in five counties, and none of 14 southwestern Gulf coast sites in two counties. Occupancy modeling yielded detection probabilities of 0.76 ± 0.075 (95% Confidence Interval) and 0.79 ± 0.060 for Atlantic coast and interior ridge sites, respectively. The mean occupancy probability was 0.39 for Atlantic coast sites and 0.80 for interior ridge sites, with occupancy probability increasing with site patch size. Since 1994, greater habitat loss occurred in Atlantic coast localities than in interior ridge localities, with 30.3% of 33 Atlantic coast localities and 8.5% of 118 interior ridge localities with < 200 ha of suitable habitat experiencing ≥ 50% habitat loss. Populations on interior ridges were more likely to persist in smaller habitat patches than along the Atlantic coast, where 15 conservation lands have *S. woodi* populations. Populations appear to be secure in the interior ridge evolutionarily significant unit (ESU) on the Lake Wales and Bombing Range ridges. The Gulf coast ESU is apparently extinct, and our results suggest that the Atlantic coast ESU may warrant federal listing as Threatened because its range has contracted 77 km northward in the past 30 y.**

Key Words.—conservation; habitat loss; occupancy modeling; patch size; reptile; survey

Introduction

In 2012, the U.S. Fish and Wildlife Service was petitioned to list the Florida Scrub Lizard (*Sceloporus woodi*) under the Endangered Species Act, primarily because its naturally fragmented scrub habitat has been significantly fragmented by agricultural (primarily citrus) and urban development (Adkins Giese et al. 2012). This endemic Florida, USA, species occurred historically in 16 counties in three disjunct areas: interior ridges (Mount Dora, Winter Haven, Bombing Range, and Lake Wales ridges) from Putnam County to Highlands County, Atlantic Coastal Ridge from Brevard County to northern Miami-Dade County, and the southwestern Gulf coast in Lee and Collier counties (Fig. 1). Morphological analyses along with paleogeography suggest that *S. woodi* evolved on the Lake Wales Ridge in the Pliocene and dispersed northward in the early Pleistocene, later dispersing in the late Pleistocene from Ocala National Forest on the Mount Dora Ridge to the Atlantic coast and from the southern Lake Wales Ridge to the Gulf coast (Jackson 1973). Molecular analyses suggest that some populations on the Lake Wales Ridge have persisted in isolation for > 1 million y (Clark et al. 1999). Populations occupying different major scrub archipelagos differ by 3–10% and likely qualify as evolutionarily significant units (Branch et al. 2003).

Sceloporus woodi inhabits xeric upland habitats, primarily ones with open, sandy areas (Fig. 2) near trees or shrub clumps that provide escape cover, shade, and occasionally perch sites. Scrub is the primary habitat occupied, but adjacent sandhill, scrubby flatwoods, and young, frequently disked citrus groves may be used (Jackson 1973; Lee 1974; Enge et al. 1986). Scrub communities occur on sand ridges along former shorelines and are characterized by very well-drained, nutrient-poor soils, a relatively open canopy, an evergreen shrub understory, and sparse ground cover. Scrub habitat typically burns catastrophically only once every 5–70 y, typically killing Sand Pines (*Pinus clausa*) and Florida Rosemary (*Ceratiola ericoides*; Menges 2007; Florida Natural Areas Inventory 2010). Scrub oaks (*Quercus chapmanii*, *Q. geminata*, *Q. myrtifolia*) and most other shrubs regenerate by sprouting from root-shoots after fire, often forming low, dense clumps that provide shade and escape cover for *S. woodi* in the barren, burned landscape. The prolonged absence of fire in scrub may result in a xeric hammock or dense Sand Pine Forest whose closed canopy and litter layer are unfavorable for *S. woodi* populations (Greenberg et al. 1994; Tiebout

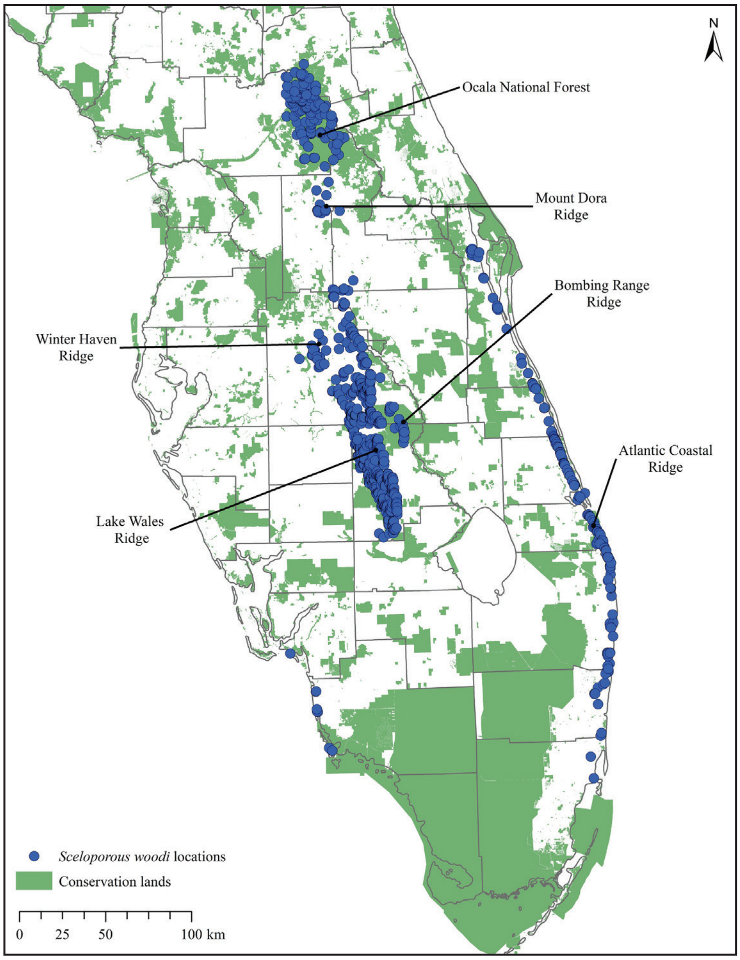


Figure 1. All records of the Florida Scrub Lizard (*Sceloporus woodi*) from 1919 to 2017 in Florida, USA, with inhabited ridges labeled. We did not survey Ocala National Forest.

and Anderson 2001), which can persist only if open, disturbed areas or *C. ericoides* are present (Enge et al. 1986; Ashton and Knipps 2011). In rosemary scrub, the extensive barren sand after fire typically declines to 30–40% or more after about 5 y and remains so for at least 30 y (Hawkes and Menges 1996; Ashton and Knipps 2011; Fig. 3). Leachates of the allelopathic *C. ericoides* inhibit germination of other plant species (Hewitt and Menges 2008), but fruticose ground lichens (*Cladonia* spp. and *Cladina* spp.) and Sand Spikemoss (*Selaginella arenicola*) may form dense carpets on sand patches in rosemary scrub by about 12 y after fire (Johnson and Abrahamson 1990; Menges and Kohfeldt 1995). Thick clumps of lichens reduce recruitment of herbs (Hawkes and Menges 2003) but also inhibit the mobility and foraging of S. woodi (Fig. 3), possibly resulting in population declines (McCoy et al. 2004).

Scrubby flatwoods have an open canopy of Longleaf Pine (*P. palustris*) and/or Slash Pine (*P. elliottii*), a shrubby understory, and a denser ground cover of forbs and grasses than in scrub. Sandhill is characterized by an open Longleaf Pine canopy, a sparse midstory of Turkey Oak (*Q. laevis*), and a moderate to dense ground cover of grasses, herbs, and low shrubs. Sceloporus woodi populations can inhabit scrubby flatwoods and sandhill if disturbed areas of bare sand are present or sterile soils or frequent fires reduce the grassy ground cover (Jackson 1973; Fabry 2007; Kaunert and McBrayer 2015). The

Figure 2. Male (left) and female (right) Florida Scrub Lizard (*Sceloporus woodi*) from St. Lucie County, Florida, USA. (Photographed by Kevin Enge).

Figure 3. (A) Allelopathic Florida Rosemary (*Ceratiola ericoides*) maintains bare, sandy areas important to the survival of the Florida Scrub Lizard (*Sceloporus woodi*) in this mature scrub in Highlands County, Florida, USA. (B) A dense carpet of ground lichens and Sand Spike-moss (*Selaginella arenicola*), which is detrimental to population persistence of *S. woodi*, at one of only two remaining occupied sites on the Winter Haven Ridge in Polk County, Florida, USA. (Photographed by Kevin Enge).

natural fire return interval of sandhill is 1–3 y and of scrubby flatwoods is typically 5–8 y but may be up to 15 y (Florida Natural Areas Inventory 2010). In scrubby flatwoods, the amount of barren sand typically declines from about 65% immediately after fire to < 10% within 5 y and then stabilizes at about 10% in the continued absence of fire (Young and Menges 1999).

Enge et al. (1986) surveyed 529 sites in 15 counties and detected *S. woodi* in 270 sites in 12 counties. They recommended not federally listing *S. woodi* as Threatened, despite the loss of most historically occupied sites in Lake County (except in Ocala National Forest) and northern Polk County and the probable extirpation of Gulf coast populations. We surveyed these sites plus other potential sites 30 y later using the same methodology to determine if the distribution of *S. woodi* has changed significantly and whether the species now warrants federal listing.

Materials and Methods

***Study approach*.**—We conducted visual encounter surveys for *S. woodi* using the same methods and observer as Enge et al. (1986). The original survey was conducted from 8 April to 5 August and on 11 November 1986. We surveyed again 5 May to 12 July 2016, 12 September to 11 November 2016, 20 March to 24 August 2017, and 10 October to 1 November 2017. We typically avoided surveying during the hottest times of the year when lizards were difficult to detect except in the morning and early evening. The emphasis of the 1986 survey was to detect the presence of *S. woodi* at as many localities as possible, and time constraints typically prevented resurveys of a locality where *S. woodi* was not detected. A locality is a discrete habitat patch with little or no suspected *S. woodi* exchange because of likely barriers to dispersal such as major roads, streams, some railroad tracks, and unsuitable habitat. Because of high habitat specificity and limited dispersal ability, *Sceloporus woodi* seldom disperse > 200 m to new localities when their habitat becomes unsuitable, and their maximum dispersal distance is 750 m (Tiebout and Anderson 1997; Hokit et al. 1999). In some cases, we surveyed multiple sites in localities with extensive habitat.

Our study had an occupancy modeling component, so we resurveyed many localities, including those where *S. woodi* was detected during a prior survey. We tried to survey a site for 10 min, whereas the 1986 study often terminated the survey once a lizard was detected. The 1986 study surveyed Ocala National Forest (Lake, Marion, and Putnam counties, Florida, USA), but we opted not to survey this protected area, which still contains extensive suitable habitat and widespread *S. woodi* populations (Orton 2017). Unlike the 1986 survey, we surveyed Jonathan Dickinson State Park, which contains extensive suitable habitat and widespread *S. woodi* populations. Some localities with known *S. woodi* populations were not surveyed in 1986 because of inaccessibility or other reasons. To look at changes in distribution since approximately 1986, we combined all sites with *S. woodi* records from 1983 through 1990 into one time period that included scrub surveys conducted by Christman (1988), Mushinsky and McCoy (1995), and Florida Natural Areas Inventory (FNAI). We used remote sensing to determine which of about 200 sites where *S. woodi* was recorded during surveys in 1983–1990 did not need to be searched because suitable habitat no longer existed. We considered populations to be extinct in these sites.

We were also interested in compiling a complete picture of current *S. woodi* distribution and did not confine our surveys to known sites with *S. woodi* populations. We used a GIS landcover layer and Google Earth imagery to identify additional areas with barren, sandy microhabitats in scrub, scrubby flatwoods, or sandhill, and we discovered some smaller areas while driving.

Some sites with suspected *S. woodi* populations could not be surveyed because they were inaccessible, often on posted private property. Whenever possible, we surveyed sites on posted private property by walking the fence line along the public right-of-way, but this habitat was often suboptimal.

The lead author walked bare, sandy areas in appropriate xeric habitats (i.e., scrub, sandhill, xeric hammock, scrubby flatwoods, and ruderal) and recorded the number of *S. woodi* observed, survey time, elapsed time before the first *S. woodi* was sighted, distance walked as determined by a track log recorded with a Garmin GPSMAP® 64st unit (Garmin International, Inc., Olathe, Kansas, USA), and environmental variables (temperature, sky conditions, wind). During the first visit to a site, the surveyor recorded the predominant sandy microhabitat searched along with habitat type, predominant canopy and shrub species, average shrub height, and percentage coverage of canopy, shrubs, ground cover, litter, and bare sand. We classified habitats as ruderal if they had been cleared in the past or had > 50% bare sand because of heavy off-road vehicle (ORV) use. Sandy microhabitats were grouped into (1) roads; (2) firebreaks, fence lines, and powerlines; (3) trails; (4) ORV areas; (5) clearings; (6) road shoulders; and (7) natural sand patches. The ORV areas were paths created by frequent recreational ORV traffic and large, denuded areas from heavy ORV use. Paths created by ORVs and trails were often sinuous, but the former tended to be wider and sandier with better visibility. For sites with multiple microhabitat types, we identified the predominant microhabitat searched or the microhabitat where the most *S. woodi* were observed. Sandy microhabitats searched in occupied Atlantic coast sites were primarily roads, trails, clearings, and ORV areas, whereas those in occupied interior ridge sites were primarily roads, ORV areas, firebreaks, road shoulders, and clearings. Roads and trails were mostly on conservation lands, whereas clearings and ORV areas were mostly on private lands. We ranked sites as having good, fair, poor, or unsuitable habitat for *S. woodi*. Good habitat had a mostly open canopy and extensive areas of bare sand adjacent to suitable escape cover. Fair habitat had some bare sand adjacent to suitable escape cover (e.g., typical scrubby flatwoods). Poor habitat had little or no bare sand adjacent to escape cover but had xeric soils (e.g., xeric hammock). Unsuitable habitat lacked xeric soils or was completely developed or overgrown.

We surveyed between 0800 and 1900 provided the air temperature was at least 20° C. Surveys lasted 1–26 min; the target time was 10 min, which was the elapsed time for 61.5% of 231 successful surveys (i.e., *S. woodi* was detected) of interior ridge sites and 73.8% of 107 successful surveys of Atlantic coast sites. We terminated surveys earlier than 10 min if all suitable habitat was searched. We surveyed > 15 min mostly at historical sites with suitable habitat where *S. woodi* was scarce or absent or at sites with long loop trails that took longer to walk. Historical sites are ones where *S. woodi* were detected during previous surveys. On sites with firm sand, about 700 m could be walked in 10 min if time was not spent stopping to search for and identify lizards that were heard or only briefly seen. We typically surveyed sites only once if they had poor habitat, were difficult to access, required staff accompaniment, or were outside the known range of the species.

We typically surveyed Atlantic coast sites with fair or good habitat three to four times, regardless of whether *S. woodi* was detected on previous visits. We surveyed 96 Atlantic coast sites once, 14 sites twice, 84 sites three times, 31 sites four times, and six historical sites in Palm Beach County five times. Because of the large number of interior ridge sites identified for surveys (n = 398), we typically did not resurvey sites if *S. woodi* was detected during the first visit. We surveyed 254 interior ridge sites once, 63 sites twice, 72 sites three times, and 11 sites four times. We surveyed the four most suitable Gulf coast sites four times. Single, unsuccessful surveys were conducted in 26.1% of interior ridge sites, 36.2% of Atlantic coast sites, and 57.1% of Gulf coast sites. Many of these sites had poor habitat or were outside the known range of the species. We considered sites in which we did not detect *S. woodi* during at least two surveys to be unoccupied, but *S. woodi* could have been present at these sites, particularly those not included in occupancy modeling because of insufficient survey times.

Occupancy modeling.—We used Occupancy Modeling to estimate survey detection probability, occupancy probability, and variables affecting survey detection and site occupancy. Detection probability is the probability of detecting at least one *S. woodi* in an occupied site, and occupancy probability is the probability that a site contains *S. woodi*. The minimum survey time for an interior ridge site to be included in the occupancy model was 3.5 min, because a mean of 2.7 min was required to detect *S. woodi*. For Atlantic coast sites, the minimum survey time for inclusion was 4 min, because a mean of 3.2 min was required to detect *S. woodi*. We surveyed too few Gulf Coast sites to use Occupancy Modeling.

We implemented Occupancy Models using the unmarked package (Fiske and Chandler 2011) in R version 3.3.3 (R Core Team 2017). We modeled Atlantic coast and interior ridge populations separately using a single-season occupancy model implemented via the occu function (MacKenzie et al. 2002). We standardized all continuous variables to mean zero and unit variance using the decostand function with the standardize method in the Vegan R package to aid in model convergence (Oksanen et al. 2017). We visually inspected for collinearity; none were correlated enough (all $r \leq 0.7$) to warrant exclusion.

We evaluated each model set using Akaike's Information Criterion (AIC), the difference between the model AIC and the lowest AIC value for the model set (ΔAIC), and the Akaike weight to determine the amount of evidence for each model (Burnham and Anderson 2002) and compared against a null model with no covariates.

For both interior ridge and Atlantic coast sites, detection covariates included search time, time of day, cloud cover, ambient air temperature, and whether the sampling event occurred before or after the first appearance of hatchlings (approximately 20 June). Females lay two to four clutches annually with two to eight (usually four to five) eggs per clutch, and hatchlings appear from June through early November (Jackson and Telford 1974; McCoy et al. 2004). One third of *S. woodi* observed after 20 June were young-of-year. Occupancy covariates were patch size, habitat type, percentage bare sand, percentage shrub cover, percentage canopy closure, sandy microhabitat searched, and habitat type. We visually estimated percentage bare sand, litter, and vegetative ground cover, but we included only percentage bare sand in the model because this covariate was considered the most important to *S. woodi*. We divided percentage shrub cover and percentage canopy closure into the following percentage categories: 0–5, 6–25, 26–50, 51–75, and 76–100%. We included distance to the nearest known occupied patch as an occupancy covariate for Atlantic coast sites, but we did not calculate distances between interior ridge sites because many patches could not be surveyed because they were on private land and/or far from public roads. We easily calculated distances between Atlantic coast scrub patches because of their linear arrangement and we could survey most sites because they were accessible and publicly owned.

We then used the predict function to generate graphs displaying the effect of each covariate on either abundance or detection for both Atlantic and interior ridge populations. When generating prediction intervals for each covariate, we chose mean values of the other covariates to use in the model. For categorical variables, we selected the most common category.

Spatial analyses and mapping.—We determined patch size and distance to the nearest known occupied patch (i.e., locality) using Google Earth Pro (Google, Inc., Mountain View, California, USA). The closest patch boundaries were used when measuring distances. We determined patch size by drawing polygons around suitable habitat. Patch boundaries consisted of aforementioned barriers to lizard dispersal. We calculated the percentage habitat loss for each habitat patch by drawing polygons around 1994/1995 imagery (the earliest available using the timeline feature in Google Earth Pro) and comparing it with 2017 imagery. We could determine percentage habitat loss accurately since 1994 only for discrete, mostly homogeneous habitat patches < 200 ha in size. Larger habitat patches typically contain a mosaic of habitat types, some of which might represent barriers to lizard dispersal between populations and occur on conservation lands that have experienced relatively little habitat loss. Fire exclusion and urban, residential, or agricultural development sometimes isolate patches of suitable habitat from the surrounding landscape matrix, but intervening poor habitats may not represent barriers to dispersing lizards. We designated localities as fragmented if they were situated in partially developed subdivisions or were heterogeneous areas with multiple xeric upland patches. In fragmented habitats, we used 2017 imagery to calculate the size of the suitable habitat patch that was surveyed, and we used 1994/1995 imagery to calculate the size of nearby suitable habitat patches to which it was formerly connected. We did not, however, calculate percentage habitat loss in fragmented habitats because nearby disconnected habitats could serve as sources of recolonization. We also did not determine the size of xeric habitat patches > 200 ha, which often contain a mosaic of xeric habitats of varying suitability to *S. woodi*. We used Google Earth imagery to assess the habitat suitability of inaccessible historical sites.

We depicted our survey results by mapping sites with extant *S. woodi* populations, sites with apparently extinct populations (includes historical sites with unsuitable habitat), and sites with suitable habitat but no *S. woodi* detections (Figs. 4 and 5). We surveyed some sites outside the known range of the species based on erroneous reports in databases or misidentified museum specimens. We did not map records within the same locality that were < 500 m apart. We mapped all museum and FNAI records but typically omitted a record with imprecise locality information (true of many records before the advent of GPS), unless it represented a significant historical record.

Results

Distribution.—The lead author walked 541 km while surveying 402 sites in six counties on the interior ridges, 224 sites in five counties on the Atlantic coast, and 14 sites in two counties on the southwestern Gulf coast. We did not survey 182 potential *S. woodi* localities identified using Google Earth imagery because ground-truthing revealed them to be inaccessible or unsuitable. On the Atlantic coast, we detected *S. woodi* in 21.2% of 52 historical (1983–1990) localities with suitable habitat (Table 1), excluding two localities in Martin County and one locality in Palm Beach County that could not be surveyed. For the remaining 38 historical localities in which we did not detect the species, 29.5% had fair habitat, 21.3% had poor habitat, and 24.6% had unsuitable habitat. We detected *S. woodi* in 17.5% of 166 new sites surveyed (Table 1), including eight conservation lands

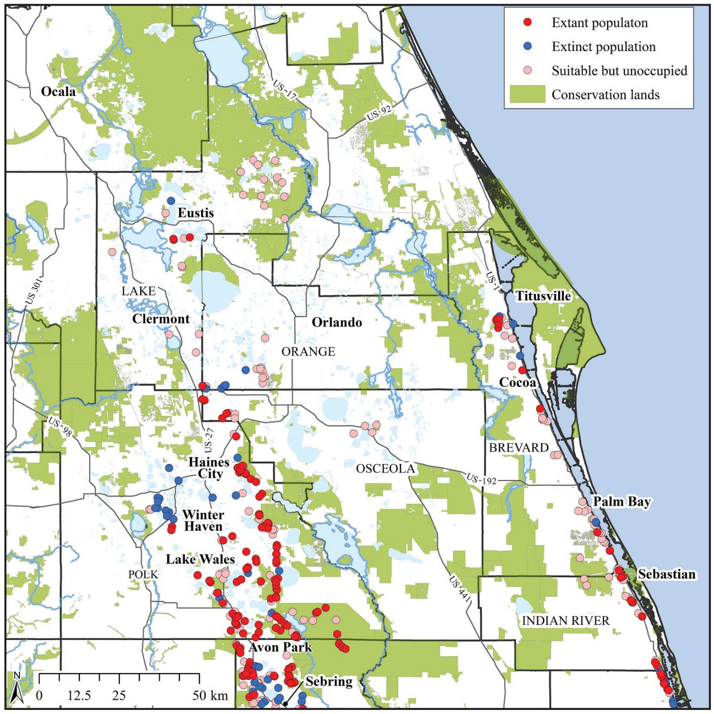


Figure 4. Results of 2016–2017 surveys for the Florida Scrub Lizard (*Sceloporus woodi*) in the northern extent of its range in Florida, USA, showing sites with extant populations, sites with apparently extinct populations, and sites with suitable habitat but no *S. woodi* detections.

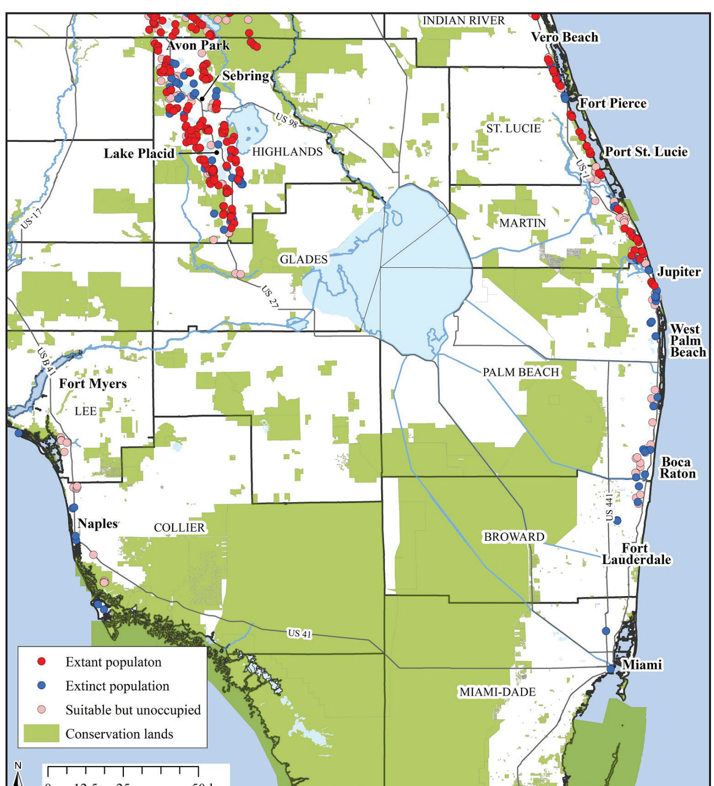


Figure 5. Results of 2016–2017 surveys for the Florida Scrub Lizard (*Sceloporus woodi*) in the southern extent of its range in Florida, USA, showing sites with extant populations, sites with apparently extinct populations, and sites with suitable habitat but no *S. woodi* detections.

Table 1. Results of 2016–2017 surveys for the Florida Scrub Lizard (*Sceloporus woodi*) in historical (1983–1990) and new localities in various counties in Florida, USA. The unoccupied historical localities listed are only those that contain suitable habitat; some could not be surveyed and might still be occupied. Headings are number of historical localities (NHL), number of occupied historical localities (NOHL), number of unoccupied historical localities (NUHL), number of new localities surveyed (NNLS), and number of occupied new localities (NONL).

County	NHL	NOHL	NUHL	NNLS	NNOL
Brevard	9	1	3	49	5
Indian River	6	3	0	19	2
Saint Lucie	10	5	3	25	10
Martin	14	7	5	30	7
Palm Beach	13	1	7	30	1
Broward	4	0	2	10	0
Lake	2	2	0	32	2
Orange	4	0	0	20	1
Osceola	1	1	0	14	4
Polk	52	31	16	101	54
Highlands	89	44	26	133	80
Glades	0	0	0	2	0
Lee	0	0	0	5	0
Collier	1	0	0	9	0
Total	205	95	62	482	170

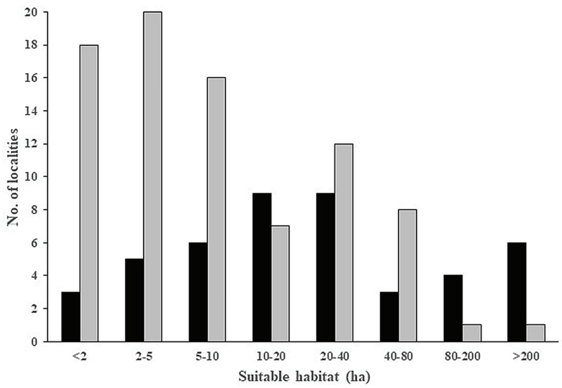
in five counties (Supplemental Information Table S1). Breaking down the Atlantic coast populations further, we observed *S. woodi* in only one of nine historical localities in Brevard County, one of 16 historical localities (two of 22 historical sites) in Palm Beach County, and none of four historical localities in Broward County (Table 1). All eight historical localities in Palm Beach County that still contain suitable habitat are on conservation lands.

On interior ridges, we detected *S. woodi* in 56.1% of 139 surveyed historical localities with suitable habitat (Table 1). For the remaining historical localities, 19.0% had fair habitat, 15.7% had poor habitat, and 13.2% had unsuitable habitat. We detected *S. woodi* in both historical localities in Lake County, one in Osceola County, none in Orange County, 31 in Polk County, and 44 in Highlands County (Table 1). We discovered two new sites in Lake County, one new site in Orange County, and four new sites in Osceola County (Table 4). *Sceloporus woodi* occur on at least 41 parcels of conservation land in Polk and Highlands counties but apparently no longer occur on both parcels of the Lake Blue Unit of Lake Wales Ridge Wildlife and Environmental Area (WEA), Polk County (Supplemental Information Table S1). We detected *S. woodi* in 46.7% of 302 new sites surveyed (Table 1). All occupied localities in Lake, Orange, and Osceola counties are on private property (Fig. 4).

Sites with suitable habitat were more likely to be occupied on the interior ridges than on the Atlantic coast. We detected *S. woodi* in 52.0% of 402 surveyed interior ridge sites but only in 24.1% of 224 surveyed Atlantic coast sites (Table 1). Sites with suitable habitat but no *S. woodi* detections comprised 21.9% of interior ridge sites, 39.7% of Atlantic coast sites, and 42.9% of Gulf coast sites (Figs. 4 and 5). We detected *S. woodi* in only two interior ridge localities and one Atlantic coast locality with poor habitat. We found *S. woodi* in only one locality in Orange County (Fig. 4) and no localities in Lee and Collier counties (Fig. 5; Table 1), despite the presence of suitable habitat. We failed to observe *S. woodi* during 21.1% of 421 surveys of occupied sites, and we observed only one *S. woodi* during 24.2% of surveys of occupied sites.

Patch size, isolation, and habitat loss.—The smallest isolated patch occupied by *S. woodi* was a 1.0 ha scrub in St. Lucie County that had decreased 60% in size since 1994. Only four of 29 patches of suitable habitat < 2 ha in size that were surveyed as part of Occupancy Modeling were occupied, plus two other patches that were not surveyed long enough to be included in the occupancy models. A 1.4 ha patch in Polk County and a 1.8 ha patch in St. Lucie County had not changed in size since 1994, indicating that a patch of suitable habitat as small as 1.4 ha can support a *S. woodi* population in the long term.

Surveys of comparable-sized patches of suitable habitat detected *S. woodi* in a greater proportion of interior ridge patches than in Atlantic coast patches. In Atlantic coast patches surveyed at least twice, we found *S. woodi* in 50.0% of 58 patches with ≥ 10 ha of suitable habitat but in only 20.6% of 68 patches with < 10 ha of suitable habitat (Fig. 6). We selected 10 ha because this apparently represented the minimum patch size that was often occupied by *S. woodi* along the Atlantic coast, but this threshold was smaller for interior ridge populations, where habitat patches 2–5 ha in size were twice as likely to be occupied as unoccupied (Fig. 6). On interior ridges, we found *S. woodi* in 84.2% of 183 patches with ≥ 10 ha of suitable habitat and in 59.7% of 72 patches with < 10 ha of suitable habitat (Fig. 6). Occupancy differed between patches larger or smaller than 10 ha in Atlantic coast (X^2 = 12.04, df = 1, P < 0.001) and interior ridge (X^2 = 17.55, df = 1, P < 0.001) localities. On the Atlantic coast, occupancy was 30.8% for 13 historical localities with < 10 ha of suitable habitat and 66.7% for 18 historical localities with > 10 ha of suitable habitat that were surveyed long enough to be included in occupancy models. Habitat fragmentation by urban development on the Atlantic coast has likely resulted in population extinctions, particularly in remnant habitat patches < 10 ha in size. Continued occupancy of historical localities differed depending on whether patch size was smaller or larger than 10 ha in Atlantic coast localities (X^2 = 3.89,



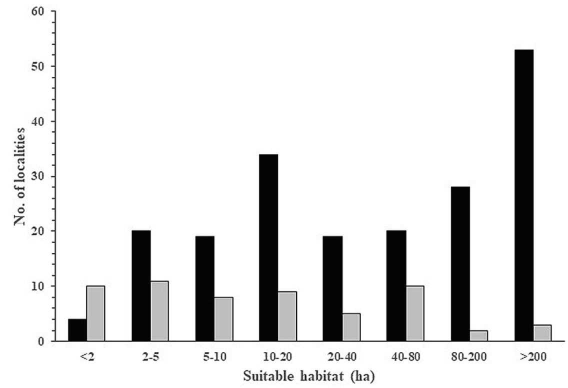


Figure 6. Patch sizes of Atlantic coast (left) and interior ridge (right) localities with suitable habitat that were occupied (black) and unoccupied (gray) by Florida Scrub Lizards (*Sceloporus woodi*) based upon 2016–2017 surveys in Florida, USA.

df = 1, $P = 0.048$) but not in interior ridge localities ($X^2 = 0.80$, df = 1, $P = 0.372$). On interior ridges, occupancy was 89.1% for 64 historical localities with < 10 ha of suitable habitat and 93.9% for 49 historical localities with ≥ 10 ha of suitable habitat.

Of 41 occupied localities along the Atlantic coast, 53.7% were ≤ 200 m from another occupied locality, and 92.7% were < 5 km from another occupied locality. The maximum distance from another occupied locality was 26.7 km for the Helen and Allan Cruikshank Sanctuary in Brevard County, where only one *S. woodi* was observed during three surveys totaling 30 min, despite good habitat. Historical localities in southern Palm Beach and Broward counties are now apparently unoccupied and situated ≥ 54 km from the nearest occupied locality in northern Palm Beach County (Fig. 5). The distance between the closest occupied localities on the Winter Haven and Lake Wales ridges in Polk County was 13.5 km (Fig. 4). The few remaining occupied localities near Tavares in Lake County were at least 45 km north of the nearest occupied locality in Orange County (Fig. 4), but unsurveyed and likely occupied sites to the north in Ocala National Forest were about half that distance (Fig. 1). Most occupied interior ridge localities were < 5 km from another occupied locality.

Of 33 Atlantic coast *S. woodi* localities with < 200 ha of suitable habitat, 21.2% experienced no habitat loss, 36.4% experienced < 20% habitat loss, and 30.3% experienced ≥ 50% habitat loss since 1994. We could not accurately determine patch size of four fragmented localities. The range of *S. woodi* along the Atlantic coast has contracted 77 km northward in the past 30 y; two conservation lands near Jupiter in northern Palm Beach County apparently now represent the southern extent of the range of the species (Fig. 5). Populations are apparently extinct in the four historical localities in Broward County, and the last record from Miami-Dade County was in 1966 (Indiana State University, Biological Sciences Department #1738). Conservation lands with habitat patches > 160 ha in size are Seabranch Preserve State Park and Jonathan Dickinson State Park in Martin County and Savannas Preserve State Park in St. Lucie and Martin counties. We observed *S. woodi* in four large habitat patches in Jonathan Dickinson State Park, which was not surveyed in 1986 because lizards were already known to be present.

Since 1994, occupied interior ridge localities tended to experience less habitat loss than occupied Atlantic coast localities. Of 118 interior ridge localities with < 200 ha of suitable habitat, 37.3% experienced no habitat loss, 75.4% experienced < 20% habitat loss, and 8.5% experienced ≥ 50% habitat loss since 1994. Habitat patches > 200 ha (n = 24) experienced little habitat loss. Most of the 16 occupied patches we classified as fragmented were in large, partially developed subdivisions in scrub habitat in Polk and Highlands counties. The only two remaining occupied localities on the Winter Haven Ridge in Polk County were on private property and in the Lake McLeod Unit of Lake Wales Ridge National Wildlife Refuge (NWR; Figs. 3 and 5). Historically, numerous *S. woodi* localities were present on the Mount Dora Ridge near Eustis and Tavares in Lake County (Fig. 1), but extensive development has eliminated all except four localities south of Lake Dora (Fig. 4), which have decreased 11–67% in size since 1994.

Occupancy models.—The best occupancy model for Atlantic coast *S. woodi* populations had search time and time of day as covariates for detection probability (Supplemental Information Table S2), and patch size, percentage bare sand, percentage shrub cover, microhabitat type, and distance to the nearest occupied patch as site covariates for occupancy probability (Supplemental Information Tables S3 and S4). Only the parameter estimate for patch size was significantly different from zero, however, indicating that occupancy probability increased with patch size. The null occupancy model reported a mean occupancy probability of 0.39 ±

0.08 (95% Confidence Interval).

The best occupancy model for interior ridge *S. woodi* populations had hatchling status and search time as covariates for detection probability (Supplemental Information Table S5), and patch size, percentage bare sand, percentage canopy cover, percentage shrub cover, and microhabitat type as site covariates for occupancy probability (Supplemental Information Tables S6 and S7). Only the detection covariates hatchling status and search time and the occupancy covariate patch size had parameter estimates significantly different from zero, indicating that detection probability increased after appearance of hatchlings and with search time. Occupancy probability increased with patch size. The null model with no covariates reported a mean occupancy probability of 0.80 ± 0.05.

Detection.—It took a mean of 3.2 ± 0.32 (standard error) min to detect the first *S. woodi* during successful surveys of 99 Atlantic coast sites and 2.7 ± 0.46 min during successful surveys of 228 interior ridge sites. The elapsed time when the first *S. woodi* was observed at a site ranged from 1 sec to 14 min. We observed the first *S. woodi* in ≤ 1 min for 36.4% and 36.0% of successful surveys of Atlantic coast and interior ridge sites, respectively. We observed a mean of 0.30 *S. woodi*/min during 1,268 min of surveys of occupied Atlantic coast sites, ranging from 0.11 lizards/min in Palm Beach County to 0.48 lizards/min in Martin County. We observed a mean of 0.34 *S. woodi*/min during 2,381 min of surveys of occupied interior ridge sites, ranging from 0.21 lizards/min in Lake County to 0.39 lizards/min in Osceola County. We observed the most *S. woodi* (37 in 10 min) in Seabranch Preserve State Park, Martin County.

The null occupancy model for Atlantic coast sites reported a detection probability of 0.76 ± 0.075 (95% CI), which means the probability of not detecting *S. woodi* in occupied sites visited three, four, and five times was 0.01, 0.003, and 0.0008, respectively. The null model with no covariates for interior ridge sites reported a detection probability of 0.79 ± 0.06, which means the probability of not detecting *S. woodi* in occupied sites that were visited three times was 0.009 and four times was 0.002. In occupied scrubs, the most commonly observed lizard species were *S. woodi* (n = 1,185), Eastern Six-lined Racerunner (*Aspidoscelis s. sexlineata*; n = 85), and Brown Anole (*Anolis sagrei*; n = 77). We failed to observe and identify 266 lizards heard rustling in leaves under shrubs or briefly glimpsed; we suspect most were *S. woodi* or *A. sagrei*.

Discussion

We conducted the most extensive survey ever for *S. woodi*, visiting all accessible sites with suitable habitat that were surveyed 30 y earlier by Enge et al. (1986), except for Ocala National Forest, plus additional sites with suitable habitat that we identified using remote sensing. We found that *S. woodi* populations persisted throughout the historical range of the species on the Lake Wales and Bombing Range ridges but had disappeared from much of the Winter Haven Ridge in Polk County and the Mount Dora Ridge in Lake County. During the past 30 y along the Atlantic coast, all populations apparently went extinct at the southern extent of the range of the species in highly urban Broward County and all except the northern 10% of Palm Beach County, and most populations disappeared at the northern extent of its range in Brevard County. Only one or two Gulf coast populations may have been extant 30 y ago, and these are now extinct. Because the lead author conducted all surveys in 1986 and 2016−2017, the variable of observer bias was eliminated when comparing occupancy trends of these two status assessments.

Detection and site occupancy.—According to null occupancy models, Atlantic coast and interior ridge sites had similar, high detection probabilities, but the influence of various site covariates differed between regions. Detection probability at interior ridge sites increased with search time and when hatchlings were potentially present. We observed recent hatchlings from 20 June into October. Young-of-year sometimes outnumbered adults during surveys and were often easier to identify because of their shorter flushing distance (Stiller 2011). When hatchlings emerge, densities may reach 124 lizards/ha, but survival rates are low and population size fluctuates (McCoy et al. 2004). Closed population models showed that *S. woodi* abundance varied substantially over time and between patches of scrub, with peak abundances generally occurring in early to mid-summer (Halstead 2008).

We opted to include the type of sand microhabitat searched when calculating the probability of occupancy but not detection. However, *S. woodi* tended to be visible from farther away and thus easier to identify before escaping into cover in large vs. small sand patches, straight (e.g., roads) vs. sinuous (e.g., trails) linear disturbances, and wide (e.g., roads) vs. narrow (e.g., firebreaks) linear disturbances. The extent that *S. woodi* used the open sandy areas searched depended partly upon the condition of the surrounding habitat. For example, if a sand road represented the only bare sand present in overgrown habitat, most *S. woodi* in the area would be found using the road. This would not be the case if the surrounding habitat had sand patches that could be used by *S. woodi*.

Occupancy modeling indicated that interior ridge sites with suitable habitat were more than twice as likely as Atlantic coast sites to have *S. woodi*, although occupancy probability for interior ridge and Atlantic coast sites both tended to increase with patch size. Given our high detection probabilities, visiting sites three to four times virtually guaranteed that *S. woodi* would be detected if they were present. Thus, our lack of success in finding *S. woodi* in Broward County and most of Palm Beach County suggests those populations are extirpated.

Excluding sites surveyed outside the known range of the species, Enge et al. (1986) observed *S. woodi* in 56.6% of 136 Atlantic coast sites in 1986, but in our recent surveys, we found them in only 31.7% of 164 sites with suitable habitat. The decline in site occupancy of Atlantic coast sites is probably even > 25%, because only four sites were surveyed more than once in 1986; additional surveys would likely have detected *S. woodi* in some sites designated unoccupied. In contrast, we surveyed many sites at least three times in 2016–2017; the probability of not detecting *S. woodi* at an occupied site after three surveys was only 1%. The decline in site occupancy was especially marked at the northern extent of the range of the species in Brevard County (42.1% to 16.7%) and at the southern extent in Palm Beach (67.7% to 8.8%), and Broward (27.3% to 0%) counties.

Site occupancy has apparently not declined in the past 30 y in interior ridge sites with suitable habitat. In 1986, *S. woodi* was observed in 46.7% of 261 interior ridge sites, excluding sites outside the known range and Lake County sites in or near Ocala National Forest. Our recent survey detected *S. woodi* in 65.5% of 319 interior ridge sites; our greater success was probably because we surveyed 145 sites more than once, whereas only six sites were surveyed more than once in 1986. The mean occupancy probability was even higher (0.80). Site occupancy may be higher now than 30 y ago because more sites are located on conservation lands with better habitat management.

***Population declines and extinctions*.**—We suspect the primary reasons for *S. woodi* population extinctions are habitat loss from land clearing and habitat degradation from ecological succession due to fire exclusion, deleterious land management practices, or invasion by exotic flora. Because suitable habitat along the Atlantic coast occurs in a narrow strip that ranges from a few hundred meters to a few kilometers wide, any development, major highway, or waterway that bisects this strip effectively fragments populations. In contrast, suitable habitat on the interior ridges occurs in a landscape matrix where xeric uplands naturally occurred as habitat fragments of various sizes. Interior ridge populations were more likely to persist in smaller habitat patches than Atlantic coast populations, possibly because dispersal was more likely among the numerous xeric upland habitat patches present in Polk and Highlands counties, which tended to be closer together and often separated by citrus groves, low-intensity urban development, or pine flatwoods.

Populations inhabiting small, isolated patches of xeric habitat are most threatened by stochastic events or poor habitat management. Smaller populations are more prone to extinction than large populations because of chance fluctuations in demographic and environmental processes (Richter-Dyn and Goel 1972; Goodman 1987). Patch size may directly influence habitat quality, individual fitness, demography, and consequently survival of local populations (Groombridge 1992; Thomas 1994). A *S. woodi* population in a small (0.75 ha) habitat fragment declined over a 3-y period because of a decline in survivorship of adult females (McCoy et al. 2004). Production of hatchlings, recruitment, survivorship, and lizard abundance were positively associated with habitat patches 2–6 ha in size (Hokit and Branch 2003). We found long-term persistence of *S. woodi* populations in habitat patches as small as 1.4 ha, but occupancy probability increased with patch size. Despite its vagility, *S. woodi* is a poor disperser and seldom recolonizes isolated habitat patches from nearby populations (Hokit et al. 1999). Habitat fragmentation and patch isolation probably contributed to extinction of *S. woodi* populations in Broward and Palm Beach counties.

Ecological succession in scrub typically leads to poor habitat conditions and declining *S. woodi* populations (Tiebout and Anderson 2001; Kaunert and McBrayer 2015). Fire is important in arresting ecological succession and creating the open conditions and bare, sandy areas preferred by *S. woodi*, but recently burned scrubs do not provide favorable conditions for *S. woodi* survival unless patches of unburned vegetation remain or until scrub oaks regenerate sufficiently to provide adequate shade and escape cover. Intense fires in small scrub sites could potentially eliminate *S. woodi* populations. Leaf litter, lichens, and coarse woody debris increase in the absence of fire in scrub, and the amount of open space decreases during the first 10 y after fire (Tiebout and Anderson 2001). In overgrown scrub, barren sandy areas may become restricted to the perimeter of the scrub or to linear anthropogenic disturbances, such as sand roads, where *S. woodi* are probably more susceptible to predation by birds, mammals, and snakes. Recreational ORV traffic often results in more extensive vegetative destruction and soil disturbance than other anthropogenic disturbances (e.g., sand nature trails, roads, and firebreaks) and may impact invertebrate prey populations and occasionally kill lizards, particularly slower and less wary young individuals. Mechanical treatment (e.g., roller-chopping or grinding) of all vegetation in an isolated scrub parcel prior to burning could extirpate a *S. woodi* population; the mulch layer produced does not allow lizards to effectively forage or maneuver until it burns or decomposes. A scrub does not become suitable for *S. woodi* until at least 2 y after roller-chopping (Kaunert and McBrayer 2015).

Predation or competition from nonnative wildlife species may contribute to *S. woodi* population extinction, particularly in small habitat patches. Predation by feral Cats (*Felis cattus*), particularly in small, urban scrub preserves, may contribute to population extinction. Nonnative *A. sagrei* might compete for food and perch sites with *S. woodi* but tend to have low densities in the open scrub habitats preferred by *S. woodi*. *Anolis sagrei* appeared to be particularly abundant at sites in heavily urbanized Palm Beach and Broward counties during the 1986 status survey, but *A. sagrei* now occurs throughout the range of *S. woodi*. The Northern Curly-tailed Lizard (*Leiochephalus carinatus*) is continuously distributed along the Atlantic coast in Palm Beach County and northern Broward County (Smith et al. 2004) and was observed in some scrub preserves. This nonnative species, which is substantially larger than *S. woodi*, could be a significant competitor or a predator of hatchlings.

Scrubs in Palm Beach and Broward counties appeared to have the heaviest invasion by exotic vegetation, which may have contributed to the decline or extirpation of *S. woodi* populations. Most of these invaders decrease the amount of sunlight reaching the ground, reducing thermoregulatory opportunities for *S. woodi*, and the extent of bare sand areas. Love Vine (*Cassytha filiformis*), a native parasitic plant, was particularly common in coastal scrubs south of Indian River County, where it often enshrouded shrubs and even trees. *Cassytha filiformis* has apparently proliferated at many sites during the past 30 years, possibly because of lack of fire. We never observed *S. woodi* in areas where mats of *C. filiformis* extended from woody vegetation onto much of the adjacent sand surface, potentially inhibiting mobility and foraging of lizards.

Anthropogenic disturbances that create open, sandy areas (e.g., roads, firebreaks, and trails) can allow *S. woodi* populations to persist in unburned scrub, sandhill, and even xeric hammock habitats, particularly on private lands lacking *Ceratiola ericoides* and other allelopathic plant species. In contrast, land clearing for developments or agriculture typically renders the habitat unsuitable for long-term survival of *S. woodi* populations. Recreational ORV use has maintained bare sandy areas and allowed *S. woodi* populations to persist, particularly on parcels of private land in interior ridge sandhill habitat and in Atlantic coast scrubs. Some ORV-disturbed sites remained relatively unchanged since the 1986 survey. Even when ORV disturbance has ceased because of fencing, the barren areas created may persist and remain favorable for *S. woodi* for decades.

Status.—Enge et al. (1986) recommended that *S. woodi* not be federally listed as Threatened, but subsequent population declines and extinctions in portions of the range of the species warrant a reassessment. For listing consideration under the U.S. Endangered Species Act, a species can be divided into distinct population segments, but these must be designated by the U.S. Fish and Wildlife Service. Instead, we are using evolutionarily significant units (ESU). We are considering the interior ridges as one ESU, although the Bombing Range Ridge and the central Lake Wales Ridge form one haplotype cluster, the southern Lake Wales Ridge forms another haplotype cluster, and populations on the Mount Dora Ridge are 4.4% divergent from the Lake Wales Ridge (Branch et al. 2003). Our survey results indicate that this ESU probably does not warrant federal listing, despite clearing of approximately 85% of scrub and sandhill habitats on the Lake Wales Ridge for citrus groves or subdivisions (Turner et al. 2006) and habitat degradation associated with lack of fire. Only one occupied locality is present in Orange County, only two occupied localities apparently remain on the Winter Haven Ridge in Polk County, and extensive development on the Mount Dora Ridge around Tavares in Lake County has eliminated most populations. *Sceloporus woodi* populations are present on at least 41 conservation lands in Polk and Highlands counties, however, where an aggressive government program of land-buying was initiated in 1990 on the Lake Wales Ridge because of the many imperiled, endemic species of plants and animals.

Scrub habitat along the Atlantic Coastal Ridge once formed a nearly continuous band from Brevard County to Broward County and extended as far south as northern Miami-Dade County. Atlantic coast populations are highly divergent (7.8–8.0%) from populations on the central ridges (Branch et al. 2003), and the Atlantic coast ESU probably warrants federal designation as Threatened because many formerly occupied sites have been developed or become degraded by ecological succession to closed-canopied habitats lacking bare, sandy areas. The narrow Atlantic Coastal Ridge is highly fragmented by urban and suburban development, and some occupied localities with *S. woodi* populations are owned by development companies. Despite purchases by the state or counties of some scrub sites since the 1986 status assessment, the occupied range of this ESU has contracted 77 km northward in the past 30 y. The species was last observed in Broward County about 1990, and populations disappeared from 15 of 16 historical localities and two additional conservation lands in Palm Beach County by the early 2000s according to database records and area biologists. The species was relatively common in Palm Beach County 30 y ago, as evidenced by Enge et al. (1986) finding it in 22 of 32 sites (16 occupied localities) during single surveys and observing a mean of 0.25 *S. woodi*/min. In contrast, we observed a mean of 0.11 *S. woodi*/min at the only two Palm Beach County localities with extant populations. Five historical localities in Palm Beach County have been developed, but most others still contain apparently suitable habitat in county-owned scrub preserves. Enge et al. (1986) observed a mean of only 0.04 *S. woodi*/min during 70 min of surveys in two occupied localities in Broward County, suggesting that populations were already in decline. Habitat fragmentation and isolation probably contributed to population declines and eventual extirpation in these two counties. Only 2% of scrub habitat remains in Broward County, and Palm Beach County has lost > 95% of its scrub habitat (Fernald 1989). Only one of eight historical localities in Brevard County, the northern extent of this ESU, still has an extant population. Despite suitable habitat in several preserves owned by Brevard County, we found only low-density populations in Valkaria Scrub Sanctuary and the Helen and Allan Cruikshank Sanctuary. The other known populations in Brevard County are on private land.

Populations of *S. woodi* in the southwestern Gulf coast ESU are apparently extinct. The population on Marco Island, Collier County, was extirpated in 1986 when the last scrub habitat was cleared (Enge et al. 1986). The small scrub has been developed where Branch et al. (2003) collected 11 genetic samples in the 1990s near Naples, Collier County. The only known site for *S. woodi* in Lee County was the northern end of Estero Island, where a specimen was collected in 1949 (UF #4086). Some suitable habitat remains along the Gulf coast, particularly in Railhead Scrub Preserve in North Naples, but we failed to detect the species during multiple visits to several potential sites in Lee and Collier counties.

Sceloporus woodi no longer occurs in four counties, and its continued existence on the Winter Haven Ridge, part of the Mount Dora Ridge, and the Lake Wales Ridge in Orange and Osceola counties is in doubt because all populations occur on private land. The purchase and proper management of occupied parcels in these areas would help preserve the present distribution and genetic diversity of the species. *Sceloporus woodi* is widely distributed and secure on the Lake Wales and Bombing Range ridges in Polk and Highlands counties. Populations on the narrow and highly fragmented Atlantic Coast Ridge are secure on several large conservation lands in St. Lucie and Martin counties, but populations are apparently not doing as well in Brevard, Indian River, and Palm Beach counties primarily because of smaller patch sizes and improper habitat management.

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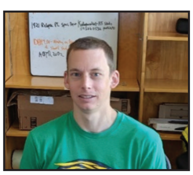
Kevin Enge received his B.S. in Wildlife and Biology from the University of Wisconsin -Stevens Point, USA, and M.S. in Wildlife Ecology from the University of Florida, Gainesville, USA. He has worked for the Florida Fish and Wildlife Conservation Commission since 1989 and is currently a Research Scientist in the Reptile and Amphibian Subsection of the Wildlife Research Section, where he primarily conducts herpetofaunal surveys. He coedited the 2019 book Amphibians and Reptiles of Florida and has authored over 130 papers. (Photographed by Bess Brown).



Brett Tornwall received his B.S. in Wildlife Ecology from the University of Florida, Gainesville, USA, M.S. in Biology from Appalachian State University, Boone, North Carolina, USA, and Ph.D. in Biology from Virginia Tech, Blacksburg, USA. He worked for the Florida Fish and Wildlife Conservation Commission as an American Alligator (*Alligator mississippiensis*) Technician and later as a Statistician. His research interests include dispersal and metacommunity theory. He is currently a Statistician with the Children's Oncology Group at the University of Florida. (Photographed by Noah Weller).

Brittany Bankovich received her B.S. in Biology from the University of Akron, Ohio, USA, and M.S. in Wildlife Ecology from the University of Florida, Gainesville, USA. She is a Geographic Information Systems Analyst with the Florida Fish and Wildlife Conservation Commission (Fish and Wildlife Research Institute, Center for Spatial Analysis). Her research interests include spatial ecology and remote sensing. (Photographed by Don Hardeman).