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Running Head – Population size of a translocated lizard

Title – Dispersal and population state of an endangered island lizard following a conservation translocation

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Abstract – Population size is widely used as a unit of ecological analysis, yet to estimate population size requires accounting for observed and latent heterogeneity influencing dispersion of individuals across landscapes. In newly established populations, such as when animals are translocated for conservation, dispersal and availability of resources influence patterns of abundance. We developed a process to estimate population size

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31 using N -mixture models and spatial models for newly established and dispersing
32 populations. We used our approach to estimate the population size of critically
33 endangered St. Croix ground lizards (*Ameiva polops*) five years after translocation of 57
34 individuals to Buck Island, an offshore island of St. Croix, United States Virgin Islands.
35 Estimates of population size incorporated abiotic variables, dispersal limits, and operative
36 environmental temperature available to the lizards to account for low species detection.
37 Operative environmental temperature and distance from the translocation site were
38 always important in fitting the N -mixture model indicating effects of dispersal and
39 species biology on estimates of population size. We found that the population is
40 increasing its range across the island by 5% to 10% every six months. We spatially
41 interpolated site-specific abundance from the N -mixture model to the entire island, and
42 we estimated 1,473 (95 % CI: 940-1802) St. Croix ground lizards on Buck Island in 2013
43 corresponding to survey results. This represents a 26-fold increase since the translocation.
44 We predicted the future dispersal of the lizards to all habitats on Buck Island, with the
45 potential for the population to increase by another five times in the future. Incorporating
46 biologically relevant covariates as explicit parameters in population models can improve
47 predictions of population size and the future spread of species introduced to new
48 localities.

49 **Keywords** – Population size, N -mixture models, dispersal, occupancy, operative
50 temperature, conservation introduction, *Ameiva polops*

51 **Introduction** –

52 Despite the natural utility of population size as a fundamental unit of ecological
53 analysis (Elton 1927, Joseph et al. 2006, Krebs 2014), estimating population size is
54 difficult. Abundance and detection of species vary with environmental heterogeneity, for
55 example as habitat transitions, species interact, and landscapes change (Meot et al. 1998,
56 Watson et al. 2004, Mackenzie et al. 2006, Rodda et al. 2015). Thus mathematical models
57 have been developed to account for biases created by abundance and detection
58 probability (Royle 2004, Royle and Dorazio 2008). One such tool is the N -mixture
59 model, which estimates mean abundance N of individuals by integrating observed data
60 over a random variable count model, for e.g., a Poisson or negative binomial distribution
61 (Kéry and Royle 2010, Knappe and Korner-Nievergelt 2016). Simultaneously, imperfect

62 detection p is modeled by integrating p as a prior binomial parameter (see more detailed
63 derivation of the general model in Royle, 2004). To date, N -mixture models have
64 described basic changes in populations varying along environmental and biological
65 gradients when detection is imperfect (Royle and Nichols 2003). For example, N -mixture
66 models have revealed effects of hiking trails on salamanders (Milanovich et al. 2014),
67 drought on alligators (Waddle et al. 2015), and localized competition between native and
68 invasive geckos (Buckland et al. 2014). In the present study, we integrated multiple
69 physiologically relevant covariates into an N -mixture modeling framework to account for
70 dispersal of individuals in a newly established population of the endangered St. Croix
71 ground lizard (*Ameiva polops*), five years after a conservation introduction (translocation
72 outside the native range; Ewen et al. 2012, Fitzgerald et al. 2015). The study provides
73 important insights about how relevant environmental variables that may influence
74 dispersal and how N -mixture models can be used to understand dispersal dynamics in
75 introduced populations. The approach can be useful for monitoring both planned
76 conservation translocations, and the spread of exotic species. While one of our goals was
77 to determine the population size of a rapidly spread endangered lizard, we also attempted
78 to tackle the difficult process of integrating biologically informed covariates into N -
79 mixture modeling processes. We developed a five-step process to account for relevant
80 species' biological traits that can be applied to dispersing populations when detection is
81 less than perfect.

82 Available habitat is a critical factor mediating the dispersal dynamics of new
83 populations, and of particular importance when identifying appropriate sites for
84 conservation introductions. Landscape configuration affects the distribution of
85 temperatures in microhabitats where ectothermic animals move, forage and interact
86 (Huey et al. 2009). Temperatures existing within available habitat are commonly
87 measured by a heat transfer metric called the operative environmental temperature. The
88 operative environmental temperature is an index of potential heat transfer between
89 ectotherms and their environment measured by thermometers that are calibrated to live,
90 individual animals or calculated with heat transfer equations (Dzialowski 2005). The
91 distribution of operative temperatures across a landscape can be thought of as a
92 physiological index for potential activity and habitat suitability, providing a biological

93 basis for understanding variation in the relative abundance of animals (Bakken and
94 Angilletta 2013, Sears and Angilletta 2015). In a modeling framework, operative
95 environmental temperature tests whether thermally available habitat affects latent
96 abundance and impacts on detection.

97 Because N -mixture models have the ability to test a range of environmental and
98 biological variables, they bring great potential to the challenges of monitoring spreading
99 populations (Mazzerolle et al. 2007). For both native species relocated for conservation
100 and non-native species introduced accidentally, initial locality is often known.
101 Spatiotemporal gradients, which characterize expanding populations as individuals
102 radiate from an introduction locality, last until an equilibrium state has been reached
103 across the available region (Bled et al. 2011). Incorporating dispersal gradients into an N -
104 mixture model explicitly allows estimation of the spread in addition to true abundance of
105 introduced species (Boulangéat et al. 2012). Dynamic occupancy models are emerging
106 using these techniques (Bastille-Rousseau et al. 2016). Historically, however, relative
107 abundance models, for e.g., autologistic and linear regressions, used a variety of simple
108 and complex distance metrics to address dispersal (Verboom et al. 1991). Commonly,
109 nearest-neighbor occupancy was quantified as a binary variable with accompanying data,
110 for example, Euclidean distance (Williams et al. 2008). By incorporating dispersal as a
111 covariate corrects the N -mixture model for effects of bias towards the introduction
112 locality. The expected result of including mechanisms to understand population
113 abundance is improved occupancy and abundance estimates (Joseph et al. 2009).

114 With the information to account for spatial heterogeneity and dispersal, a robust
115 number of surveys are completed to count *observed* abundance within sites (Mackenzie et
116 al. 2006). To arrive at *true* abundance within each site, we use the N -mixture model, to
117 represent the population state at the present time step. For established populations,
118 modeled abundance also represents the population state at the present time step. The
119 abundance model could also reflect abundance throughout its range, for example, the
120 range-wide abundance of Island Scrub-Jays across Santa Cruz Island, CA was generated
121 using N -mixture model parameters (Sillett et al. 2012). In the case of a new population
122 that is spreading, a dispersal-corrected N -mixture model could be fitted across the
123 landscape, but it would estimate the future, post-dispersal population state rather than the

124 present population state. We believe that a dispersal-corrected binomial N -mixture model
125 is useful in creating hypotheses for future occupancy and abundance of translocated
126 species and interpolation between sites can achieve that goal (Dickinson et al. 2001).

127 Our goal was to determine the population size of the endangered St. Croix ground
128 lizard, translocated in 2008 to an island refuge offshore of St. Croix, U.S. Virgin Islands
129 (Fitzgerald et al. 2015). In addition to providing important information on the population
130 state of the critically endangered St. Croix ground lizard, we provide a process to
131 estimate the population state of a dispersing population that has more general application
132 to the problem of estimating the abundance of introduced species while they are
133 spreading. For example our methodology may work to estimate population growth and
134 spread of invasive species (e.g., boas in Florida), and could have applicability to
135 estimating populations of animals carrying disease (e.g., salamander *Bsal*).

136 **Methods –**

137 *Study species*

138 The St. Croix ground lizard (*Ameiva polops* Cope 1863), endemic to St. Croix,
139 U.S. Virgin Islands was extirpated from the main island due to mongoose predation,
140 which became established on St. Croix in 1884 (Seaman and Randall 1962, Philibosian
141 and Ruibal 1971). Small populations of the St. Croix ground lizard persisted offshore of
142 St. Croix on 1.2 ha Protestant Cay and 5.2 ha Green Cay, and introduced to a 7.5 ha
143 dredge-spoil island Ruth Cay in 1990 (Hurtado et al. 2012). Fifty-seven animals from the
144 Green Cay population were introduced to 71 ha Buck Island in 2008 and began
145 reproducing almost immediately, and a new population was successfully established on
146 that island (Treglia and Fitzgerald 2011, Fitzgerald et al. 2015). Multiple population
147 surveys have taken place to assess the four populations since it was listed as Endangered
148 under the U.S. Endangered Species Act in 1977 (Appendix S1: Table S1).

149 The St. Croix ground lizard is a small, sexually dimorphic lizard that shuttles
150 between the sun and shade to thermoregulate in the middle of the day and is at other
151 times in one of many underground burrows (Fitzgerald et al. 2015). The maximum snout
152 to vent length of adult males is 95 mm and females reach 65 mm. These active-foraging
153 lizards inhabit relatively dry scrubland on Green Cay, sandy mangrove flats on Ruth Cay,
154 and semi-native landscaped gardens on Protestant Cay (Philibosian and Yntema 1976).

155 Previous habitat assessments indicate that the lizards prefer areas with deep leaf litter,
156 herbaceous ground cover, woody stems which may break up the soil and create space for
157 burrows, loose soils, and sun patches (Moser et al. 2010). Buck Island has undergone
158 forty years of native habitat restoration based on historic pollen records to restore
159 Caribbean coastal forest, scrubland, woodland, manchineel forest, and sandy beaches
160 (Moser et al. 2010, Witmer and Hillis-Starr 2002).

161 *Surveys*

162 We conducted surveys to quantify dispersal of the St. Croix ground lizard on
163 Buck Island in May 2013, May 2014, October 2014, May 2015, and October 2015 for a
164 total of five separate seasons. All 63 sites were surveyed five times during each season
165 using a visual encounter method, where surveys were terminated after 20 minutes (Rodda
166 et al. 2005). The sites were distributed throughout the entire island and randomly located
167 using ArcGis 10.1 (ESRI) stratified by habitat type (Moser et al. 2010). To ensure
168 independence of surveys, we constrained circular 40 m diameter sites (1260 m^2) to occur
169 at least 80 m apart based on information on the home range $\bar{x} = 190 \text{ m}^2$ of the animals
170 from the source population on Green Cay (Meier et al. 1993). Importantly, all surveys at
171 a site were completed within 3 days during a season to eliminate the potential for
172 migration of individuals between sites (Kendall 1999).

173 During the first season, in May 2013, six observers completed 192 additional
174 abundance surveys at 32 sites on the western half of the island, where we measured
175 dispersal and occupancy on Buck Island during the presence or absence surveys.
176 Individual observers conducted 20 min time-constrained searches for lizards. Each site
177 was surveyed 2 times on a given day, and each site was surveyed on three consecutive
178 days. The first observer walked around a marked circle with a radius of 8 m from the
179 center of the site (50.24 linear m), and a second observer walked around a marked circle
180 with a radius of 15 m from the center of the site (94.2 linear m). They walked in opposing
181 directions. The observers then switched radius and repeated the survey in the counter
182 direction without disclosing information on lizard sightings until the conclusion of all
183 three days. Each survey was used as an independent count to inform the final model.
184 Surveys began at 1130 h, 1230 h, or 1330 h and alternated so that observers surveyed

185 each site in each time period. The timeframe corresponds with the species' peak daily
186 activity from 1000 h to 1600 h (Wiley 1983, Meier et al. 1993).

187 *Covariates*

188 We selected macrohabitat and microhabitat features based on the known
189 associations of the species and included topography and operative environmental
190 temperatures as covariates. We measured microhabitat variables within 1 m² quadrats
191 placed in the four cardinal directions approximately 3 m from the center-point of each
192 site and averaged the four data points to acquire a single value in each microhabitat
193 category including: percent herbaceous ground cover on a Braun-Blanquet (1932) index,
194 the number of woody stems > 3 cm in diameter, and average leaf litter depth (cm) of four
195 random points. We calculated the Euclidean distance from the 2008 release area
196 (Fitzgerald et al. 2015) to the survey sites using ArcGis 10.1 (hereafter, distance-from-
197 release). We deployed temperature data-loggers to measure substrate temperature (HOBO
198 Pendant Temperature Logger, Onset Computer Corp, Bourne, MA, USA). We modeled
199 operative environmental temperature with copper models in the shape of lizards, with
200 heads, tails, and legs made from copper foil and tubing measuring 7 cm by 1 cm by 1 cm
201 painted grey (Dzialowski 2005). We placed an iButton[®] temperature logger inside the
202 lizard model to measure the operative temperature every ten minutes over all 3 days of
203 the survey period. We assigned the average and maximum temperature for the substrate
204 and operative temperature models as covariates in the hour we surveyed the site.

205 From 30 m² remotely sensed data, the elevation was extracted from a digital
206 elevation model (Gesch 2007). We indexed soil types as percent sand, clay, or water in
207 program R (Davis 2002, Debeaudette 2009). The land surface temperature and the
208 normalized difference vegetation index (NDVI) were derived from Landsat 8 following
209 Weng et al. (2004) and values from the NASA Landsat guide (USGS 2013) in R.

210 A Multiple Response Permutation Procedure (MRPP) analysis with a Sorensen
211 distance matrix was used to determine if the microhabitat variables we measured within
212 each site homogeneously represented the *a priori* habitat types (forest, woodland,
213 shrubland, manchineel, and beach) by repeatedly sorting the sites into the most
214 homogeneous groups. We used two-dimensional nonmetric multidimensional scaling
215 (NMDS) to visualize the habitat variables, and overlaid modeled abundance on the

216 ordinated sites for both the measured and raster variables. We created a convex hull
217 around the sites by habitat type. We reported the fit of the ordination to the observed data
218 matrix as stress, where stress < 0.2 indicated an appropriate fit (McCune et al. 2002).

219 *Lizard body temperature*

220 We caught and transported ten lizards from Buck Island to mainland St. Croix to
221 measure the preferred temperature and thermal tolerance of the lizards. Animals were
222 allowed to walk freely in a thermal gradient constructed from plywood measuring 4 feet
223 long by ½ foot wide by 3 feet tall. Temperatures in the gradient ranged from 20 °C to 60
224 °C. Cloacal temperatures of lizards were measured every ten minutes with a K-type
225 thermocouple and digital thermometer. When four consecutive temperature readings
226 within $\pm 1^\circ\text{C}$ were obtained from the subject we assumed the animal was
227 thermoregulating at its selected thermoregulatory temperature (T_{sel}). Thermal tolerance
228 breadth is a standard measure to determine the extreme temperature bounds where
229 animals retain homeostatic control (Hertz et al. 1993). Cold and heat tolerance trials for
230 each individual were taken after animals achieved their preferred body temperature for at
231 least one hour so that the magnitude of the temperature change did not confound the
232 temperatures at which individuals retained homeostatic control (Angilletta 2009). To
233 measure heat tolerance (critical thermal maximum, CT_{max}), individuals were tethered
234 under a heat lamp until the onset of seizures (Lutterschmidt and Hutchison 1997). To
235 measure cold tolerance (critical thermal minimum, CT_{min}), we exposed animals to cold
236 by placing individuals in a ziplock container and floating each individual in a 5 °C ice
237 bath checking for a righting response when flipped from a ventral to a dorsal position.
238 There was no more than momentary stress for any individual animal and no mortality.
239 The animals were allowed to recover before release the following day at the site of
240 capture on Buck Island.

241 *Occupancy modeling*

242 We estimated lizard occupancy across the island using a zero-inflated binomial
243 occupancy model (MacKenzie et al. 2006, Royle and Dorazio 2008). We used habitat
244 type and distance-from-release as covariates in the occupancy model. We ranked models
245 with and without each covariate using Akaike's information criterion (AICc) model

246 selection weight, where the simplest model that best fits the data received the lowest
247 score.

248 *Abundance estimates*

249 We estimated lizard abundance with an N -mixture model using a negative
250 binomial distribution (R package ‘unmarked’ version 0.10.2, Fiske and Chandler 2011).
251 We fit the null model, which did not include any covariates, and the universal model,
252 which included all site covariates with the function ‘pcount’ (Royle 2004). We used
253 stepwise selection to see which environmental variables drove differences in abundance
254 and detection (‘MuMIn’ version 19.9.5, Barton 2013). We assessed the best models with
255 Akaike’s information criterion (AICc), and we used a Wilcoxon rank sum statistic to test
256 the concordance between population estimates from the measured covariates and the
257 raster layers. We used parametric bootstrap sampling ($N = 1000$ runs) from the function
258 ‘parboot’ to evaluate the model goodness-of-fit (GOF) using a Freeman-Tukey test
259 statistic, which allows small observed values in the model.

260 To calculate the current population, we exported the abundance site estimates to
261 ArcGis 10.1 and interpolated a surface scaled for root mean square deviation on 30 m^2
262 grid cells. The ‘predict’ function in ‘unmarked’ allowed us to estimate the future
263 abundance state (Kéry et al. 2005). We summed the mean abundance and 95%
264 confidence intervals to arrive at the population estimates from the final N -mixture model
265 and its results. A spatial interpolation estimated the population abundance within each
266 pixel where surveys were not completed using the resultant mean abundance versus
267 available habitat between sites. The future abundance estimate was projected by applying
268 the final N -mixture model parameters to each pixel with the same set of environmental
269 data but setting the distance-from-release to zero to model the post-dispersal abundance
270 of lizards. For both the current and future states, we summed the mean abundance and 95
271 % confidence intervals to arrive at total population estimates.

272 To present our methods as a step-wise protocol, we created a diagram that
273 summarizes our process (Fig. 1). Five years post-translocation, we collected
274 environmental and biological variables including remotely sensed environmental
275 features, distance-from-release, and operative environmental temperature (Step 1). We
276 measured the population’s occupancy across the island over three years to determine if a

277 directional dispersal front characterized the pattern of dispersal in this population (Step 2
278 – 3). We selected sites within a 100 m buffer of the dispersal front to estimate true
279 abundance with a *N*-mixture model in 2013 (Step 4). We estimated the current and future
280 population states by spatially interpolating the modeled abundance between the sites and
281 fitting the binomial *N*-mixture model, respectively (Step 5).

282 **Results** –

283 *Environmental Covariates*

284 Within all sites, leaf litter depth ranged from 0 to 7.5 cm, woody stems ranged
285 from 0 to 20 per m², and canopy covered from 3 to 91 % of the overhead space (Table 1).
286 During the day, substrate temperature ranged from 27.48 °C to 67.50 °C. The operative
287 temperature models at each site ranged from 27.60 °C to 63.50 °C. The mean operative
288 temperature collected at a site within 10 minutes of a lizard observation was 40.30 °C (95
289 % quartiles: 36.12 °C – 43.36 °C). The NMDS for the measured variables (stress
290 =0.1080) and the raster variables (stress = 0.1130) indicated significant overlap of
291 microhabitat features of Buck Island, thus our *a priori* habitat categories were
292 independent of the microhabitat data that we collected ($R^2 = 0.987$).

293 *Lizard temperature trials*

294 The ten lizard subjects weighed 6.7 g on average (range: 5.4 - 15.7 g). Mean
295 thermal tolerance breadth was 26.08 °C; mean *CTmin* was 19.36 °C (95 % quartile: 17.68
296 - 21.10 °C) and mean *CTmax* was 45.44 °C (95 % quartile: 45.0 - 46.0 °C). The mean
297 *Tsel* was 39.84 °C (95 % quartile: 39.17 - 40.50 °C). We found that the selected
298 temperatures and heat tolerance of the species fell within the range of available operative
299 environmental temperatures on Buck Island (Fig. 2).

300 *Dispersal and occupancy*

301 Patterns of dispersal across the population were tracked over three years (Fig. 3).
302 In May 2013, we found site occupancy was 41.0 % based on a total of 305 surveys (95 %
303 CI: 29.0 - 54.28 %). From the model, we inferred that observers detected lizards if
304 present at a site 79.7% (95 % CI: 72.1 – 85.6 %) of the time. We only found two lizards
305 on the eastern 47 % of the island (33.3 ha) in May 2013. We found an increasing number
306 of sites occupied with subsequent surveys (Fig. 3). We used these surveys to inform the

307 proportion of sites including a 200 m eastern buffer of absence sites to survey for
308 abundance.

309 When we re-surveyed the sites in May 2014, we found lizards had dispersed to
310 seven previously unoccupied sites adjacent to sites occupied the previous year. In
311 October 2014, we found three additional sites occupied. Overall, lizards occupied 60.3 %
312 (95 % CI: 47.3 – 72.0 %) and 65.5 % (95% CI: 52.5 – 76.6 %) of the island by May and
313 October 2014, respectively. Detection in 2014 increased from 2013, with observers
314 detecting lizards 94.2 % (95 % CI: 85.6 – 97.8 %) and 86.9 % (95 % CI: 77.9 – 92.6 %)
315 of the time. Lizards had dispersed to four more previously unoccupied sites by May 2015,
316 and an additional four sites by October 2015. Occupancy reached 74.1 % (95 % CI: 61.4
317 – 83.7 %) and 81 % (95 % CI: 68.9 – 89.1 %) of the island by May and October 2015,
318 respectively. Detection remained high, with observers detecting lizards 96.7 % (95 % CI:
319 93.3 – 98.4 %) and 97.8 % (95 % CI: 94.9 – 99.1 %) of the time. All years showed good
320 model goodness-of-fit (May 2013 GOF: $P = 0.483$; May 2014 GOF: $P = 0.535$; Oct 2014
321 GOF: $P = 0.534$; May 2013 GOF: $P = 0.489$; May 2013 GOF: $P = 0.539$). We did not
322 observe lizards at the far eastern site where we observed two male individuals in May
323 2013, despite 18 surveys over two years.

324 *Abundance*

325 The May 2013 surveys to estimate lizard abundance in the occupied area included
326 the 32 westernmost sites (presence-absence surveys took place island-wide). Lizard
327 counts ranged from 0 to 18, with an average of 6.3 individuals per site. More than two-
328 thirds (69.15 %) of all lizards we observed were found at sites < 200 m from the 2008
329 release site (Fig. 4). Observations by the pair of observers were consistent among survey
330 days (First observer: $P = 0.266$, $df = 2$, $\chi^2 = 2.647$; Second observer: $P = 0.545$, $df = 2$,
331 $\chi^2 = 1.210$) and between the observers at each site within the survey period ($P = 0.546$, df
332 $= 31$, $t = 1.23$). Of the individual observations that we made in 2013 during the
333 abundance surveys, we found the majority of lizards observed in full sun ($N = 1,322$),
334 with fewer observations of lizards in full shade ($N = 26$) or in partial shade ($N = 92$). We
335 observed most ground lizards under shrubs ($N = 626$), but we also observed lizards
336 among herbaceous vegetation ($N = 220$). Yet, lizard counts varied significantly among
337 sites ($P < 0.0001$, $df = 31$, $\chi^2 = 189.67$) and by habitat type ($P < 0.0001$, $df = 4$, $\chi^2 =$

338 29.54). We observed 16 lizards at the beach site, zero at the manchineel forest site, 167
339 (per site \bar{x} = 12.8, range: 3 - 27) in woodland sites, 42 (per site \bar{x} = 7, range: 0 - 19) in
340 forest sites, and 66 (per site \bar{x} = 3.2, range: 0 - 13) in shrubland sites.

341 *Abundance Models*

342 We ranked models that allowed only abundance or only detection to vary in order
343 to choose covariates (Appendix S2: Table S1). We found the top abundance model
344 carried 28.1 % of AICc weights. Factors influencing abundance included average
345 substrate and operative temperatures, maximum operative temperature, distance-from-
346 release, leaf litter depth, percent herbaceous cover, and the number of woody stems
347 (Appendix S2: Table S1: *Abundance Only*). The top detection driven model carried 33.7
348 % of AICc weight. Detection was largely driven by average operative temperature,
349 maximum operative and substrate temperatures, habitat type, percent herbaceous cover,
350 and distance-from-release (Appendix S2: Table S1: *Detection Only*).

351 For the final model, we used the significant covariates from the top abundance
352 and top detection models, and allowed distance-from-release to interact with all layers.
353 This produced a model used to estimate the population size for the entire island (GOF P
354 = 0.636, Table 2). The model revealed the mean abundance by integrating the observed
355 counts over the negative binomial distribution. The estimate of abundance N at each site
356 was corrected for the habitat heterogeneity, physiologically informed operative
357 temperature, and the dispersal of the lizards which was then used to estimate the
358 detection of lizards by integrating the product on a binomial likelihood distribution where
359 detection was influenced by habitat, elevation, and temperature. See Royle (2004) for
360 derivation of the general N -mixture model and Joseph et al. (2009) for the special case of
361 using a negative binomial distribution for the N -mixture model estimator. Population
362 estimates based on this model indicated a total of 739 (\pm 27) lizards (95% bootstrap CI:
363 489 – 1,006) at the surveyed sites. The final model estimated 35 lizards in the
364 recreation/beach site, one lizard at the manchineel forest, 503 lizards (\bar{x} = 38.7, range: 6 -
365 85 per site) at woodland sites, 128 lizards (\bar{x} = 21.3, range: 0 - 80 per site) in forest, and
366 140 lizards (per site \bar{x} = 12.7, range: 1- 26) in shrubland sites.

367 The final model indicated average detection during counts was 20.1 % (CI: 18.5
368 % -32.1 %). We observed the most lizards near the 2008 release site (maximum of 39

369 individuals) and < 17 at any site > 125 m from the translocation site. The relationship
370 between distance-from-release and number of lizards observed at sites was statistically
371 significant ($R^2 = 0.912$; $F = 75.86$, $df = 30$; $P < 0.001$). The model indicated that
372 detection did not vary at increasing distance-from-release. Detection was density-
373 independent presumably because our survey methodology and length of surveys was
374 sufficient if a lizard was present, even if local density was low (Fig. 4).

375 *Current and Future Population Size*

376 We spatially interpolated the population abundance at sites (Fig. 5A) to the entire
377 island using the final May 2013 model accounting for latent abundance and detection bias
378 (GOF $P = 0.46$). The interpolation estimates the population size throughout the island,
379 not only at the survey sites. The island-wide lizard population in 2013 was estimated at
380 1,473 individuals (95 % CI: 940 - 1,802). The final model predicts lizard occupancy
381 across Buck Island reaching 8,336 individuals in the post-dispersal future population state
382 (95 % CI: 6,590 - 10,501). The model indicated areas across eastern portions of Buck
383 Island where the lizard had not yet been found as suitable for St. Croix ground lizards
384 (Fig. 5B).

385 *Discussion –*

386 We estimated the current and future population states of St. Croix ground lizards
387 on Buck Island by incorporating biologically relevant covariates like dispersal and
388 operative temperature in occupancy models and integrating a spatial interpolation model
389 with an N -mixture model. Spatially extending the site-specific model results allowed us
390 to estimate abundance across the whole island at the present time-step (2013) and project
391 the model parameters across the island to predict the future population state after lizards
392 had occupied all areas of habitat. We found an effect of elevation and distance-from-
393 release on abundance, but not observers' ability to detect presence. We believe that
394 dispersal is continuing, and it will have ended when distance-from-release is no longer a
395 significant covariate related to latent abundance. In this case, the island will occupy all
396 areas of Buck Island where suitable habitat exists, and possibly some areas where
397 unsuitable habitat exists. If our predictions are accurate, the future population size will
398 continue to increase up to 6,590 - 10,501 lizards. Simulated data with marked and
399 counted animals using known-fate (capture-recapture) and N -mixture models have

400 provided evidence that a sample of marked animals is representative of the population of
401 interest, and conversely that *N*-mixture models are representative of the abundance of the
402 population (Zipkin et al. 2014, Schmidt et al. 2015). One view is that a combination of
403 intensive (capture-mark-recapture) and extensive (unmarked) datasets will produce the
404 most robust estimates of population states. The limitations and risk related to marking
405 small (<10 g) endangered burrowing lizards precluded extensive marking of any subset of
406 this population for comparison. However, detection probability of marked St. Croix
407 ground lizards during the translocation event (range: 20.1 - 25.1%) was very similar to
408 detection probabilities in this study (Treglia and Fitzgerald 2011). The distribution and
409 abundance predictions from this study are easily testable through application of the same
410 methodological approach with future data collected at the same survey sites. As such, we
411 recommend the abundance of the St. Croix ground lizard monitored at least every five
412 years to maintain consistency in the time interval between the translocation and the first
413 abundance survey post-translocation.

414 We found that a biologically relevant covariate, operative temperature, improved
415 the fit of the *N*-mixture model because lizards are selecting for sites within their operative
416 temperature. Incorporating operative temperature also improved our ability to model the
417 population size of St. Croix ground lizards on Buck Island, with lower operative
418 temperatures correlating with very low abundance and detection of lizards across all sites.
419 We can presume this is because fewer lizards were available for detection at low
420 operative temperatures. Surprisingly, the operative temperature did not vary significantly
421 among habitat types. Individuals used all vegetation types, but we observed more lizards
422 at woodland (41.0 %) sites and fewer lizards at forest (34.3 %) and shrubland (24.7 %) sites.
423 Woodland sites, where we observed most lizards, were wetter with less leaf litter
424 and less canopy than the other two habitats. Forest and shrubland sites are typically drier,
425 and these sites had, respectively, more canopy (higher NDVI) and dense understory. The
426 habitat associations we used are different than reported in previous studies of the species,
427 where variables such as 'sun patches', 'deep leaf litter' were important to relative
428 abundance (Philibosian and Ruibal 1971, McNair and Lombard 2004). The Buck Island
429 population lives on an island with more topography and higher elevation (0 – 70 m) than
430 the other three populations, which occur on islands 1 - 10 m above sea level. We found a

431 negative correlation of this species' abundance and elevation. A negative interaction
432 between high elevation and distance-from-release sites indicates that lizards are
433 dispersing around rather than over the peaks on Buck Island. The highest ridges are also
434 areas that are relatively hot and dry. Overall, the uneven distribution of lizards on Buck
435 Island suggests that current reforestation actions taking place as part of a holistic
436 restoration program will also serve to enhance habitat for the St. Croix ground lizard
437 throughout the island. In particular, planting woodland species should create a matrix of
438 sun and shade that increases opportunities for effective thermoregulation over a greater
439 areal extent.

440 Our models lead us to predict that St. Croix ground lizards will continue to
441 disperse and eventually occupy areas across the entire island. The model predicted habitat
442 for lizards at the site where we observed two adult male individuals in the eastern part of
443 Buck Island in 2013 (Fig. 3). Besides the two adults we observed in 2013, St. Croix
444 ground lizards have not been observed in the east again, despite 18 formal surveys and
445 during three years of rodent pest control across the island by biologists purposefully
446 looking for St. Croix ground lizards during their work. Outliers are mathematically
447 certain in dispersing populations of reintroduced animals (Yott et al. 2011), and the
448 dispersal distribution of St. Croix ground lizards indicates low densities can exist across
449 the entire island. That we observed two outlying individuals lends confidence to our
450 approach in using distance-from-release in the models. Similarly, studies measuring
451 movement of translocated and resident species have found linear and geometric trends in
452 movements of translocated musk turtles (Attum et al. 2013) and patterns related to least
453 cost pathways for translocated wild ass (Davidson et al. 2013).

454 Recent conservation challenges such as invasive species, climate change, and the
455 increasing realization that population persistence will require human intervention call for
456 continual development of methodological and modeling approaches. While the challenge
457 of estimating new population states is old, creating reproducible analytical methods that
458 can account for spatial and biological heterogeneity is more relevant today than ever
459 (Sexton et al. 2009). New models are emerging that allow for the inclusion of
460 biologically relevant parameters and processes in a landscape context. These sorts of
461 approaches, like the one we have taken in this work, should become increasingly useful

462 to understanding the plausibility and limits of conservation introductions and to
463 confronting invasive species problems (Sutherland et al. 2015, Yamaura et al. 2016).
464 Population size of translocated species and invasive species is difficult to model,
465 especially when populations are growing, dispersing, and occupying new habitats.
466 Including mechanistic covariates in models improves the ability to approximate
467 population states over time and make hypotheses for the future of reintroductions and
468 invasions (Seebacher and Franklin 2012, Kearney and Porter 2009). We demonstrated
469 one way to assess the population state of dispersing individuals by integrating models
470 accounting for latent abundance, covariates related to the biology and movement of a
471 focal species, and spatial models. Population state estimation using the workflow
472 presented here can present opportunities to test predictions related to population state
473 estimation and more generally biologically driven hypotheses to enhance the
474 characterization of new populations before individuals have arranged themselves and/or
475 arrived to all available habitats.

476

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494 *Literature Cited* –

- 495 Angilletta, M. 2009. Thermal adaptation: a theoretical and empirical synthesis. Oxford
496 University Press, Oxford, England.
- 497 Attum, O., C. Cutshall, K. Eberly, H. Day, and B. Tietjen. 2013. Is there really no place
498 like home? Movement, site fidelity, and survival probability of translocated and resident
499 turtles. *Biodiversity and Conservation* 22(13-14): 3185-3195.
- 500 Bakken, G., and M. Angilletta. 2013. How to avoid errors when quantifying thermal
501 environments. *Functional Ecology* 28(1): 96 - 107.
- 502 Barton, K. 2013. MuMIn: Multi-model inference. <[http://CRAN.R-](http://CRAN.R-project.org/package=MuMIn)
503 [project.org/package=MuMIn](http://CRAN.R-project.org/package=MuMIn)>.
- 504 Bastille-Rousseau, G., J. Potts, C. Yackulic, J. Frair, E. Ellington, and S. Blake. 2016.
505 Flexible characterization of animal movement pattern using net squared displacement
506 and a latent state model. *Movement Ecology* 4: 1 - 12.
- 507 Bled, F., J. Sauer, K. Pardieck, P. Doherty, and J. Royle. 2013. Modeling Trends from
508 North American Breeding Bird Survey Data: A Spatially Explicit Approach. *PLOS ONE*
509 8(12): e81867.
- 510 Boulangeat, I., D. Gravel, and W. Thuiller. 2012. Accounting for dispersal and biotic
511 interactions to disentangle the drivers of species distributions and their abundances.
512 *Ecology Letters* 15(6): 584 - 593.
- 513 Braun-Blanquet, J. 1932. Plant sociology (Translated by G. D. Fuller and H. S. Conrad).
514 McGraw-Hill, New York. 539 pp.
- 515 Buckland, S., N. Cole, J. Aguirre-Gutierrez, L. Gallagher, S. Henshaw, A. Besbard, R.
516 Tucker, V. Bachraz, K. Ruhomaun, and S. Harris. 2014. Ecological effects of the
517 invasive giant Madagascar Day Gecko on endemic Mauritian Geckos: applications of
518 binomial-mixture and species distribution models. *PLOS ONE* 9(4): e88798.
- 519 Davidson, A., Y. Carmel, and S. Bar-David. 2013. Characterizing wild ass pathways using
520 a non-invasive approach: applying least-cost path modelling to guide field surveys and a
521 model selection analysis. *Landscape Ecology* 28(8): 1465-1478.
- 522 Davis, J. 2002. Natural Resources Conservation Service, United States Department of
523 Agriculture. Soil Survey Geographic (SSURGO) Database for Virgin Islands of the

524 United States. Available online at <http://soildatamart.nrcs.usda.gov>. Accessed
525 09/24/2013.

526 Debeaudette, D. 2009. Aggregating SSURGO Data in R. California Soil Resource Lab.

527 Dickinson, H., J. Fa, and S. Lenton. 2001. Microhabitat use by a translocated population of
528 St. Lucia whiptail lizards (*Cnemidophorus vanzoi*). *Journal of Zoology* 251: 187 - 197.

529 Dzialowski, E. 2005. Use of operative temperature and standard operative temperature
530 models in thermal biology. *Journal of Thermal Biology* 30: 317 - 334.

531 Elton, C. 1927. The nature and origin of soil-polygons in Spitsbergen. *Quarterly Journal of*
532 *the Geological Society* 83(5): 163 - NP.

533 Fiske, I. J., and R. B. Chandler. 2011. unmarked: An R Package for Fitting Hierarchical
534 Models of Wildlife Occurrence and Abundance. *Journal of Statistical Software* 43: 1 -
535 23.

536 Fitzgerald, L., M. Treglia, N. Angeli, T. Hibbits, A. Subalusky, I. Lundgren, and Z. Hillis-
537 Starr. 2015. Correlates to successful establishment of a new population of the critically
538 endangered St. Croix ground lizard (Teiidae: *Ameiva polops*). *Restoration Ecology*
539 23(7): 776 - 786.

540 Gesch, D. 2007. The National Elevation Dataset. Pp. 99 - 118. In Maune, D. (ed.), *Digital*
541 *Elevation Model Technologies and Applications: The DEM Users Manual, 2nd Edition:*
542 *Bethesda, Maryland, American Society for Photogrammetry and Remote Sensing.*

543 Hertz, P., R. Huey, and R. Stevenson. 1993. Evaluating temperature regulation by field-
544 active ectotherms: the fallacy of the inappropriate question. *American Naturalist* 145(5):
545 796 - 818.

546 Huey, R., C. Deutsch, J. Tewksbury, L. Vitt, P. Hertz, H. Pérez, and T. Garland. 2009.
547 Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal*
548 *Society of London B: Biological Sciences*, pp. rspb-2008.

549 Hurtado, L., C. Santamaria, and L. Fitzgerald. 2012. Conservation genetics of the critically
550 endangered St. Croix ground lizard (*Ameiva polops* Cope 1863). *Conservation Genetics*
551 13: 665 - 679.

552 Joseph, L., S. Field, C. Wilcox, and H. Possingham. 2006. Presence–Absence versus
553 Abundance Data for Monitoring Threatened Species. *Conservation Biology* 20: 1679 -
554 1687.

555 Joseph, L., C. Elkin, T. Martin, and H. Possingham. 2009. Modeling abundance using N -
556 mixture models: the importance of considering ecological mechanisms. *Ecological*
557 *Applications* 19(3): 631-642.

558 Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological
559 and spatial data to predict species' ranges. *Ecology Letters* 12(4): 334 - 350.

560 Kendall, W. 1999. Robustness of closed capture-recapture methods to violations of the
561 closure assumption. *Ecology* 90: 2517 - 2525.

562 Kéry, M. and J. Royle. 2010. Hierarchical modelling and estimation of abundance and
563 population trends in metapopulation designs. *Journal of Animal Ecology* 79: 453–461.

564 Kéry, M., J. Royle, and H. Schmid. 2005. Modeling avian abundance from replicated
565 counts using N -mixture models. *Ecological Applications* 15(4): 1450 - 1461.

566 Knappe, J., and F. Korner-Nievergelt. 2016. On assumptions behind estimates of abundance
567 from counts at multiple sites. *Methods in Ecology and Evolution* 7(2): 206 - 209.

568 Krebs, C. 2014. *Ecological Methodology*, 3rd ed. Addison-Wesley Longman, Inc., Menlo
569 Park, California. 744 pp.

570 Lutterschmidt, W. and V. Hutchinson. 1997. The critical maximum: history and critique.
571 *Canadian Journal of Zoology*. 75(10): 1561 - 1574.

572 MacKenzie, D., J. Nichols, J. Royle, K. Pollock, L. Bailey, and J. Hines. 2006. *Occupancy*
573 *Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*.
574 Academic Press (Elsevier), San Diego, California. 324 pp.

575 Mazzerolle, M., L. Bailey, W. Kendall, J. Royle, S. Converse, and J. Nichols. 2007.
576 Making great leaps forward: accounting for detectability in herpetological field studies.
577 *Journal of Herpetology* 41(4): 672 - 689.

578 McCune, B., J. Grace, and D. Urban. 2002. *Analysis of ecological communities*. Vol. 28.
579 Glendon Beach, Oregon: MjM software design. 304 pp.

580 McNair, D., and C. Lombard. 2004. Population estimates, habitat associations, and
581 management of *Ameiva polops* (Cope) at Green Cay, United States Virgin Islands.
582 *Caribbean Journal of Science* 40: 353 - 361.

583 Meier, A., R. Noble, and S. Rathburn. 1993. Population status and notes on the biology and
584 behavior of the St. Croix ground lizard on Green Cay (St. Croix USVI). *Caribbean*
585 *Journal of Science* 29:147 - 152.

586 Meot, A., P. Legendre, and D. Borcard. 1998. Partialling out the spatial component of
587 ecological variation: questions and propositions in the linear modelling framework.
588 Environmental and Ecological Statistics 5(1): 1 - 27.

589 Milanovich, J., D. Hocking, W. Peterman, and J. Crawford. 2015. Effective use of trails for
590 assessing terrestrial salamander abundance and detection: A case study at Great Smoky
591 Mountains National Park. Natural Areas Journal 35(4): 590 - 598.

592 Moser, J., K. Whelan, R. Shamblin, A. Atkinson, and J. Patterson. 2010. Buck Island Reef
593 National Monument, U.S. Virgin Islands, Vegetation Mapping Project 2009. Natural
594 Resource Technical Report. NPS/SFCN/NRTR – 2010/293. National Park Service, Fort
595 Collins, Colorado. 25 pp.

596 Philibosian, R., and J. Yntema. 1976. Records and status of some reptiles and amphibians
597 in the Virgin Islands. 1968-1975. Herpetologica 32: 81 - 85.

598 Philibosian, R., and R. Ruibal. 1971. Conservation of the lizard *Ameiva polops* in the
599 Virgin Islands. Herpetologica 27: 450 - 454.

600 R Development Core Team. 2011. R: A language and environment for statistical
601 computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-
602 07-0, url: <http://www.R-project.org>.

603 Rodda, G., E. Campbell, T. Fritts, and C. Clark. 2005. The predictive power of visual
604 searching. Herpetological Review 36(3): 259 - 264.

605 Rodda, G., K. Dean-Bradley, E. Campbell, T. Fritts, B. Lardner, A. Adams, and R. Reed.
606 2015. Stability of detectability over 17 years at a single site and other lizard detection
607 comparisons from Guam. Journal of Herpetology 49(4): 513 - 521.

608 Royle, J. 2004. *N*-mixture models for estimating population size from spatially replicated
609 counts. Biometrics 60(1): 108 - 115.

610 Royle, J., and J. Nichols. 2003. Estimating abundance from repeated presence-absence data
611 or point counts. Ecology 84(3): 777 - 790.

612 Royle, J., and R. Dorazio. 2008. Hierarchical modeling and inference in ecology. Academic
613 Press, California, USA. 444 pp.

614 Schmidt, J., D. Johnson, M. Lindberg, and L. Adams. 2015. Estimating demographic
615 parameters using a combination of known-fate and open *N*-mixture models. Ecology
616 96(10): 2583-2589.

617 Seaman, G., and J. Randall. 1962. The Mongoose as a Predator in the Virgin Islands.
618 *Journal of Mammalogy* 43(4): 544 – 546.

619 Sears, M. and M. Angilletta. 2015. Costs and Benefits of Thermoregulation Revisited: Both
620 the Heterogeneity and Spatial Structure of Temperature Drive Energetic Costs.
621 *American Naturalist* 185(4): E94-E102.

622 Seddon, P., W.M. Strauss, and J. Innes. 2012. Animal Translocations: What Are They and
623 Why Do We Do Them? Pp. 1 – 32. *In* Ewen, J., D. Armstrong, K. Parker, and P. Seddon
624 (ed.), *Reintroduction Biology: Integrating Science and Management*: Wiley-Blackwell,
625 Oxford. xxv + 499 pp.

626 Seebacher, F., and C. Franklin. 2012. Determining environmental causes of biological
627 effects: the need for a mechanistic physiological dimension in conservation
628 biology. *Philosophical Transactions of the Royal Society of London B: Biological*
629 *Sciences* 367(1596): 1607 - 1614.

630 Sexton, J., P. McIntyre, A. Anger, and K. Rice. 2009. Evolution and Ecology of Species
631 Range Limits. *Annual Review of Ecology, Evolution, and Systematics* 40: 415 - 436.

632 Sillett T., R. Chandler, J. Royle, M. Kéry, and S. Morrison. 2012. Hierarchical distance-
633 sampling models to estimate population size and habitat-specific abundance of an island
634 endemic. *Ecological Applications* 22: 1997 – 2006.

635 Sutherland, C., A. Fuller, and J. Royle. 2015. Modelling non-Euclidean movement and
636 landscape connectivity in highly structured ecological networks. *Methods in Ecology*
637 *and Evolution* 6(2): 169 - 177.

638 Treglia M., and L. A. Fitzgerald. 2011. Translocation of the St. Croix ground lizard to
639 Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands. Pp. 109 - 115. *In*
640 Soorae P.S. (Ed.). *Global Re-introduction Perspectives: 2011. More case studies from*
641 *around the globe*. Gland, Switzerland: IUCN/SSC Re-introduction Specialist Group and
642 Abu Dhabi, UAE: Environment Agency-Abu Dhabi.

643 U. S. Fish and Wildlife Service. 1984. St. Croix ground lizard Recovery Plan. U.S. Fish
644 and Wildlife Service, Atlanta, Georgia. 26 pp.

645 U.S. Geological Survey. 2013. Earth Resources Observation & Science Center, United
646 States Department of Interior. Landsat 8 GeoTIFF Data Product for

647 'LC80030482013139LGN01'. Available online at <http://earthexplorer.usgs.gov>.
648 Accessed 10/25/2013.

649 Verboom, J., A. Schotman, P. Opdam, and J. Metz. 1991. European Nuthatch
650 Metapopulations in a Fragmented Agricultural Landscape. *Oikos* 61(2): 149 – 156.

651 Waddle, H., L. Brandt, B. Jeffery, and F. Mazzotti. 2015. Dry years decrease abundance of
652 alligators in the Florida Everglades. *Wetlands* doi: 10.1007/s13157-015-0677-8.

653 Watson, J., R. Whittaker, and T. Dawson. 2004. Habitat structure and proximity to forest
654 edge affect the abundance and distribution of forest-dependent birds in tropical coastal
655 forests of southeastern Madagascar. *Biological Conservation* 120(3): 311 - 327.

656 Weng, Q., D. Lu, and J. Schubring. 2004. Estimation of land surface temperature-
657 vegetation abundance relationship for urban heat island studies. *Remote Sensing of*
658 *Environment* 89: 467 - 483.

659 Wiley, J. 1984. The ecology and behavior of the St. Croix ground lizard (*Ameiva polops*)
660 an endangered species. Report on file at the Caribbean Island National Wildlife Refuge,
661 Boquerón, Puerto Rico, USA. 35 pp.

662 Williams, N., A. Hahs, and J. Morgan. 2008. A dispersal-constrained habitat suitability
663 model for predicting invasion of alpine vegetation. *Ecological Applications* 18(2): 347 -
664 359.

665 Witmer, G., and Z. Hillis-Starr. 2002. The Eradication of Introduced Rats at Buck Island
666 Reef National Monument, St. Croix, U.S. Virgin Islands. Report to the National Park
667 Service, U.S. Department of the Interior. 67 pp.

668 Yamaura, Y., M. Kéry, J. Royle. 2016. Study of biological communities subject to
669 imperfect detection: bias and precision of community *N*-mixture abundance models in
670 small-sample situations. *Ecological Research* 31(3): 289 - 305.

671 Yott, A., R. Rosatte, J. Schaefer, J. Hamr, and J. Fryxell. 2011. Movement and spread of a
672 founding population of reintroduced elk (*Cervus elaphs*) in Ontario, Canada. *Restoration*
673 *Ecology* 19:70 - 77.

674 Zipkin, E. T. Sillett, E. Campbell Grant, R. Chandler, and J. Royle. 2014. Inferences about
675 population dynamics from count data using multistate model: a comparison to capture-
676 recapture approaches. *Ecology and Evolution* 4(4): 417 – 426.

677 **Tables –**

678 **Table 1.** Summary statistics for environmental covariates averaged by habitat type on
 679 Buck Island. The range for each variable is in parentheses.

	<i>Forest</i> (<i>n=9</i>)	<i>Shrubland</i> (<i>n=13</i>)	<i>Woodland</i> (<i>n=14</i>)	<i>All</i>
Leaf litter depth (cm)	2.12 (0.25 - 6.00)	2.27 (0.13 - 7.50)	1.73 (0.13 - 4.50)	2.03 (0.13 - 7.50)
Canopy Cover (%)	40.59 (5.50 - 91.00)	43.44 (14.50 - 73.75)	30.88 (4.50 - 48.75)	38.02 (4.50 - 91.00)
Woody stems (#)	6.72 (0.25 - 18.00)	7.79 (0.00 - 20.50)	4.71 (0.75 - 13.75)	6.37 (0 - 20.5)
Avg. substrate temperature (°C)	28.19 (27.59 - 28.91)	28.93 (27.71 - 30.38)	28.29 (27.48 - 29.04)	28.50 (27.48 - 30.38)
Avg. operative temperature (°C)	28.25 (27.60 - 29.31)	28.79 (27.99 - 30.01)	28.56 (27.82 - 30.03)	28.57 (27.6 - 30.03)
Max. substrate temperature (°C)	49.66 (38.27 - 67.50)	56.26 (42.00 - 67.50)	51.84 (40.5 - 62.00)	52.95 (38.27 - 67.5)
Max. operative temperature (°C)	52.81 (29.50 - 63.50)	53.10 (47.76 - 62.50)	53.60 (46.00 - 62.50)	53.22 (29.5 - 63.5)
Elevation (m)	31.31 (2.89 - 67.45)	36.43 (13.70 - 70.10)	35.60 (13.79 - 64.65)	34.84 (2.89 - 70.1)

Soil moisture (scaled)	1.01 (0.77 – 1.13)	1.04 (0.58 – 1.13)	1.09 (0.86 – 1.13)	1.05 (0.58 – 1.13)
NDVI (scaled)	1.41 (0.24 – 1.83)	1.73 (1.52 – 2.09)	1.73 (1.34 – 2.00)	1.65 (0.24 – 2.09)

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684 **Table 2.** The *N*-mixture model used to create current and future population state

685 estimates.

	<i>Estimate</i>	<i>SE</i>	<i>z</i>	<i>P</i>
Abundance				
Intercept	-2.16	2.88	-0.75	0.45
Woodland	-0.66	0.22	-3.02	0.00
Shrubland	-0.57	0.35	-1.64	0.10
Manchineel	0.00	5650.00	0.00	1.00
Recreation	-0.01	6260.00	0.00	1.00
Elevation	1.27	0.27	4.70	0.00
Temp	6.27	2.81	2.23	0.03
Dist	0.01	0.01	0.79	0.43
Woodland*Dist	0.00	0.00	1.02	0.31
Shrubland*Dist	0.00	0.00	0.38	0.70
Manchineel*Dist	-0.01	11.50	0.00	1.00
Recreation*Dist	-0.10	853.00	0.00	1.00
Elevation*Dist	-0.01	0.00	-5.88	0.00
Temp*Dist	-0.01	0.01	-0.88	0.38
Detection				
Intercept	-4.80	1.57	-3.05	0.00

Sand	-0.26	0.10	-2.66	0.01
Woodland	-0.26	0.14	-1.79	0.07
Shrubland	-0.12	0.16	-0.76	0.45
Manchineel	0.11	0.28	0.39	0.69
Recreation	0.60	0.48	1.26	0.21
Elevation	-0.09	0.11	-0.86	0.39
Water	-0.05	0.46	-0.10	0.92
NDVI	0.26	0.26	1.00	0.32
Temp	3.13	1.67	1.87	0.06

686

687

688 **Figure Legends**

689 **Fig. 1.** The five-step iterative process used to estimate populations of the St. Croix
690 ground lizard. At each step, a decision can be made to include the data (*Yes*) or to move
691 onto the next step (*No*). If the decision is made to include the data (*Yes*), then the second
692 step (*No*) is included additionally. This approach is amenable for modeling new and
693 dispersing populations.

694 **Fig. 2.** The frequency histogram of available operative temperatures (*OTM*) recorded
695 during the survey hours indicates that areas are available for the St. Croix ground lizard
696 to thermoregulate. The thermal preference (*Tpref*) and heat tolerance (*CTmax*) of the
697 lizard fall within the range of available operative temperatures while the lizard's cold
698 tolerance limit (*CTmin*) is far lower than all recorded operative temperatures. Median
699 temperatures of *CTmax*, *Tpref*, and *CTmin* are flanked by range limits (dotted lines).

700 **Fig. 3.** The mean St. Croix ground lizard occupancy on the island increased 46% overall
701 based on annual and biannual surveys conducted from the year 2013 to 2015. Numbers in
702 parentheses indicate 95 % confidence intervals.

703 **Fig. 4.** St. Croix ground lizards dispersed in all directions from the 2008 release sites
704 (black squares inset map). Color scale indicates number of lizards per 30 m² grid cell (A).
705 The detection of St. Croix ground lizards was independent of dispersal (B).

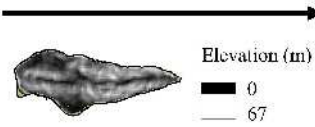
706 **Fig. 5.** The current (A) and future (B) population state of St. Croix ground lizards on
707 Buck Island. The future abundance was fit with the binomial N -mixture model
708 parameters on a 30 m² scale. The abundance ranges from 0 (purple) to 100 (green)
709 individuals per grid cell.

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Variables

Step 1: Determine if biologically relevant variables can be measured across the landscape.

No. Yes



1a. Measure biological relevant variables across region.
In this study, we measured operative temperature.

1b. Measure abiotic variables across the landscape.

In this study, we created indices of vegetation, temperatures, substrate, and elevation (pictured).

Dispersal

Step 2: Determine if the population is newly introduced, and approximate the introduction point.

No. Yes

2a. Calculate distance metric characterizing distance from introduction point.

2b. Plan sampling for discrete time periods if dispersal is integrated into the population models.

Occupancy

Step 3: Determine if occupancy estimate is desired end-product.

No. Yes

3a. Calculate occupancy with model.
In this study, we estimated occupancy at 63 sites over five survey occasions (t).

3b. Calculate occupancy with appropriate unmarked model as in (3a), but continue to model site-specific abundance (4).

Site-specific abundance

Step 4: Estimate site-specific abundance with a model. Determine if regional abundance is a desired end-product.

In this study, we estimated abundance at 43 sites from the occupied region at sampling t=1.



Abundance (7 individuals) ● 0 ● 16-25 ● 46-55
■ Occupancy only ● 1-5 ● 26-35 ● > 56
● 6-15 ● 36-45

No. Yes

4a. Calculate abundance with detection-correction model.

4b. Continue to find region-wide and/or future abundance with the fitted site-specific abundance model (5).

Regional abundance

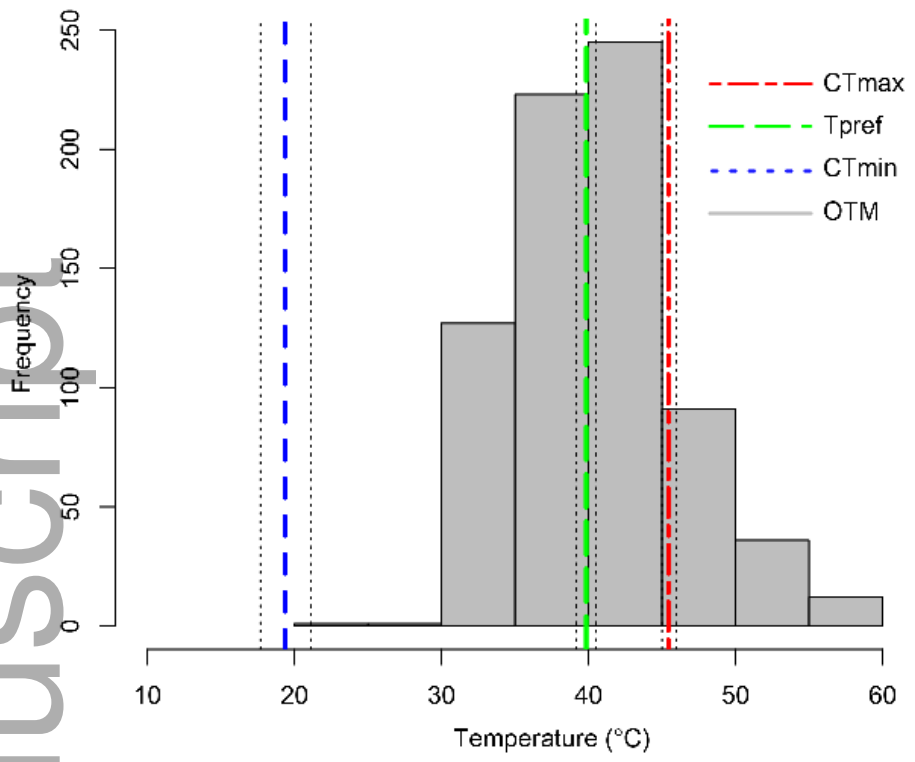
Step 5: If current population size is desired, then interpolate the site-specific abundance results

If future density is desired, use fitted model results to predictively model the population across the landscape in both the currently occupied and unoccupied zones.



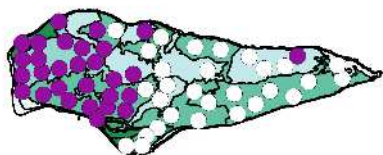
In this study, we predicted post-dispersal density of lizards.

eap_1650_f1.tif



eap_1650_f2.tif

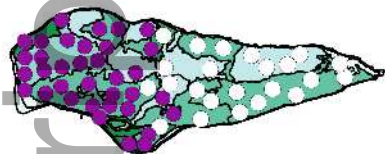
A. May 2013 - 41.0% occupancy (29.0 - 54.2)



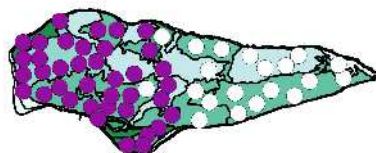
Site occupancy

- Absent
- Present

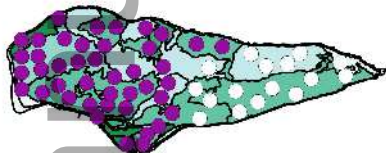
B. May 2014 - 60.3% occupancy (47.3 - 72.0)



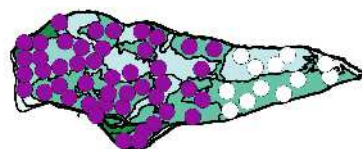
C. Oct 2014 - 65.5% occupancy (52.5 - 76.8)



D. May 2015 - 74.1% occupancy (61.4 - 83.7)



E. Oct 2015 - 87.0% occupancy (68.9 - 89.1)



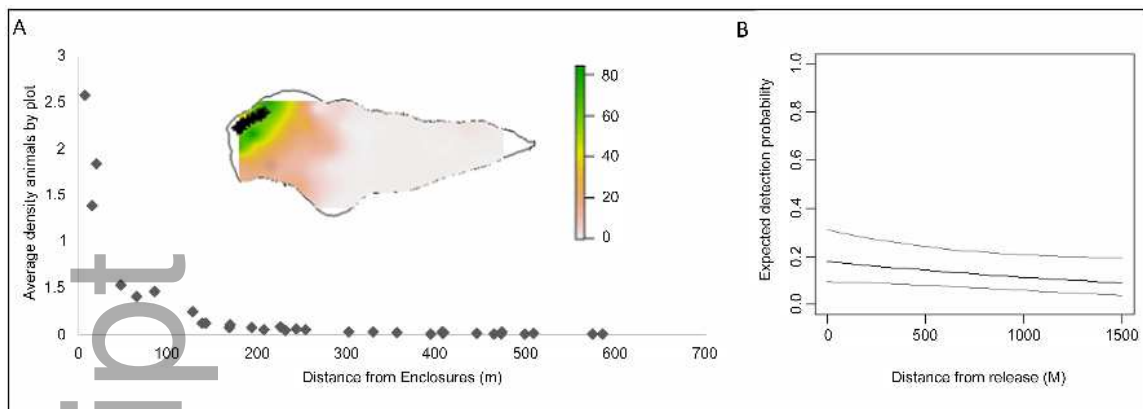
0 1000 2000 m



Habitat types

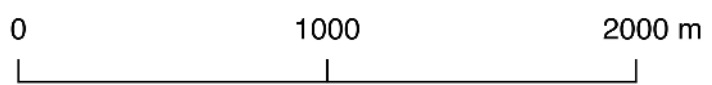
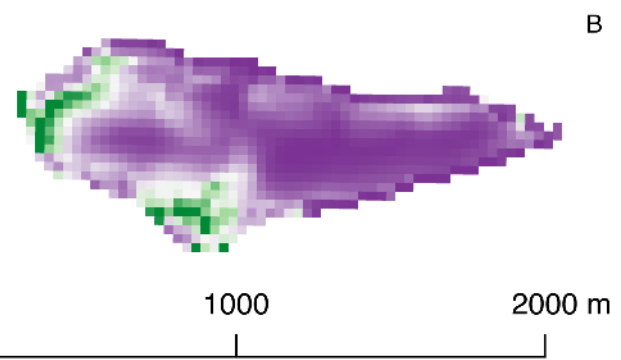
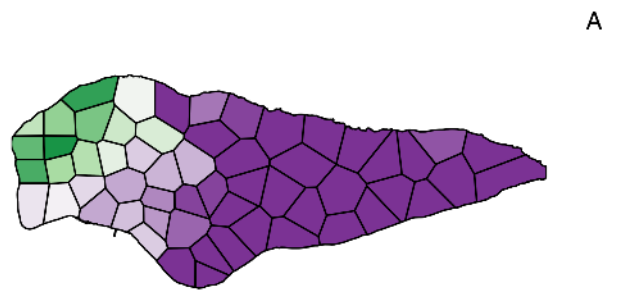
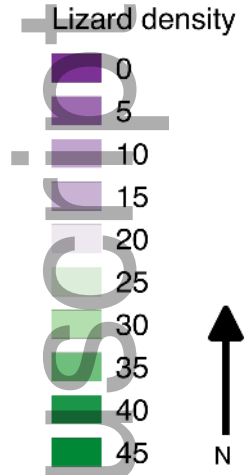
- Beach
- Forest
- Shrubland
- Woodland

eap_1650_f3.tif



eap_1650_f4.tif

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eap_1650_f5.tif

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