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# Modeling relative habitat suitability and movement behavior of invasive Burmese pythons in southern Florida

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IN SOUTHERN FLORIDA

For the degree of Master of Science

Is approved by the final examining committee:

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MODELING RELATIVE HABITAT SUITABILITY AND MOVEMENT BEHAVIOR  
OF INVASIVE BURMESE PYTHONS IN SOUTHERN FLORIDA

A Thesis

Submitted to the Faculty

of

Purdue University

by

Holly E. Mutascio

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of

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## ABSTRACT

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Invasive Burmese pythons are established in the Everglades and are altering the ecology of southern Florida. Their distribution in Florida is expanding northward into more urbanized and fragmented habitats. An understanding of the suitability of habitat throughout southern Florida for Burmese pythons and their interaction with Florida's landscapes through movement behavior is vital for predicting the python's ability to persist in habitats outside of the Everglades. In this thesis, we use ecological modeling to predict habitat suitability and to investigate personality-dependent dispersal.

First, we used presence-only ecological niche modeling with correction for sampling bias to identify the key landscape variables in predicting habitat suitability for pythons at the present stage of the invasion. We found estuarine habitat and freshwater wetlands to be the important variables to contribute to python habitat suitability when considered at the scale of a Burmese python's home range.

Then we used an individual based model to explore risk-taking behavior on a shy-bold continuum of animal personality of dispersing juvenile Burmese pythons on the leading edge of the population's expansion from the Everglades into Homestead and south Miami, Florida. We observed that a behaviorally plastic strategy best resembled

empirically derived patterns of the python's expansion into increasingly urbanized landscapes.

## CHAPTER 1. MODELING RELATIVE HABITAT SUITABILITY FOR INVASIVE BURMESE PYTHONS (*PYTHON MOLURUS BIVITTATUS*) CORRECTING FOR SAMPLING BIAS

### 1.1 Introduction

Invasive Burmese pythons (*Python molurus bivittatus*) are causing serious environmental impacts throughout southern Florida. Burmese pythons have been established in the region since the mid-1980s (Willson et al. 2011) as evidenced by regular observations in Everglades National Park (ENP) (Snow et al. 2007b) an increasing number of sightings in progressively northern locations of the state (Andreadis 2011), observations of individuals from a variety of size classes (Meshaka et al. 2000), and documented breeding (Andreadis 2011; Engeman et al. 2011). Burmese pythons are highly successful invaders due to their evasive behavior, cryptic coloration, flexible dietary preferences, broad habitat utilization, low energetic requirements, long lives, and high fecundity (Reed 2005; Willson et al. 2011; Reed et al. 2012). They are known to consume many species of birds, mammals, and American alligators (*Alligator mississippiensis*) (Snow et al. 2007a; Dove et al. 2011). They are thought to be responsible for the severe declines of several mammal populations in ENP (Dorcas et al. 2012; McCleery et al. 2015) and could worsen the decline of the endangered Key Largo woodrat (*Neotoma floridana smalli*) (Greene et al. 2007). There is also concern that Burmese pythons may compete with other top predators, including the American alligator

the Florida panther (*Puma concolor coryi*), and the federally threatened eastern indigo snake (*Drymarchon corais couperi*) (Reed 2005; Snow et al. 2007b), and that ecological changes associated with their invasion may impact restoration activities in the Everglades and Florida Keys (Harvey et al. 2009).

To develop effective management strategies for the Burmese python, there is a need to understand their ecological requirements, particularly of their habitat use in Florida. In their native range, Burmese pythons are habitat generalists and occupy a variety of landscapes such as estuarine mangrove forests, marshes, swamps, scrub jungle, rainforests, and grasslands (Wall 1921; Whitaker 1978; Bhupathy and Vuayan 1989; Ernst and Zug 1996; Snow et al. 2007b). They are also skilled swimmers and usually occupy areas located near a permanent water source (Minton 1966; Snow et al. 2007b). Florida's Everglades offer similar habitat types to the python's native landscape and given that python density is high in ENP (Reed et al. 2010), it can be ascertained that its landscape features provide suitable habitat. As large numbers of pythons now occupy areas in southern Florida dissimilar to the Everglades, such as the greater Naples area (Conservancy of Southwest Florida 2015), these areas must also contain suitable habitat. Linking python presence to specific landscape features will elucidate python habitat use in these areas beyond the Everglades system.

Ecological niche models (ENM), also known as species distribution models (SDM) or habitat distribution models, can be useful tools for understanding invasive species distributions (Baldwin 2009; Václavík and Meentemeyer 2009). ENMs relate environmental variables to species occurrences and statistically or theoretically predict geographic distribution by approximating the species niche (Peterson 2006; Sillero 2011).



These models have frequently been employed in the field of invasion biology to predict the potential ranges of invasive species. To achieve this, researchers commonly use “climate matching”, which estimates a species’ native climate space using its native distribution in order to project the climate space onto new geographic areas that are vulnerable to invasion (Peterson 2003; Rodda et al. 2011). Predicting the potential invasive range of a species based on its native range using climate-matching and other ENM techniques has been met with heavy criticism due to subtle differences in modeling approaches (e.g., using maximum entropy versus maximum likelihood when making claims of species occurrence; Fitzpatrick et al. 2013) and mistakes made when making inferences about a species’ niche (Rodda et al. 2011). Furthermore, inferences from presence-only data, which are often the only datasets available on invasive species, are built on assumptions that are often violated. Appropriate analysis of presence-only data requires that sampling effort and detection probability are known, or are constant relative to the environmental variables being considered (Yackulic et al. 2013). These assumptions can be particularly difficult to meet when little is known about the extent and magnitude of an invasion.

ENMs can be used to understand the relative habitat suitability of an invasive in a novel environment to gain a better understanding of their habitat use and ecological requirements (Peterson 2006). Species select specific habitats because their features facilitate particular behaviors such as foraging, predator avoidance, thermoregulation, and reproduction (Hansen and Urban 1992; Krausman 1999; Morris 2003). Thus an understanding of an invading species’ habitat use can be valuable to elucidating its invasion success and allows researchers to identify areas where invasives are most likely

to occur in order to conduct targeted behavioral studies. This is particularly important for the Burmese python system as this species' cryptic behavior makes it difficult to study its ecology and to find effective population management solutions.

The expansion of Burmese pythons throughout southern Florida provides a well-explored example of the challenges of the application of ENMs, and particularly the use of program MaxEnt (Phillips et al. 2004; SJ Phillips et al. 2006), to predict invasions. Rodda et al. (2008) first used an early ENM climate envelope modeling technique to identify areas vulnerable to python establishment. They fit a climate envelope around presence locations of Indian pythons in their native range and projected the climate envelope onto the US in order to identify areas climatically suitable for Burmese python habitat (Rodda et al. 2008). Their results suggested that pythons could potentially invade much of the southern US. However, these models were criticized for being under-parameterized which in turn over-predicted the python's native range (Pryon et al. 2008). Using a similar technique that is also rooted in ecological niche theory with the same end goal as Rodda et al. (2008), Pryon et al. (2008) used program MaxEnt to model the distribution of pythons in their native range and projected this model onto the US. Their results predicted a smaller potential range in the US, confined to a small area of southern Texas and to southern Florida. This finding was also criticized because the models were over-parameterized, the projected climate space was based on the realized rather than fundamental niche, pseudo-absence points were selected from a global rather than localized pool, and some of their presence records were of blood pythons (*Python brongersmai*) instead of Indian pythons (Rodda et al. 2011). Finally, the current range of pythons in Florida has already expanded beyond Pryon et al. (2008) predicted range. The

results of these two studies demonstrate the importance of the accuracy and relevancy of the parameters, particularly pseudo-absence points, being used in ENMs. They also emphasize the need to consider of the type of niche being modeled when interpreting the results of a particular ENM application.

More recently, researchers and managers have redirected their efforts from predicting the Burmese python's potential range to understanding its habitat use. Hart et al. (2015) and Walters et al. (2016) examined python home ranges and habitat use using locational data from radio-tagged pythons within ENP and identified important fine-scale landscape features selected for by pythons. These were primarily slough, coastal, and tree islands (Hart et al. 2015) and broad-leafed, edge, and elevated habitats (Walters et al. 2016). These results provided valuable insights for the Everglades python population, but python populations have expanded their range outside of this core area where habitat use is less understood.

In this study, we used presence-only ENM to identify key environmental variables in predicting suitable habitat for pythons in the southern half of Florida to understand python habitat preference at a broad scale and across a wide geographical area at the current stage in the invasion. Because habitat selection of a given species is most effectively understood at multiple spatial resolutions (Mayor et al. 2009), we hope to build on current knowledge of python habitat use in the southernmost areas of Florida while forming a basis for future studies of python habitat in the northernmost part of their present range. Our models predict suitability at a broader resolution than telemetry studies, but at a finer resolution than previous ENM modeling in the python system. Our goal was to create ENM predictions with rigorous criteria for background point selection

in order to correct for geographical sampling bias. We also aimed to make appropriate inferences by considering the relationship between the ENM predictions and the continued expansion of the Burmese python population in Florida. By doing so, we are not specifically predicting a potential range of this species; rather, we aim to build our knowledge of relative habitat suitability in order to guide future behavioral research and management efforts.

Based upon current understanding of the python's native range, we predict that variables such as proximity to water and land cover classes comprising wet areas will be the strongest predictors of habitat suitability. We also expect that environmental variables considered at the home range scale will best reflect python habitat use, and have the strongest influence on our models. Habitat at the presence location is not necessarily representative of the habitat used by pythons across their life history since they move throughout a large area and make long distance movements (Pittman et al. 2014; Hart et al. 2015).

## **1.2 Methods**

### *1.2.1 Study area*

Southern Florida is a mosaic of urbanized, agricultural, forested, and wetland landscapes, bordered by estuarine and coastal land habitats. It exhibits wet and dry seasonality, with average annual precipitation of approximately 1,412 mm and an average temperature of 23.9°C ([www.usclimatedata.com/climate/naples/florida/united-states/usfl0338/2016/1](http://www.usclimatedata.com/climate/naples/florida/united-states/usfl0338/2016/1)).

We selected the geographical extent to model by drawing a minimum convex polygon around our presence points (see: 1.1.1 Burmese python presence data) and adding a 4.22 km buffer, the radius of Hart et al.'s (2015) home range estimate of 22.5 km<sup>2</sup>. This allowed for the consideration of the home range of pythons on the edge of the study extent.

### *1.2.2 Burmese python presence data*

We used presence-only occurrence data sourced from the Early Detection & Distribution Mapping System (EDDMapS) database. This web-based mapping system pools data on invasive species presence locations from multiple databases, organizations, and volunteer-submitted observations (EEDMapS 2015). All data are reviewed and verified by experts and are made publically available (C. Barger, Center for Invasive Species and Information Technology, personal communication). Observations often include information about the method used to verify the record, the precision of the geographic coordinates, and written comments about the geographic location and physical description of the animal recorded. More than 2,000 sightings of Burmese pythons have been entered into EDDMapS with most observations occurring after the mid-2000s. Due to their evasive and secretive behavior (Dorcas and Willson 2013) and the difficulty in traversing Florida's terrain, the majority of sightings occurred on or along roads or in urban areas. It can be assumed that the majority of living pythons reported were captured and likely euthanized; therefore, these data can be considered independent sightings (Florida Fish and Wildlife Conservation Commission n.d.; Harvey et al. 2009).

We inspected each occurrence and eliminated points from our final dataset if they fell under the criteria outlined in Table 1-1 to ensure our model included only presences from “wild” pythons rather than released pets. These criteria also allowed us to examine location accuracy given that reviewers sometimes need to estimate coordinates, particularly those reported from a systematic method or verbal description (L. Connor, Florida Fish and Wildlife Conservation Commission, personal communication). After evaluating these criteria, we still suspected that some coordinates had been recorded with locational error, particularly when a set of points were located parallel to a road segment instead of overlapping the segment. We reexamined all data points located off-road to determine if the observation in fact occurred on a road. If, based on written comments or location descriptions, it was clear that the snake was initially spotted on a road, we reassigned the observation’s coordinates to the nearest location on a road using programs Geospatial Modeling Environment (GME) v. 0.7.3.0 (Beyer 2012) and ArcMap v. 10.2.2 (ESRI, Redlands, CA, USA).

Our final python presence dataset was downloaded from EDDMapS on October 15, 2015. Using our selection criteria, we determined that 2,014 of the presences satisfactorily met our criteria to be included in our analyses. Presences ranged from the Florida Keys to just west of Sarasota and north of Port St. Lucie, but nearly all search effort to date has been concentrated within ENP and the Homestead region (~90%), and the greater Naples metropolitan area (~2.5%) (Figure 1-1).

### 1.2.3 Environmental variables

Previous applications of predictive habitat distribution modeling to the south Florida Burmese python invasion (e.g. Pyron et al. 2008, Rodda et al. 2008, Rodda et al. 2011) have relied exclusively on climate variables. These studies aimed to predict the range of Burmese pythons throughout North America whereas our study aims to predict relative habitat suitability within southern Florida. We used land cover variables because these factors capture the variability of the geographic space being modeled at this intermediate scale in comparison to variables such as climate, which are more appropriate at broader scales (Peterson 2011). We obtained land use/land cover (LULC) data from the Florida Cooperative Land Cover Map, version 3.0 ([myfwc.com/research/gis/applications/articles/Cooperative-Land-Cover](http://myfwc.com/research/gis/applications/articles/Cooperative-Land-Cover)) and merged additional geospatial data on canals and ditches from the South Florida Water Management District (South Florida Water Management District GIS Data Catalogue, [http://www.sfwmd.gov/gisapps/sfwmdxwebdc/dataview.asp?query=unq\\_id=1959](http://www.sfwmd.gov/gisapps/sfwmdxwebdc/dataview.asp?query=unq_id=1959)), St. Johns River Water Management District (St. Johns River Water Management District GIS Development and Data Collection, [ftp://secure.sjrwmd.com/disk6b/lcover\\_luse/lcover2009/](ftp://secure.sjrwmd.com/disk6b/lcover_luse/lcover2009/)), and Southwest Water Management District (Southwest Water Management District Shapefile Library, [https://www.swfwmd.state.fl.us/data/gis/libraries/physical\\_dense/lu11.php](https://www.swfwmd.state.fl.us/data/gis/libraries/physical_dense/lu11.php)). We aggregated habitat classifications into 18 categories (see: Appendix A).

We chose three landscape variables to model habitat suitability: fine-scale land cover, home range-level land cover, and distance to open freshwater or wetland. The fine-scale land cover variable comprised of the cover classification within each 30-m cell. The

home range-level land cover variable considered the cover classification most prominent within a circle the size of a python home range surrounding each 30-m pixel. We used focal statistics in the Spatial Analyst extension in ArcMap to calculate the majority LULC type with a moving circular window analysis of radius 4.22 km, based on Hart et al.'s (2015) home range estimate of 22.5 km<sup>2</sup>. Considering python presence at the home range-level accounts for pythons' ability to make long distance movement. It also accounts for the likelihood that pythons are primarily sighted on roads that intersect their home ranges rather than in habitat characteristics that are correlated with roads. The distance to open freshwater or wetland variable comprised of the Euclidean distance in meters to the closest source of fresh water (lakes, ponds, streams, rivers, canals, ditches) or freshwater wetland. Although it has been shown that wild-caught Burmese pythons from Florida are capable of surviving in brackish water with no access to freshwater for several months, we did not include brackish water in this variable since it is assumed that individuals in brackish water will eventually need access to freshwater (Hart et al. 2012). We calculated distance using the Euclidean Distance tool in the Spatial Analyst extension in ArcMap. We chose this variable because Burmese pythons are semi-aquatic and their movements have been linked to presence of surface water (Hart et al. 2015).

We ran correlation analyses on our 3 environmental variables using the correlation test in the program ENMTools v. 1.3 (Warren et al. 2010; Warren and Seifert 2011). All three pairwise comparisons had Pearson correlation coefficients <0.7 and thus were not spatially associated.



#### *1.2.4 Habitat suitability modeling*

We used MaxEnt version 3.3.3k because it has become widely accepted as one of the highest performing and accurate ENM methods (Pearson et al. 2007; Wilting et al. 2010; Elith et al. 2011), particularly when assumptions of sampling bias are addressed in model implementation (Clements et al. 2012; Kramer-Schadt et al. 2013; Syfert et al. 2013). Within MaxEnt, we used all feature types, 5000 iterations,  $10^{-5}$  convergence threshold, 0.5 prevalence, and a regularization multiplier of 3 to build habitat suitability models for each bias correction method using the same set of python presence points and environmental variables. (Phillips et al. 2004; SJ Phillips et al. 2006; Phillips and Dudík 2008). It has been demonstrated that a regularization multiplier of 3, rather than 1, lowers the risk of over-fitting while also smoothing the model output across the landscape (Elith et al. 2011; Merow et al. 2013). We also tested a range of regularization multipliers but the value did not impact final model performance. Each model scenario was replicated 10 times.

#### *1.2.5 Correcting for geographical sampling bias*

Caution must be exercised in ENM to ensure that model assumptions are met. Presence-only models assume that data are random or at least representative of the range of environmental variables exploited by the focal species (Syfert et al. 2013). Burmese python data in EDDMapS exhibit strong geographical sampling bias due to the inaccessibility of much of Florida's landscape and changes in effort to search for and report pythons over time (Willson et al. 2011). Sightings occurred predominantly along

roads, most notably along ENP's main park road. Outside of ENP and nearby Big Cypress National Preserve (BCNP), sightings largely occurred in urban landscapes.

It is possible to correct for bias in presence-only data collection if some knowledge of sampling effort is known (Yackulic et al. 2013; Stolar and Nielson, 2014). MaxEnt makes use of background points to gather information on the set of environmental conditions available to the focal species in the region being analyzed in order to relate habitat suitability to the available environment (Phillips et al. 2009). Background point selection can thus be manipulated to match the bias inherent in the presence input data, allowing MaxEnt to focus on the differentiation between the presence distribution and the background distribution rather than the sampling bias (Phillips 2008).

We tested several scenarios for biasing background point selection that made use of MaxEnt's default, bias grid option, or "samples with data" (SWD) format. Table 1-2 describes the 10 bias correction scenarios we tested, how each accounts for the sampling effort in our dataset, and how each was integrated into the modeling process. All spatial and statistical analyses described in Table 1-2 were conducted in ArcMap, GME, and R v. 3.1.1 (R Development Core Team 2011). We compared the 10 bias correction scenarios to determine which captured the sampling effort in the EDDMapS dataset best.

### *1.2.6 Model analysis*

MaxEnt model performance is commonly evaluated using the area under (AUC) the receiver operating characteristic (ROC) curve (Elith et al. 2011; Baldwin et al. 2009). We used MaxEnt's default cross-validation setting, which splits the presence only dataset

into training data, in order to fit the model, and into test data, in order to evaluate the model's predictions (Merow et al. 2013). While AUC values are generally considered to be good statistical measures of discrimination ability, the use of this approach alone has been heavily criticized in ENM because it incorrectly treats background points as true absence points (Peterson et al. 2008; Lobo et al. 2014; Fourcade et al. 2014). Instead, we employed a partial ROC (pROC) approach as recommended by Peterson et al. (2008). pROC evaluates the predictive performance of a model iteratively by only considering omission errors and the areas proportionally predicated as suitable (Escobar et al. 2013). When  $\geq 95\%$  of the replicated pROC AUC ratios are  $> 1.0$ , models can be considered to perform better than null models (Escobar et al. 2013). We calculated pROCs for each model scenario with Barve's (2008) pROC software using 1000 iterations and a 5% omission error. As long as model performance was positively confirmed by the pROC, we were confident using the AUC values generated by the default cross-validation setting in program MaxEnt to compare between model scenarios and to choose our best model since the only differences between scenarios was in background point selection.

We evaluated model output similarity between scenarios using the niche overlap analysis in ENMTools. Although traditionally used to compare niches between different species, we used this analysis to determine if our bias scenarios generated niches that differed from one another. This analysis calculates Schoener's (1968) *D* index, an ecologically meaningful measure, as well as the Hellinger similarity statistic *I* (Van der Vaart 1998), a statistically robust measure (Warren et al. 2010). Both indices provide a value between 0 (no overlap) to 1 (complete overlap) (Thompson et al. 2011).

We assessed the relative significance of each environmental variable using percent contribution jackknife tests (Elith et al. 2011). MaxEnt provides a heuristic measure of variable importance by quantifying the increases in gain by each variable within the model (Baldwin 2009). When used in combination with heuristic gain, the jackknife test excludes variables from analysis one at a time, thereby determining the relative strengths of each variable in explaining the model output (Yost et al. 2008; Baldwin 2009).

### 1.3 Results

#### 1.3.1 Selection of best habitat suitability model

All of the bias correction scenarios yielded pROC AUC ratios above 1.0, indicating that the habitat suitability models performed significantly better than random predictions (Figure 1-2). Therefore, we did not eliminate any models from consideration based on pROC values. First, we narrowed down the best grid values for the binary bias grid scenario (B-1:0 through B-1000:1, Table 1-2). The B-1:0 scenario had similar pROC AUC ratios and AUC values to the B-100:1, B-500:1, and B-1000:1 scenarios (Figure 1-2; Table 1-3). Scenarios B-5:1, B-10:1, and B-20:1 performed better, and the B-5:1 scenario performed the best with an AUC value of 0.817. Despite these differences in model performance, all final suitability maps had high degrees of overlap with Schoener's *D* indices and Hellinger similarity statistics (*I*) above 0.800 (Table 1-3).

Next we applied the 5:1 scale to the interpolated surface of roads bias grid scenario (KERN5) and compared the model performance to the KERN1 scenario. These two models had very similar pROC AUC ratios, the same AUC value (0.816), and 100%

overlap according to the *D* and *I* indices (Figure 1-2), indicating that these two scales generated the same habitat suitability model for this particular bias file scenario.

Lastly, we compared the overlap between all 10 of the bias correction scenarios using the B-5:1 binary bias grid scenario. All comparisons had *I* statistics over 0.900 and most had *D* indices above 0.800 (Table 1-4). Ten comparisons had *D* indices below 0.800. All of these comparisons were between an SWD strategy and a bias grid strategy. All 4 SWD scenarios yielded the highest AUC values, the only scenarios above 0.900. We chose the B-SWD scenario as the overall best model for habitat suitability because it had an AUC of 0.938, although the LOG-RD-SWD had the second highest AUC of 0.923.

### *1.3.2 Habitat suitability factors*

Home range-level land cover was the most important environmental variable to influence our final habitat suitability model with 63.3% overall variable contribution. Distance to open freshwater or wetland contributed 24.7% and fine-scale land cover contributed 12.1%. At the home range-level scale, estuarine habitat and freshwater non-forested wetlands were the most important cover types that contributed to python habitat suitability (Table 1-5). Estuarine habitat remained a powerful predictor of suitability at the fine-scale in addition to all 3 freshwater wetland cover types. Urbanized habitats, bodies of water, and natural rivers or streams were poor predictors of habitat suitability, although canals and ditches were relatively important predictors at the fine-scale. The probability of suitability was approximately 0.616 within 30-m of open freshwater and

wetland and sharply decreased to 0.383 at a distance of 125-m (Figure 1-3). Probability of suitability rose to 0.554 as distance increased to 3700-m from an open water source.

The probability of habitat suitability map was highly concurrent with the home range-level habitat layer (77.2% of all grid cells classified as estuary and 91.3% of all grid cells classified as freshwater non-forested wetland at the home range-level had a probability of habitat suitability above 0.5; Figure 1-4). Regions of high suitability were also associated with the most important fine-scale land cover types (97.7% of all grid cells classified as estuary, 21.5% of all grid cells classified as canal/ditch, and 52.0% of all 3 freshwater wetland habitats at the fine-scale had predicted probability of habitat suitability above 0.5). This output demonstrates the model's predictive ability in associating python occurrence in Florida with realistic habitat variables, given that high suitability is in the Everglades region where pythons are confirmed as established (Snow et al. 2007b). The majority of known python occurrences from the EDDMapS dataset occur in regions with relative habitat suitability between 0.50-0.75 (Figure 1-5). This figure is disproportionate to the availability of habitat classified as 0.50-0.75 suitable, demonstrating the high density of pythons in the Everglades region.

#### **1.4 Discussion**

The goal of this study was to identify the key environmental variables for predicting Burmese python habitat suitability in southern Florida at the present stage of invasion. As expected, habitat variables considered at a home range-level scale contributed the most to our model of relative habitat suitability. Current home range estimates show that individual Burmese pythons range throughout a large spatial area and

it has been demonstrated that they are capable of making long distances movements over a single day (Pittman et al. 2014; Hart et al. 2015). Kapfer et al. (2010) studied the relationship between home range size and habitat preferences in bullsnakes (*Pituophis catenifer sayi*), a mobile snake similarly often found in an agricultural/natural landscape mosaic. Bullsnaek home range size increased as proportion of unsuitable habitat within their range increased, suggesting that individuals needed to travel further to reach more preferable habitat (Kapfer et al. 2010). Longer dispersal distances in mammals are also linked to large home range size (Bowman et al. 2002). This relationship between movement and home range size could explain why the Burmese python invasion is moving northward (Conservancy of Southwest Florida 2015) and why some of the EDDMapS occurrence points intersect with habitat of relatively low suitability (Figure 1-5). As python density in the Everglades likely reaches carrying capacity, individual dispersers may need to travel further to find enough suitable habitat to meet their resource needs.

Overall, python presence was strongly influenced by water availability and most associated with freshwater non-forested wetlands and estuarine habitat at the home range-level. These cover types are widely available in the Everglades and are likely similar to the mangrove forests, marshes, and swamps from their native range (Snow et al. 2007b). At the 30m x 30m resolution estuarine habitat remained highly indicative of python presence while agricultural lands and canals became important predictors. Recent radio telemetry studies on adults have shown that pythons will often use agricultural levees and canals to make straight-line movements (Pittman et al. in review). Reed et al. (2011) noted high python densities in agricultural fields east of ENP and suggested that pythons

may have been attracted to these areas by high rodent abundance (which, in turn, was associated with vegetable availability and generally high primary productivity). Other fine-scale land cover types that were moderately associated with python presence included forested and shrub/scrub landscapes. Particularly within a freshwater wetland or estuarine matrix, these pockets of habitat may be important refuges for avoiding predation or nesting, or for avoiding detection by prey due to their propensity to ambush predation (Walters 2016).

#### *1.4.1 Correcting geographical sampling bias*

Given extensive criticism of MaxEnt's default settings (e.g., Rodda et al. 2011; Merow et al. 2013; Syfert et al. 2013), we expected that our DEF scenario would be the lowest performing scenario. In contrast, our usage of MaxEnt's default background point selection performed relatively well and generated a habitat suitability map with high niche overlap compared to the other scenarios that made use of bias grids or the SWD format. However, our use of the default settings did include a minimal correction for geographical sampling bias. MaxEnt draws background points from across the user-defined modeling extent. Instead of selecting points from across the globe, or even from the full area of Florida, we limited the extent of our sampling area at the start of the modeling process to a buffered MCP around the range of Burmese python presences. In turn, this reduced background selection to a localized geographical area within Florida.

We expected the LOG and LOG-RD scenarios to be among the strongest models but they were in fact the lowest performing scenarios. In contrast, the LOG-SWD and LOG-RD-SWD scenarios were the fourth and second best models respectively. The



logistic regression of sampling effort was meant to capture not only the bias associated with the correlation between sightings and presence of roads, but also the bias associated with effort to survey roads for pythons. Very little to no effort to systematically and randomly sample locations in Florida for pythons has taken place to date, and most conscious effort to look for pythons has disproportionately occurred in the ENP and Naples areas. When we created the distance of surveyed roads variable to input into our logistic regression, we took roads surveyed by the Everglades Invasive Reptile and Amphibian Monitoring Program and by dedicated researchers from the Conservancy of Southwest Florida into consideration. These two areas are located in the southern region of our modeling extent, thus creating bias in the sampling points found in EDDMapS. The logistic regression used to generate the LOG and LOG-RD scenarios reflects this latitudinal bias in sampling effort; therefore, it was surprising that the LOG and LOG-RD models performed poorly relative to the other models and our LOG-SWD and LOG-RD scenarios were not the top 2 best models. Despite this, the LOG-RD-SWD scenario generated results very similar to the best performing model (Figure 1-4).

More generally, bias correction scenarios that made use of a bias file did not perform as well as scenarios that made use of the SWD format. When the SWD format is used, all 10,000 background points spatially represent the sampling bias they are correcting and are all weighed equally by program MaxEnt. In contrast, MaxEnt randomly scatters 10,000 background points across a bias grid and uses the grid's value to determine how much a given point should be weighed. Although this assigns more influence to the background points that best represent the sampling bias, this means that only a portion of the 10,000 background points are explaining the bias while other

background points are still able to exert an albeit small influence on the model's predictions. Our results suggest that the SWD method may be superior to using a bias file and highlight the need to further explore the efficacy of bias correction techniques with MaxEnt. This may also explain why the LOG and LOG-RD scenarios did not perform as well as expected; it is possible that the use of the bias grid by MaxEnt explains more about the poor performance of the scenario rather than the failure of the logistic regression to capture the sampling effort inherent in the occurrence data.

#### *1.4.2 Interpretation and application of relative habitat suitability*

We emphasize that our predictive surface of habitat suitability is not meant to forecast a potential range of the Burmese python invasion. ENM assumes that the population being considered is in equilibrium within its environment and that the presence data reflect all favorable environmental conditions occupied by the species (Araujo and Pearson 2005; Phillips et al. 2008; Václavík and Meentemeyer 2009; Elith et al. 2010; Robinson et al. 2010; Rodda et al. 2011; Václavík and Meentemeyer 2012). This assumption is a challenge when using ENM for an invasive species because invasives are inherently expanding their range; thus, the stage of an invasion heavily influences the extent to which a species' full realized niche can be modeled (Václavík and Meentemeyer 2012). Data collected from a species in earlier stages will likely reflect only a small portion of the conditions it may be able to inhabit in comparison to a wider range of conditions it could inhabit when in later stages (Ficetola et al. 2010; Václavík and Meentemeyer 2012). Evidence suggests that the Florida Burmese python population is still growing and expanding northward (Conservancy of Southwest Florida 2015),

thereby supporting the notion that this invasive population is not in equilibrium with this novel environment. Given this, the results of our ENM only reflect the current habitat use by pythons in southern Florida and the most appropriate interpretation is that these habitat factors reflect current relative habitat suitability.

We further stress that the factors of habitat suitability we have identified should not be interpreted as the only suitable habitats that pythons are currently using or will exclusively use in the future. Mladenoff et al. (2009) modeled habitat use of recolonizing gray wolves (*Canus lupus*) in the northern Great Lakes region over several years and found that habitat suitability changed over time. Wolves preferentially occupied the most suitable habitats during the early stages of colonization but gradually used less suitable areas as the population's density in the region increased (Mladenoff et al. 1995, 1997, 1999). Invasive cane toads (*Chaunus [Bufo] marinus*) in Australia are showing signs of post-introduction evolution and increasingly occupying areas once considered to be physiologically unsuitable (BL Phillips et al. 2006; Urban et al. 2007). Given these examples, pythons on the expanding front of the invasion may preferentially select the most suitable areas first and less suitable areas later as high densities force individuals to move to previously unoccupied areas. It is also possible that pythons are still encountering habitat types that are novel to them. For example, pythons have recently been found occupying gopher tortoise (*Gopherus polyphemus*) and armadillo (*Dasypus novemcinctus*) burrows (Metzger 2013). These burrows may provide highly suitable habitat for pythons, particularly for overwintering, but we lack the appropriate occurrence data to test this hypothesis through our MaxEnt models.

Similarly, the python's niche in their introduced habitat may be evolving as they adapt to the Floridian environment. The python population in the core, southernmost areas of our study extent are likely at or closer to equilibrium than pythons in the northernmost regions. This uneven spread of stage of invasion may help to explain the greater coverage of suitability in the southern part of our predictive surface compared to the sparser predictions further north. In addition, land use change over time has been shown to influence the distribution of invasive species (Domènech et al. 2005; Ficetola et al. 2010; Hill et al. 2012). Florida's landscape is rapidly being developed, particularly due to urbanization in the central and northern parts of the state. Some landscape features associated with this type of development, such as canals and levees, may help to facilitate the spread of pythons while others, such as dense road networks (Shepard et al. 2008), may serve as dispersal barriers and force pythons to increase their home range size and use suboptimal areas.

The results from our study can inform management activities and more targeted studies of python habitat use and behavior. Identifying the cover types with which python presence is correlated may help to efficiently locate areas where pythons may first occur in higher densities, particularly in northern Florida's fragmented landscapes. This could allow for targeted surveillance and removal activities (Wiens and Graham 2005) and help researchers to detect study sites outside of the core Everglades population. The latter is especially important because there is still a need to understand what characteristics make these cover types suitable for python use, particularly in the context of different behaviors.

## 1.5 References

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**Table 1-1.** Criteria used to determine if python presences recorded in EDDMapS were either inaccurately recorded or likely a newly released pet. Presence points downloaded from EDDMapS in spreadsheet format contain extensive metadata that can be used to evaluate the efficacy of a particular data entry.

<b>Uncertainty</b>	<b>Metadata category</b>	<b>Reason to eliminate from analysis</b>
Coordinates	Precision	Entries were listed as either “Accurate” or “Approximate”. Approximate coordinates were not accurate to 30m <sup>a</sup> , the resolution modeled in this study, and were thus eliminated from analysis. If nothing was entered in this category, the data point was also eliminated.
	Coordinate Uncertainty	Most data points did not list a coordinate uncertainty. If an entry was considered to have “accurate precision” but listed a coordinate uncertainty >30m, it was eliminated from analysis.
	Comments	If written comments indicated that the coordinates were uncertain or that the coordinates had been taken from a different location from where the animal was found, the entry was eliminated from analysis.
Possible newly released pet	Comments	The albino morph is a popular skin pattern associated with pet Burmese pythons. As a recessive gene, it is not commonly found in wild snakes and can be associated with reduced fitness. We assumed that any data entries describing an albino or “yellow” snake were thus recently released pets and could not be considered to be a part of the established, breeding population.
	Photographs	Some entries were verified with photographs that were also available on EDDMapS’s interactive webmap. If the photograph showed a yellow/albino morph, the data point was eliminated from analysis.
Species identification	Identification credibility	Entries were listed as “Credible”, “Delete”, “Possible”, or “Verified”. Any entries listed as possible or delete were eliminated from analysis as well as any entries without an identification credibility listed.
	Comments	If comments mentioned that the observer was unsure if it was a Burmese python, and there were no photographs to verify the observation, the entry was eliminated from analysis.



**Table 1-2.** Description of the 10 bias correction scenarios tested and how they were implemented in the modeling process.

<b>Strategy</b>	<b>Scenario</b>	<b>Scenario abbrev.</b>	<b>Application to python system</b>	<b>Explanation of process</b>	<b>References</b>
Random sampling of background points	Default	DEF	Default setting of MaxEnt.	Program MaxEnt randomly selects 10,000 background points from the entire extent of the study area being modeled.	Elith et al. 2011
Bias grid	Binary bias (Yes/No roads/off-road)	B-1:0 B-5:1 B-10:1 B-20:1 B-100:1 B-500:1 B-1000:1	Pythons are primarily found on roads, thus assume roads are the only bias.	Converted roads polyline feature into a raster grid where roads were given a value higher than non-road cells. We tested a number of combinations (road cells: non-road cells) of values to determine if any one combination resulted in a better performing grid: 1:0.001 (because MaxEnt requires positive, non-zero values); 5:1, 10:1, 20:1, 100:1, 500:1, 1000:1. When a bias grid is entered into the program, MaxEnt will still randomly select 10,000 background points within the modeling extent, but the value of the cell a given point intersects determines how strongly it influences the model.	Clements et al. 2012; Elith et al. 2010; Elith et al. 2011; Fourcade et al. 2014
		Binary bias (Yes/No roads/off-road), based on percentages			

Table 1-2 continued

Strategy	Scenario	Scenario abbrev.	Application to python system	Explanation of process	References
Bias grid, continued	Interpolated surface of roads	KERN1 KERN5	Python presences are biased mainly to roads, thus assume the likelihood of encountering one decreases with increasing distance from road.	Derived a kernel density map of the road polyline feature, representing a gradual decrease in sampling intensity as distance increased from a point on a road. We scaled the values assigned to each cell from 1 to approaching zero (KERN1), and also tested the best set of values from the binary bias grid scenario as an alternative scale (KERN5).	Elith et al. 2010; Fourcade et al. 2014
	Logistic regression of sampling effort	LOG	Certain variables related to sampling can predict the likelihood of encountering a python.	Estimated sampling effort for the EDDMapS data set using logistic regression in R with the following predictor variables (independent of those used in the ENM): speed limit of road, annual average daily traffic of road, Euclidean distance to road, population density, and distance to surveyed roads <sup>a</sup> . Applied the final model to geospatial layers in ArcMap to generate bias grid.	Stolar and Nielson 2014
	Logistic regression of sampling effort on roads	LOG-RD	Pythons are primarily found on roads, but there are certain variables related to sampling that can predict the likelihood of encountering a python on a road.	Converted a roads polyline feature into a raster grid and merged it with the logistic regression of sampling effort layer such that pixels off road were given a value of 0.001 (i.e., effectively zero) and pixels on a road were given a value based on the logistic regression's estimate of sampling effort	Fourcade et al. 2014; Stolar and Nielson 2014

Table 1-2 continued

Strategy	Scenario	Scenario abbrev.	Application to python system	Explanation of process	References
SWD format (“samples with data”)	Binary bias (Yes/No roads/off-road)	B-SWD	Pythons are primarily found on roads, thus assume roads are the only bias.	Randomly generated 10,000 background points that intersected with roads polyline feature in ArcMap. Used GME to merge environmental information with the geographic coordinates of each point and directly inputted into MaxEnt via .csv files.	Fourcade et al. 2014
	Binary bias (Yes/No roads/off-road), based on percentages	P-SWD	Pythons are primarily found on roads, but they can be encountered off-road a certain percentage of the time.	86.6% of python observations were on roads, while 13.4% were at an off-road location. Randomly generated 8,660 background points that intersected with roads and 1,340 that were not located on a road in ArcMap. Used GME to merge environmental information with the geographic coordinates of each point and directly inputted into MaxEnt via .csv files.	Fourcade et al. 2014
	Logistic regression of sampling effort	LOG-SWD	Certain variables related to sampling can predict the likelihood of encountering a python.	Randomly generated 10,000 background points that were locationally biased based on the logistic regression estimate of sampling bias across the geographical modeling extent. Used GME to merge environmental information with the geographic coordinates of each point and directly inputted into MaxEnt via .csv files.	Stolar and Nielson 2014

**Table 1-2** continued

<b>Strategy</b>	<b>Scenario</b>	<b>Scenario abbrev.</b>	<b>Application to python system</b>	<b>Explanation of process</b>	<b>References</b>
SWD format (“samples with data”), continued	Logistic regression of sampling effort on roads	LOG-RD-SWD	Pythons are primarily found on roads, but there are certain variables related to sampling that can predict the likelihood of encountering a python on a road.	Randomly generated 10,000 background points that intersected with roads and that were locationally biased based on the logistic regression estimate of sampling bias across the geographical modeling extent. Used GME to merge environmental information with the geographic coordinates of each point and directly inputted into MaxEnt via .csv files.	Fourcade et al. 2014; Stolar and Nielson 2014

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<sup>a</sup>See: Appendix B.

**Table 1-3.** Calculated Schoener's  $D$  indices (above gray blocks), Hellinger similarity statistics ( $I$ ) (below gray blocks), as indicators of model similarity among the binary bias grid scenarios. AUC values generated by the default cross-validation setting in MaxEnt are measures of relative model performance, reported here to compare between model scenarios.

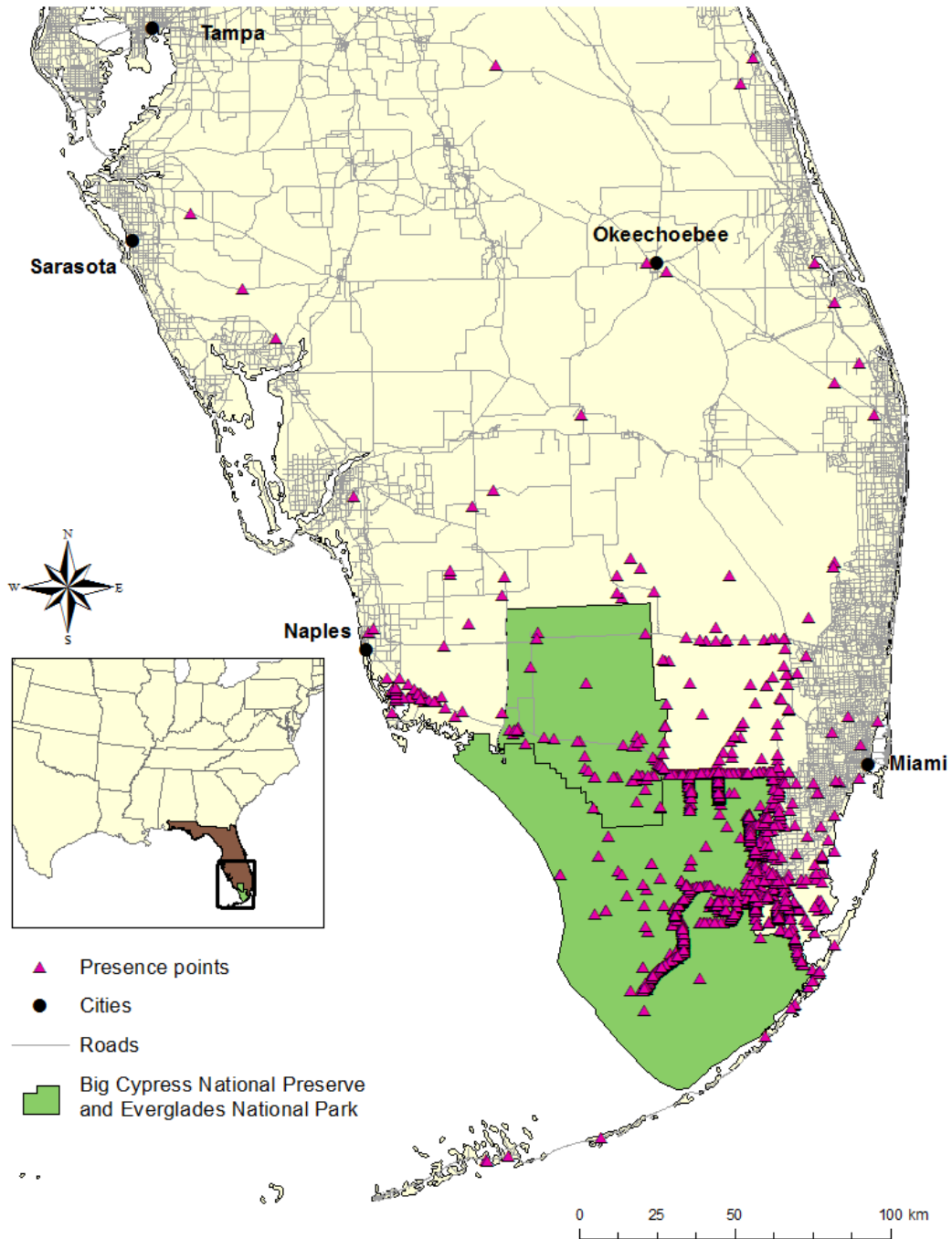
<b>Model</b>	B-1:0	B-5:1	B-10:1	B-20:1	B-100:1	B-500:1	B-1000:1
B-1:0		0.810	0.846	0.887	0.960	0.986	0.989
B-5:1	0.961		0.962	0.922	0.848	0.822	0.818
B-10:1	0.973	0.998		0.959	0.884	0.859	0.855
B-20:1	0.984	0.994	0.998		0.925	0.899	0.895
B-100:1	0.996	0.978	0.987	0.994		0.974	0.969
B-500:1	0.998	0.968	0.979	0.988	0.999		0.995
B-1000:1	0.999	0.966	0.977	0.987	0.999	0.999	
<i>AUC value</i>	<i>0.759</i>	<i>0.817</i>	<i>0.810</i>	<i>0.801</i>	<i>0.779</i>	<i>0.760</i>	<i>0.759</i>

**Table 1-4.** Calculated Schoener’s *D* indices (above gray blocks), Hellinger similarity statistics (*J*) (below gray blocks), as indicators of model similarity among the 10 bias correction scenarios. AUC values generated by the default cross-validation setting in MaxEnt are measures of relative model performance, reported here to compare between model scenarios.

<b>Model</b>	<b>DEF</b>	<b>B-5:1</b>	<b>PER</b>	<b>KERN1</b>	<b>LOG</b>	<b>LOG-RD</b>	<b>B-SWD</b>	<b>P-SWD</b>	<b>LOG-SWD</b>	<b>LOG-RD-SWD</b>
DEF		0.944	0.931	0.975	0.893	0.815	0.764	0.823	0.807	0.805
B-5:1	0.997		0.985	0.962	0.870	0.817	0.796	0.855	0.839	0.826
PER	0.995	1.000		0.949	0.859	0.816	0.805	0.864	0.843	0.831
KERN1	0.999	0.998	0.997		0.881	0.815	0.782	0.841	0.824	0.824
LOG	0.992	0.987	0.985	0.990		0.894	0.686	0.737	0.743	0.743
LOG-RD	0.972	0.974	0.973	0.972	0.988		0.661	0.707	0.733	0.734
B-SWD	0.997	0.957	0.960	0.950	0.917	0.917		0.914	0.913	0.913
P-SWD	0.968	0.979	0.981	0.973	0.945	0.939	0.994		0.917	0.917
LOG-SWD	0.960	0.972	0.974	0.965	0.944	0.946	0.986	0.992		0.955
LOG-RD-SWD	0.956	0.969	0.972	0.962	0.944	0.954	0.985	0.988	0.991	
<i>AUC value</i>	0.822	0.817	0.814	0.816	0.779	0.749	0.938	0.919	0.914	0.923

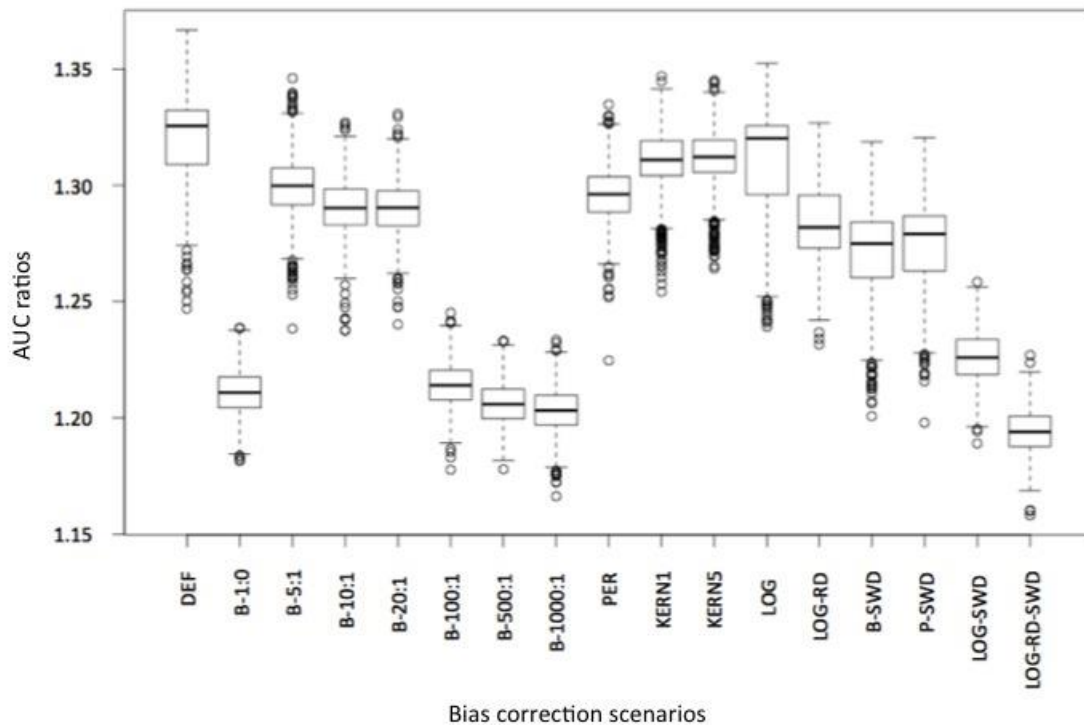
**Table 1-5.** Home-range level and fine-scale cover type suitability scores for each habitat classification for the B-SWD bias correction scenario.

Habitat classification	Home-range level	Fine-scale
Natural or artificial lakes & ponds	0.074	0.153
River or stream	-	0.209
Canal or ditch	-	0.484
Estuarine	0.179	0.860
Freshwater non-forested wetland	0.455	0.455
Freshwater forested wetland	0.021	0.456
Freshwater non-vegetated wetland	-	-
Hardwood forested uplands	-	0.456
High pine and scrub	0.074	0.456
Pine flatwoods and dry prairie	0.074	0.262
Mixed hardwood and coniferous	0.074	0.322
Shrub and brushland	-	0.470
Barren	0.074	0.456
Coastal	-	0.456
Agriculture	0.074	0.507
Rural lands	0.005	0.326
Low intensity urban	0.008	0.278
High intensity urban	0.011	0.333

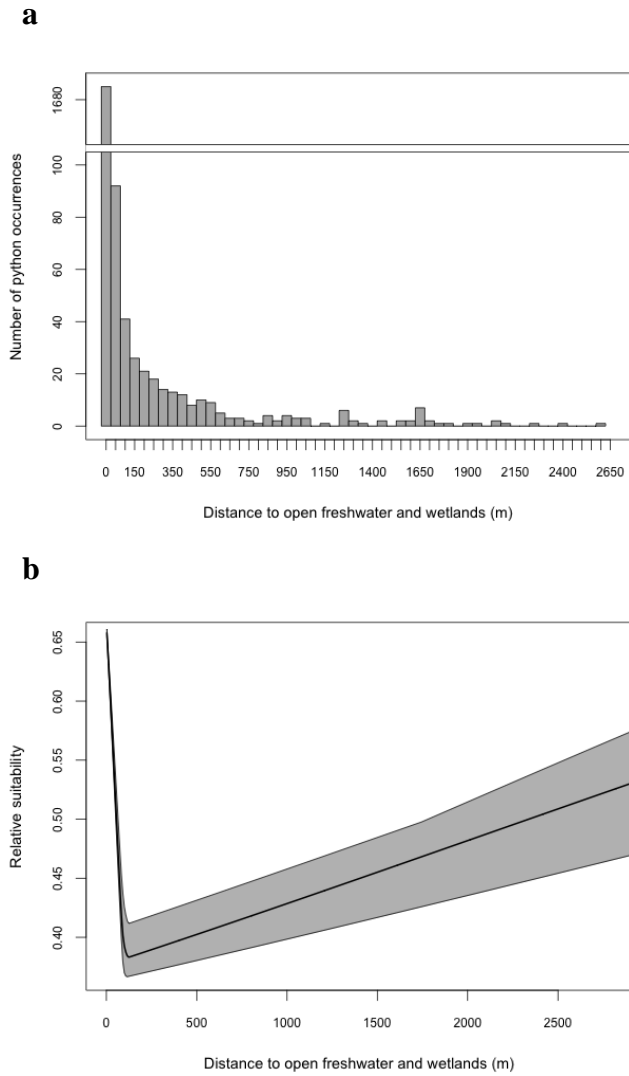


**Figure 1-1.** Map of Burmese python presences used in MaxEnt modeling scenarios in relation to roads and Everglades National Park and Big Cypress National Preserve. Data were downloaded from EDDMapS on October 15, 2015 and were culled for inaccurate entries. Note that the roads displayed in this figure are a subset of the final roads polyline feature used in all analyses.

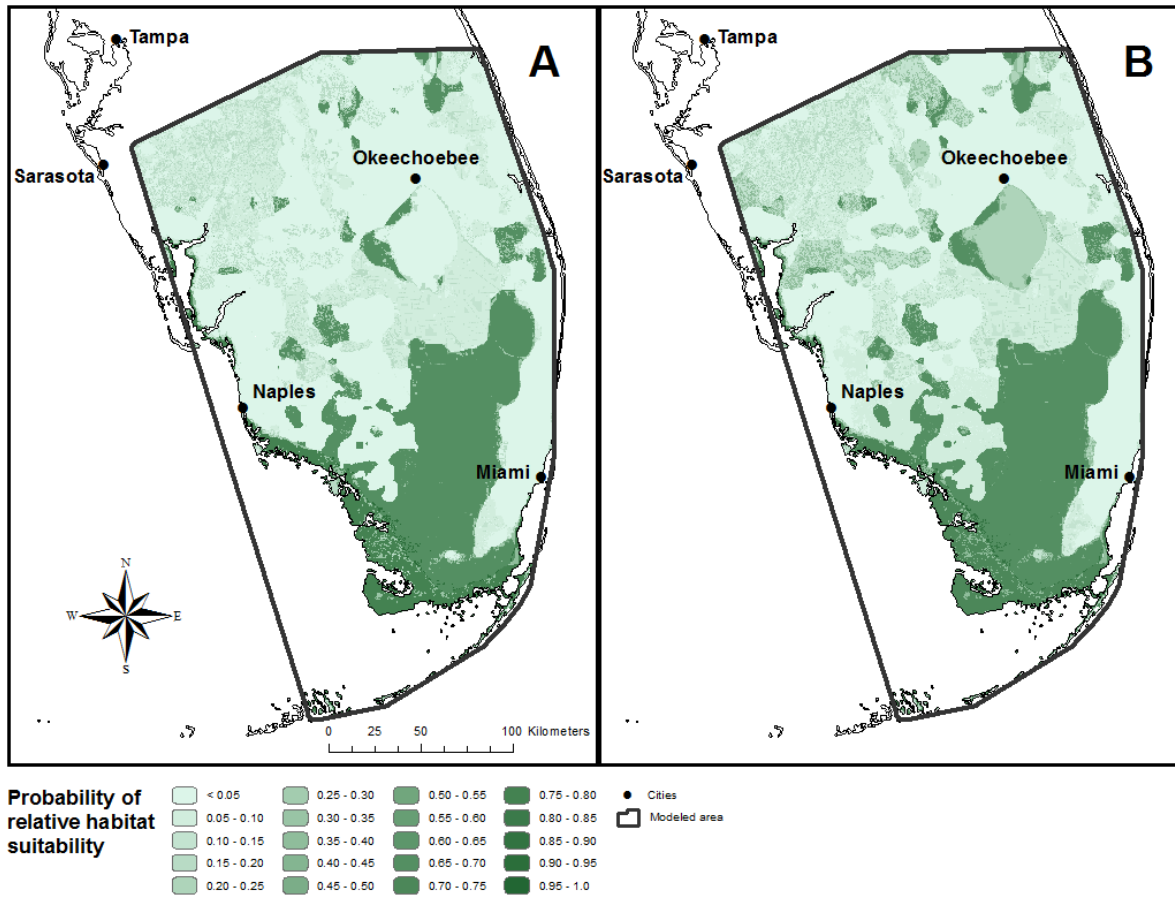




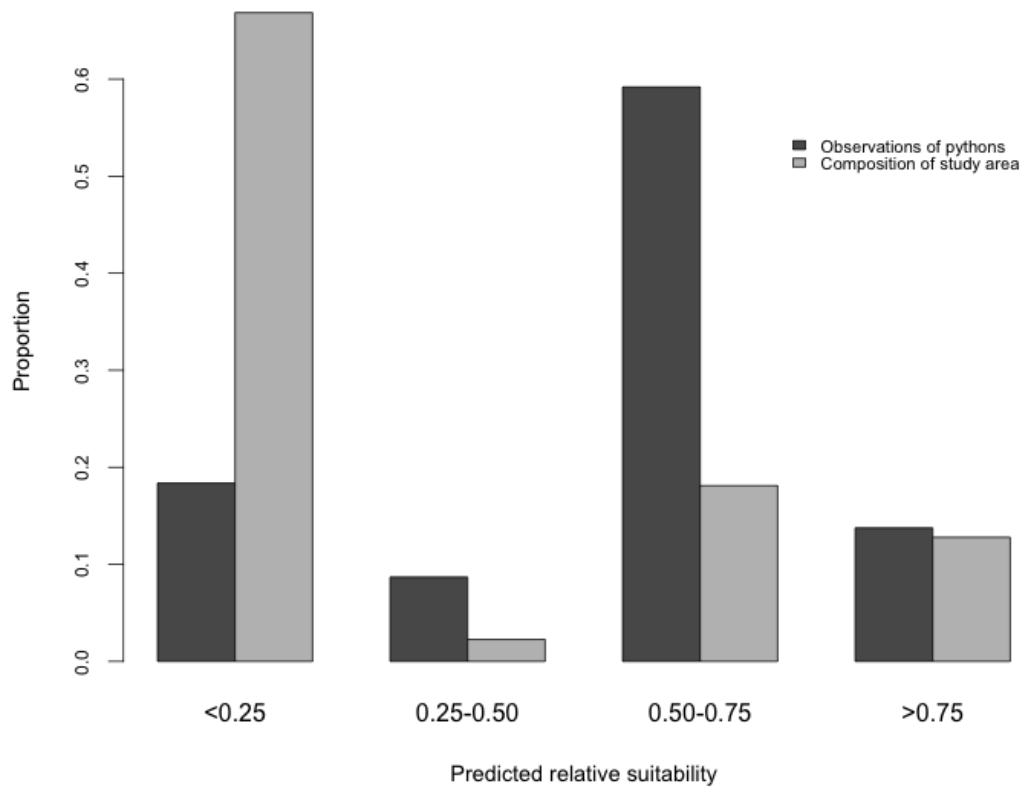
**Figure 1-2.** Summary of partial ROC AUC ratios for each bias correction scenario (n=1000). When >95% of AUC ratios are above 1.0, the model is better than a random prediction.



**Figure 1-3.** (a) Distribution of python occurrences and (b) relative suitability of habitat as a function of distance to open freshwater or wetland for the B-SWD bias correction scenario.



**Figure 1-4.** Comparison of the current predicted relative habitat suitability of southern Florida for the (a) B-SWD and (b) LOG-RD-SWD bias correction scenarios.



**Figure 1-5.** Proportion of Burmese python occurrence points from the EDDMapS database (dark gray) and grid cells from the B-SWD predicted suitability surface (light gray) that occurred/were classified for each relative suitability value.

## CHAPTER 2. INVESTIGATING MOVEMENT BEHAVIOR OF INVASIVE BURMESE PYTHONS ON A SHY-BOLD CONTINUUM USING INDIVIDUAL BASED MODELING

### 2.1 Introduction

Invasion biology has a long tradition of identifying traits that could explain between-species dissimilarities in species' abilities to succeed as invaders (Kolar and Lodge 2001; Hayes and Barry 2008; Cote et al. 2010). However, examining the average behavioral response of a population as a whole masks the variation between individuals that likely drives invasion dynamics, particularly those characteristics that may only be advantageous in certain phases of the invasion. The process of an invasion is composed of several stages starting with initial introduction and spread, establishment, and ending with integration into the ecological community (Vermeij 1996). Researchers are increasingly focusing on different behaviors that help invaders complete and transition from one stage to another while recognizing that these behaviors may not be as beneficial to the persistence of the invasive population in the next phase of the invasion (Cote et al. 2010).

Personality-dependent dispersal, where personality types such as boldness, aggressiveness, and sociability are linked to the propensity to disperse, is particularly relevant in studying the spread of invasive populations (Cote and Clobert 2007; Duckworth and Badyaev 2007; Cote et al. 2010; Sih et al. 2012). The ability of an

invasive population to spread is characterized by both high dispersal rates and long-distance dispersal (Neubert and Caswell 2000; Rehage and Sih 2004; Cote et al. 2010). The net movement of the most dispersive individuals of a population determines its rate of expansion, even when long-distance dispersal events are rare (Neubert and Caswell 2000; Bartón et al. 2012). Fraser et al. (2001) demonstrate that movement behavior is heterogeneous within a population, thus intraspecific differences in demography, behavior, or personality are important to describing dispersal kernels for an invading population. For example, recolonizing western bluebirds (*Sialia mexicana*) on an expanding front across the western United States were more likely to be aggressive and to thus outcompete sister taxa; however, individuals behind the front in the established range were more likely to be less aggressive because high aggressiveness was correlated with poor parental care in males (Duckworth and Badyaev 2007). Invasive cane toads (*Chaunus [Bufo] marinus*) in Australia employ a range of sociality depending on their position along the colonization front (González-Bernal et al. 2014). Boldness has been linked to dispersal tendency in a variety of species including pumpkinseed sunfish (*Lepomis gibbosus*; Coleman and Wilson 1998), gobies (*Neogobius melanostomus*; Myles-Gonzalez et al. 2015), great tits (*Parus major*; Dingemanse et al. 2003), and swift foxes (*Vulpes velox*; Bremner-Harrison et al. 2004).

Boldness is the tendency of organisms to explore and move through unfamiliar space and novel situations (Wilson et al. 1993). Bold individuals tend to move greater distances and to be riskier in how they explore unfamiliar landscapes and in their antipredator response (Rehage and Sih 2004; Bartón et al. 2012; Edelsparre et al. 2013). While bolder dispersers move greater distances, they also have higher probabilities of

mortality (Azevedo and Young 2006). For example, in reintroduced swift foxes in Montana, the boldest individuals moved the furthest from their release sites but experienced lower survival compared to individuals who limited their movements (Bremner-Harrison et al. 2004). Bold male elk (*Cervus elaphus*) in Alberta, Canada had higher movement rates and greater use of risky landscapes compared to shy male elk and were more likely to be harvested by hunters (Ciuti et al. 2012). Clearly, behaviors that maximize an individual's dispersal distance are not as advantageous to individual survival (Bartón et al. 2012). This suggests that the expansion of a population is driven by within-individual variation in balancing risk and dispersal distance (Zollner and Lima 2005), or that boldness varies between-individuals with those on the expanding front bolder than the average individual in the core population and the rare, bold survivor driving the expansion (Fraser et al. 2001; Bartón et al. 2012; Lindström et al. 2013).

Among the most significant biological invasions currently taking place in the eastern United States is the Burmese python in southern Florida. Pythons are already well established in the Everglades, but they appear to be expanding their range northward into more urbanized and heterogeneous landscapes (Dorcas and Willson 2011). While south Florida's habitat is ideal for the python in some respects (e.g. abundant prey, similar climate as native range, pockets of less disturbed habitat), it is not without risks of mortality (e.g., predators, road networks, farming/moving equipment).

Knowledge of resource distribution as well as habitat suitability is important in predicting the python population's ability to persist in novel, fragmented habitats outside of the Everglades, but it is also just as important to understand their movement and behavior (Taylor et al. 1993; Fahrig 2002; Knowlton and Graham 2010). It is

increasingly recognized that dispersal and movement are key processes involved in measuring landscape connectivity for a particular species (Henein and Merriam 1990; Taylor et al. 1993). However, little is known about the behavior and movement of dispersing juvenile Burmese pythons due to their evasiveness and their use of habitat that is difficult for researchers to access. Studying the behavioral components of how pythons move through Florida's landscape thus contributes to our understanding of their ability to spread into other habitat that we do not currently recognize as suitable. Additionally, knowledge of the patterns of dispersal aids in our ability to plan targeted control methods that could prevent or at least manage the spread of Burmese pythons and other invasive species in the state (Reed et al. 2011; Hudina et al. 2014).

Our objective was to use a spatially explicit individual based model (IBM) to investigate boldness on the edge of the expanding range of Burmese pythons in southern Florida as the population expanded from the Everglades into more human-dominated landscapes. Employing an IBM allows one to investigate the interaction between individual behaviors and landscape configuration and characteristics, an interaction that drives animal movement behavior (Zollner and Lima 1999), and to examine how the patterns of individual behaviors generate a system's dynamics. Our goal was to simulate individual behaviors on the leading edge so we could observe the rare dispersal events that drive a population's expansion. We predicted that individuals on the expanding front characterized as bold would move faster and further than individuals who were characterized as shy, and that the rate of expansion of bold individuals would most closely resemble the one observed in the Burmese python population between 2004-2013. We also predicted that the final range occupied by pythons as facilitated by bold



dispersers would most closely resemble the observed range occupied by pythons during this same time frame. We expected bolder individuals to experience higher rates of mortality, to make longer distance movements, and to establish home ranges further away from their release locations in comparison to shyer individuals.

## **2.2 Methods**

### *2.2.1 Model overview*

Our goal was to simulate risk-taking behavior in dispersing juvenile Burmese pythons on the leading edge of an expanding front. We created 6 behavioral scenarios on a shy-bold scale and modeled dispersal of 25 virtual pythons per scenario per dispersal season. We only modeled individuals on the leading edge of the front; at the beginning of each dispersal season, we determined the new leading edge and selected a new random sample of 25 individuals. In doing so, we were able to simulate python expansion across our study site while restricting our focus to virtual snakes on the leading edge of the population.

### *2.2.2 Modeling framework*

We used the spatially explicit individual-based model Spatially Explicit Animal Response to Composition of Habitat (SEARCH). SEARCH simulates animal dispersal and home-range establishment on a virtual landscape with a high degree of behavioral complexity (Pauli et al. 2013). The program interfaces with ArcGIS (ESRI, Redlands, CA, USA) to build a virtual landscape, which is comprised of vector-based maps representing animal movement, foraging opportunities, risk of mortality, habitat

suitability, and exclusive occupancy of resident animals (Pauli et al. 2013). Each map contains specific field definitions based on different GIS classifications, and virtual animals individually alter their behavior or physiology based on these parameters (Pauli et al. 2013). Dispersers can be introduced to the landscape via a point release map or may be “born” on the landscape through the reproduction of resident animals (Pauli et al. 2013). Each individual generates its own memory map. This represents the information it perceives from its environment and is used in making decisions. Virtual animals respond to per timestep mortality and energetics and change behavioral states (e.g., searching vs. foraging, risky vs. safe) as they interact with the landscape (Pauli et al. 2013). Parameters governing behavior, energetics, home-range requirements, and resident reproduction can be modified to include heterogeneity in animal response caused by gender, time, and behavioral state (Pauli et al. 2013; Blythe et al. 2011).

### *2.2.3 Model study area*

We simulated dispersal and home range establishment of juvenile pythons on an agricultural and urban interface in southern Florida between the southeastern Everglades, Homestead, and south Miami. Southern Florida is located in a subtropical climate characterized by a wet and a dry season. This section of the Everglades is comprised of freshwater sloughs, marl prairies, tropical hardwood hammocks, and pinelands. Agricultural lands and low-density urban development characterize Homestead, Florida, while urbanization intensity increases rapidly as Homestead connects to southern Miami and approaches the city center. These areas are anthropogenically connected via a dense road network and canal waterways.

We chose this study area because it was comprised of land cover types from which we had empirical data on juvenile python movement (see: 2.2.4 Model study system). The Early Detection & Distribution Mapping System (EDDMapS) database also provided extensive presence data recorded over 10 years in this location that we used to pattern-match (Grimm and Railsback 2013) our model outputs (see: 2.2.4 Model study system and 2.2.8 Analysis).

We selected the modeling extent by first identifying the invasion front in the EDDMapS dataset from the natural land cover types associated with the Everglades into the more heavily altered landscapes of Homestead and south Miami. The study area borders were selected based upon their clear delineation of an observed annual progression of pythons across an area of feasible size to simulate at our desired resolution. We calculated 99% kernel density estimates (KDE) around presence points for each year successively from 2002 until the present. We visually estimated that the 2004 KDE isopleth best represented the initial presence of pythons in this study area. Likewise, we estimated that the 2013 KDE isopleth best represented the expansion of the python population across the study area. Therefore, we simulated dispersal by pythons between 2004 and 2013.

#### *2.2.4 Model study system*

The model was calibrated using empirical telemetry data from a two-year field study. During July of 2014 and 2015, 28 juvenile pythons (14 snakes per year, 7 snakes per clutch and site) were implanted with radio transmitters and released at their capture

sites (Pittman et al. in review). Juveniles were radio-tracked on agricultural lands, suburban landscapes, and natural habitats with less anthropogenic influence.

### *2.2.5 Simulation scenarios*

A given simulation scenario represented a replicate for one of 6 behavioral types on the shy-bold continuum as defined in section 2.2.7 Behavioral scenarios and parameterization. Each scenario ran for a dispersal season of 6 months over a 10-year period from 2004 – 2013. We used a time step of 12 hours to accommodate the pythons' low movement patterns associated with ambush behavior, digestive requirements, shedding, and basking and program SEARCH's need for a 24-hour awake-sleep cycle.

### *2.2.6 Map inputs*

SEARCH requires one point map and four polygon maps (Pauli et al. 2013). The point map designates locations where dispersing animals not born to resident females on the map are released. This map is often used to specify locations of translocated animals or to ensure the origin of virtual dispersers in desired locations for specific research objectives. The four polygon maps were created by aggregating and reclassifying land cover types from a 30-m<sup>2</sup> land use/land cover map derived from the Florida Cooperative Land Cover Map, version 3.0 ([myfwc.com/research/gis/applications/articles/Cooperative-Land-Cover](http://myfwc.com/research/gis/applications/articles/Cooperative-Land-Cover)), which had additional geospatial data on canals and ditches from the South Florida Water Management District (South Florida Water Management District GIS Data Catalogue, [http://www.sfwmd.gov/gisapps/sfwmdxwebdc/dataview.asp?query=unq\\_id=1959](http://www.sfwmd.gov/gisapps/sfwmdxwebdc/dataview.asp?query=unq_id=1959)).

#### 2.2.6.1 Release

The release map defines the release points, or starting locations, for each individual virtual python at the start of a given simulation. For the first year of each simulation scenario, we randomly selected 25 release sites within 1-m of the 2004 KDE isopleth using the Create Random Points tool from the Data Management toolbox in ArcMap 10.2.2. For each subsequent year, we chose a new random sample of 25 individuals on the new leading edge. We determined the new front by buffering the previous years' isopleth by the furthest distance traveled by a virtual python that survived the simulated dispersal season. The new 25 release sites were then randomly selected within 1-m of the new leading edge.

Release sites could only occur on areas defined as suitable for home range establishment. However, sometimes there was a lack of suitable habitat within 1-m of the leading edge for simulations run in the years 2012 and/or 2013. In this case, virtual animals were released within 1-m of the leading edge onto any habitat except where open water occurred.

#### 2.2.6.2 Movement

We scaled up the 30-m<sup>2</sup> LULC map to a 100-m<sup>2</sup> resolution in order to cut down on computer processing when running our simulations. The 100-m<sup>2</sup> map was then aggregated and reclassified into seven land cover types: canals, agricultural lands, low intensity urban, high intensity urban, naturally-dominated habitat, open water, and core-population barrier (Figure 2-1 and Appendix C). Although our models ran at 12-hour timesteps (see: 2.2.5 Simulation scenarios), our movement parameters were calculated

based on a 24-hour period. This is due to SEARCH's need for a 24-hour sleep-awake cycle; therefore, virtual animals would move during a given day's first timestep, or 12-hour period, and would "sleep", and thus remain stationary, during the second timestep. We calibrated movement parameters using a subset of the 2014 & 2015 telemetry data. The animals in this study were primarily radio-tracked 1-2 times per week; however, they were radio-tracked for 3-10 days successively after initial release (Pittman et al. in review). These locations provided the initial parameterization for our movement model and we used pattern matching to adjust our final parameters.

#### 2.2.6.2.1 Penetrable land cover

Virtual pythons were able to move through canals, agricultural lands, low intensity urban, high intensity urban, and naturally dominated habitat. The likelihood of entering or leaving a particular habitat type was determined by the boundary crossing ranking. The probability that a virtual snake will cross over the boundary of one habitat type to another is defined by the following equation,

$$p = n/c$$

where  $p$  is the probability of crossing the boundary,  $n$  is the rank of the new habitat, and  $c$  is the rank of the current habitat (Blythe et al. 2011). A random number,  $r$ , is drawn from a uniform distribution, and if  $r$  is greater than  $p$ , the animal remains in its current habitat and vice versa if  $r$  is less than  $p$  (Blythe et al. 2011). Observations of juvenile Burmese pythons suggest that they use canals as corridors to make long distance movements, and that they favor agricultural lands over natural habitat and are least likely to enter high intensity urban (Pittman et al. in review) Thus, canals were parameterized to have an

extremely high boundary crossing ranking (200; Table 2-1) compared to the other habitat types. This parameterization retained virtual snakes within the canal boundary for several timesteps, mimicking empirical movement data. Agricultural lands were given the next highest boundary crossing ranking (7), followed by natural habitat, low intensity urban, and high intensity urban (Table 2-1).

Animals in SEARCH move via a correlated random walk with turning angles between successive timesteps selected from a wrapped Cauchy distribution (see: Batschelet 1965; Pauli et al. 2013). In the field, pythons moved faster and straighter in landscapes with heavier anthropogenic alteration (i.e., agricultural lands and urban landscapes) compared to those with less human influence (i.e., naturally dominated habitat) (Table 2-1). In particular, they moved the furthest and the straightest through canals. Pattern matching during model testing revealed that we needed to parameterize our models with a lower than expected per timestep mean vector length (MVL), 0.9799, in order to keep pythons inside the boundary of the canal polygon. Because this per timestep MVL caused virtual pythons to regularly encounter and reflect off the canal boundary, we tripled the mean step length (MSL) estimated from the telemetry dataset (empirical: 76-m, modeled: 228-m) (Table 2-1; Pittman et al. in review). This pattern-matching process emphasized matching realistic movement patterns across the duration of an animal's movement in a canal rather than per timestep sinuosity, which was a better fit for the temporal resolution of the movement data, we used for model parameterization.

#### 2.2.6.2.2 Impenetrable land cover

Open water was impenetrable by virtual pythons in our simulations. While pythons are excellent swimmers (Minton 1966; Snow et al. 2007) and have been sighted in estuaries (EDDMapS 2015), water bodies were not classified as suitable habitat in maximum entropy modeling for relative habitat suitability using the presence-only EDDMapS dataset (see: Chapter 1).

The core-population barrier was an artificial land cover type created to represent the area on the map behind the leading edge of the invasion. This polygon acted as a reflective boundary that prevented virtual dispersers from entering the population core. This strategy ensured that the simulated snakes were always contributing to the spread of the population's range which was consistent with our goal to only simulate a random sample of pythons on the front of the expanding population. The population-core barrier was derived from the buffered KDE used to determine the release points for each year's simulation run (see: 2.2.6.1 Release). Thus, each simulated year had a unique movement map that was based upon the output of the previous year's simulations.

#### 2.2.6.3 Food

No data were available on the energetics of dispersing juvenile pythons. Thus, for the purposes of this study, we chose to disregard energetic considerations. To accomplish this, the food map in each of our simulation scenarios was uniform with a constant probability of capturing food and a constant amount of energy gained. All animals were parameterized at the beginning of the simulation to have an excess amount of energy to sustain them through the dispersal season without the risk of starvation.



#### 2.2.6.4 Risk

The risk map represented two types of mortality common to Burmese pythons in southern Florida: predation and mortality due to interactions with anthropogenic machinery. We were only able to determine the probability of mortality per timestep for human-dominated landscapes versus naturally dominated landscapes. Therefore, our risk map was binary, containing only these two habitat types. Risk was 2.8x greater in human-dominated areas versus naturally dominated (Table 2-2; Pittman et al. in review).

#### 2.2.6.5 Social

The social map defines areas that are suitable or unsuitable for home range establishment. The criterion for suitability is based on habitat quality and the occupancy of resident animals. If a given area is classified as unsuitable, a virtual disperser is unable to establish a home range and needs to find an area classified as suitable. We used the distribution of relative habitat suitability scores from maximum entropy modeling using the presence-only EDDMapS dataset (Chapter 1) to build our base habitat suitability map. Pixels were classified as suitable in SEARCH if their value corresponded to or was greater than 2 standard deviations below the mean suitability score across all of southern Florida.

We added some variability to this suitability landscape in order to account for the existence of non-simulated pythons occupying territories at the leading edge of the invasion front. These pythons were not explicitly modeled as dispersers in our simulations, but they were nonetheless influencing home range establishment of the virtual dispersers. To represent these non-simulated snakes, we randomly assigned 100-

m<sup>2</sup> areas the designation “unsuitable” with a greater probability of an area being selected as unsuitable the closer to the southwestern corner of our modeling extent (i.e., the territory closest to the Everglades where python populations are assumed to be at their densest). We then merged this map layer with our maximum entropy-derived suitability map in ArcMap.

### *2.2.7 Behavioral scenarios and parameterization*

In order to examine risk-taking behavior of dispersing juvenile pythons, we created six behavioral scenarios representing a gradient of responses to risk on a shy-bold scale: most shy, somewhat shy, behaviorally plastic, overall intermediate, somewhat bold, and most bold (Table 2-3). These behaviors can be implemented in SEARCH by manipulating criteria for dispersers’ tendency to switch from or remain in “risky” or “safe” modes and modifying movement behaviors and risk of mortality within these modes. Animals switch modes based on user-defined probabilities. We initially selected 3 probabilities (0.1, 0.01, and 0.001) to implement a 3x3 fully-crossed design, but model testing revealed that 3 of the combinations resulted in duplicate behaviors. Therefore, we focused our investigation upon the 6 combinations that best reflected the spectrum of shy to bold we wished to investigate.

Virtual animals in SEARCH switch between behavioral states depending on their sensitivity to perceived risk based on “close calls” from prior time-steps (Blythe et al. 2011). Close calls are determined by comparing a random number drawn from a uniform distribution and the per timestep risk of mortality multiplied by a user-defined modifier that is associated with being in risky or safe mode, depending on the current state of the

virtual animal at that particular timestep. While in risky mode, individuals moved faster than baseline conditions as parameterized in the movement map and were subjected to a greater risk of mortality (Table 2-4). In safe mode, virtual snakes moved slower than baseline conditions and had a lower risk of mortality (Table 2-4).

In our simulations, bolder individuals on the shy-bold continuum were less risk adverse than shyer individuals. This meant that bolder individuals had a lower trigger for switching from safe to risky mode while shyer individuals had a higher trigger for switching from safe to risky mode. Likewise, bolder individuals had a higher trigger for switching from risky to safe mode while shyer individuals had a lower trigger for switching from risky to safe mode. Behaviorally plastic individuals had the same low trigger for switching between risky to safe and safe to risky modes, while overall intermediate individuals had a the same median trigger for switching (Table 2-3).

### *2.2.8 Analysis*

In SEARCH, animals are subjected to a number of fates during and at the end of each simulation. If they survive a given dispersal season, they either successfully establish home ranges or they fail to establish a home range and die during the inter-dispersal period. Mortality throughout the dispersal season can be caused by starvation or mortality as represented in the risk map. For our simulations, we categorized animals who established home ranges or failed to establish home ranges as “alive” at the end of a given dispersal season, and animals who succumbed to predation/mortality as “dead”.

We used a pattern-oriented approach to compare model outputs to empirical data from the EDDMapS dataset (Grimm and Railsback 2013). Patterns are viewed as

foundational to the structure and processes of a system; therefore, if a particular pattern observed empirically is not observed in a particular modeling scenario, that model is presumed to perform unrealistically and can be discarded. (Semeniuk et al. 2012).

We compared the simulated rate of expansion from each scenario to the observed spread of the python population. We quantified an index of the rate of expansion of the population's distribution in both the EDDMapS dataset and the output of each simulation scenario. First, we determined the distance between all presence points from each year compared to all presence points from the preceding year. For each point from the subsequent year, we measured its distance to all of the points in the previous year and calculated the median of all of these distances. We then averaged all of these medians across all of the points from the subsequent year and used that value as the rate of expansion between the two years. Next, we took the difference between successive values of that calculation for each annual increment. These differences were averaged to represent an index of the annual expansion of the population. See Appendix D for a visual representation of how we calculated this index. To pattern-match, we compared the thusly calculated metric from each simulation scenario using end points of virtual pythons who survived the dispersal season to the calculated metric of the empirical dataset to determine which behavioral type best represented dispersing pythons in southern Florida.

We also matched the range occupied by Burmese pythons in the EDDMapS dataset to the range occupied by the virtual pythons in each behavioral scenario. The empirically derived range was defined as the area covered by the 99% KDE polygons merged over 2004 through 2013. The simulated ranges were defined as the buffered core-

population barrier polygons merged over the same time period. We compared raster maps at a 100-m<sup>2</sup> resolution of these ranges by computing omission and commission errors and map agreement between the empirical range and each behavioral scenario's range using the square contingency table workbook, PontiusMatrix41.xlsx (available at <http://www2.clarku.edu/~rpontius/>; Pontius and Santacruz 2014). We defined 4 categories to compare: Non-invaded area, Phase 1 (the combined ranges from 2004-2007), Phase 2 (the combined ranges from 2008-2010), and Phase 3 (the combined ranges from 2011-2013). We chose these categories over comparing the range for each incremental year in order to focus the map comparison on the location of the leading edge instead of pixel-to-pixel agreement of each year's range.

## 2.3 Results

### 2.3.1 Summary statistics

When interpreting the results across the gradient of behaviors, we will generally use the term “bolder” to refer to individuals on the bold end of the shy-bold continuum, and “shyer” to refer to those on the shy end of the continuum. If we are referring to a particular behavioral scenario, we will use the category named in Table 2-3.

Bolder virtual pythons traveled greater distances and moved further from their release locations than shyer virtual pythons (Figures 2-2a and 2-2b). Shyer and bolder virtual pythons switched infrequently between modes (Figure 2-2c) where shyer pythons spent most of their time in safe mode and bolder pythons in risky mode (Figure 2-2d). Animals from the behaviorally plastic scenario switched frequently between safe and risky modes, and spent about half of their time in each mode (Figures 2-2c and 2-2d).

However, animals from the overall intermediate scenario did not switch frequently between modes; they remained in one mode for most of their dispersal period with a bias towards remaining in risky mode (Figures 2-2c and 2-2d).

Shyer pythons took a greater number of timesteps in comparison to bolder pythons (Figure 2-2e). A greater proportion of pythons from the most shy and somewhat shy scenarios were able to establish home ranges while a greater proportion of somewhat bold and most bold pythons died due to predation or other causes of mortality (Figure 2-2f). Individuals from the behaviorally plastic and overall intermediate scenarios experienced high mortality as well, with greater than 50% of individuals being subjected to mortality (Figure 2-2f).

Shyer virtual pythons that traveled the furthest distance from the prior year's leading edge were more likely to be alive at the end of the dispersal season in comparison to bold pythons, who were more likely to have died (Figure 2-3). The most dispersive behaviorally plastic pythons also were more likely to have died by the end of the season. Accordingly, the most dispersive shy animals from one year were more likely to determine the next year's leading edge while the most dispersive bold animals were more likely to succumb to mortality and have no contribution to the next year's leading edge.

### *2.3.2 Pattern matching*

The empirically derived index of the annual rate of expansion of the Burmese python population as represented in the EDDMapS data set showed that rate of spread increased by  $0.257 \text{ km} \cdot \text{year}^{-1}$  (Table 2-5). The two shyer behavioral scenarios also showed an increasing rate of spread, but the behaviorally plastic simulation scenario most

closely resembled the empirically derived index, only differing by  $0.499 \text{ km} \cdot \text{year}^{-1}$ . In contrast, the two bolder scenarios yielded slowing rates of spread: the rate slowed by nearly 6.5x for the somewhat bold scenario and by 11.5x for the most bold scenario.

Overall, the simulated ranges had low overall map agreement with the empirical range (Table 2-6). Agreement was highest between non-invaded and Phase 1 pixels, but it decreased over time from Phase 1 through Phase 3 (i.e., from 2004 – 2013). While the behaviorally plastic scenario had the third highest overall agreement with the empirical data, it consistently had the first or second highest agreement with Phases 1 through 3. Agreement within each phase was also second highest for bolder behavioral scenarios. However, the shyer behavioral scenarios had greater overall agreement because they had the greatest agreement with non-invaded area. Figure 2-4 shows the population ranges of the EDDMapS dataset and each of the behavioral scenarios.

## **2.4 Discussion**

Our IBM supported our predictions of how personality-dependent dispersal can impact the spread of an expanding population. Along the shy-bold continuum, bolder virtual snakes spent a greater proportion of time in risky mode. While spending more time in risky mode resulted in greater dispersal distances, it also resulted in higher rates of mortality. This meant that the individuals who traveled the furthest in the somewhat bold or most bold scenarios did not always contribute to the annual advancement of the front since they would die before the end of the dispersal season. Even so, the bolder survivors dispersed consistent with our expectations compared to individuals from the

shyer scenarios since the expanding edge still advanced further across the modeling extent in the bolder behavioral scenarios.

Low map agreement between the geographical extent of the empirical dataset's population range and across the 6 behavioral scenarios is likely due to the differences in how we constructed the geographical extent of EDDMapS data versus the simulated datasets for each year. Our empirical population's extent was determined by calculating 99% KDEs whereas our simulated populations' extents were created by buffering the original, empirically-derived KDE from the 2004 EDDMapS data points. This difference resulted in greater coverage of the modeled study area by the simulated pythons and a more even distribution of the simulated population compared to what was observed in the EDDMapS dataset.

We expected the most bold scenario to be the best match with our empirically observed patterns of annual rate of spread and the geographical extent of the python population. Instead, the behaviorally plastic scenario was the best fit. This result is based upon its closest match to the observed rate of expansion and the population's geographical extent, indicating strong support that Burmese pythons with adaptive flexibility in their dispersal behavior are driving the expansion of the population into south Florida's urbanized landscapes. This is further supported by the relative performance of the collectively shy and bolder scenarios simulated during different phases of the expansion: shy snakes produced population extents similar to empirical observations in Phase 1 while bolder snakes generated extents more similar to empirical observations in Phases 2 and 3. This demonstrates the success of a mixture of behaviors within the same population at different stages of a population's expansion.



Animal personality is equated to consistency in behaviors, but it is a common misconception in behavioral ecology that animal personality and behavioral plasticity exist separate from one another (Sih et al. 2004; Dingemanse et al. 2010). There is increasing evidence that animals can be relatively consistent in their behaviors while still retaining flexibility at the same time (Briffa et al. 2008). Plasticity and personality may even be linked (Sih and Bell 2008; Dingemanse et al. 2010). Animals may adjust their personality-dependent behaviors depending on social situations (e.g., social context and aggression in mice, Natarajan et al. 2009), learning (e.g., prior experience and boldness in rainbow trout, *Oncorhynchus mykiss*, Frost et al. 2007), predation risk (e.g., activity level, stress, and anti-predation behavior in Chaffinch, *Fringilla coelebs*, Quinn and Cresswell 2005), environmental variables (e.g., wind velocity and dispersal in salt marsh wolf spider, *Pardosa purbeckensis*, Bonte et al. 2007; temperature and boldness in lemon damselfish, *Pomacentrus moluccensis*, Biro et al. 2010), and environmental stability (Koolhaas et al. 1999; Sih and Bell 2008).

Broadly speaking, landscape connectivity is understood to emerge from the interaction of animal behaviors, particularly movement rules and landscape structure (Taylor et al. 1993). Fragmentation and human disturbance also impact landscape connectivity on an individual level: movement and dispersal can vary between individuals between landscape types and even within the same landscape (Baguette and Van Dyck 2007; Knowlton and Graham 2010). Therefore, our result that the behaviorally plastic scenario best matched the empirically observed population patterns demonstrates a challenge for estimating realized connectivity of landscapes for invasive species in landscapes that are being rapidly altered by human activity. If successful invasive species

demonstrate high degrees of behavioral plasticity, particularly by shifting between movement strategies in different circumstances, a successful definition of landscape connectivity may require concomitant flexibility that is not traditionally considered in estimating connectivity. Following up on this idea through the use of IBMs on the Burmese python system would benefit from explicitly relating behaviors to specific landscape characteristics and environmental variables. This would lead to a more specific knowledge of how landscape factors drive the behavioral plastic strategy and contribute to our overall understanding of how heterogeneous landscapes support viable populations (Knowlton and Graham 2010). This approach would allow future modelers to perform sensitivity analysis on the parameters for the behavioral scenarios represented in this IBM.

While bold individuals are more likely to explore novel situations, they are not necessarily better equipped to survive; rather, individuals with greater behavioral flexibility have better responses to novel conditions (Sih et al. 2004). The spread of a species may be best facilitated by populations comprised of within-species variation in traits between dispersers on the leading edge, particularly when different dispersal strategies are more successful at particular phases of an expansion and at specific population densities and disperse (Fogarty et al. 2010). Thus, it is better for an individual's fitness to balance risk and dispersal plastically than to adhere to a fully consistent behavior. This is especially true when animals are dispersing through fragmented landscapes where risk is heterogeneous across the landscape. For example, moving slowly and exhibiting vigilance or other anti-predator behaviors is beneficial when moving through risky matrix, but it is not as beneficial to an individual to partake

in these behaviors when moving through higher quality and less risky habitat (Zollner and Lima 2004). In their own IBM, Jepsen and Topping (2014) observed that populations of roe deer (*Capreolus capreolus*) with flexible behavioral strategies had higher population sizes, population persistence, and to abilities to cope with patchy landscapes than populations who were not behaviorally flexible. Burmese pythons in Florida similarly make trade offs as they move through Florida's landscape. For example, pythons use canals to make long distance movements between suitable habitat patches, but canals are risky due to the prevalence of American alligators (*Alligator mississippiensis*) (Pittman et al. in review).

Although our IBM did not support our initial prediction that bold dispersers would best describe the Burmese python population on the leading edge of an expansion, our results do not contradict the literature supporting risky movement and boldness. We were not modeling an invasive population spreading from its point of introduction. The population we modeled is best described as a core population pushing out of a naturally dominated landscape into an increasingly urbanized landscape. As established in the literature, this is the type of situation for which behavioral plasticity is most beneficial to the persistence of a population (Jepsen and Toppings 2014). It is also plausible that the patterns associated with our bolder scenarios are simply not represented in the EDDMapS dataset because bold individuals on the expansion front were subjected to mortality before they were able to establish and/or be observed. Bolder dispersers may also colonize empty patches first and later be followed by more fit individuals who persist in the patches (Fogarty et al. 2010). Further fieldwork and modeling in the Burmese python system will be needed to elucidate our understanding of within-individual behavioral

plasticity and the mechanism that may be driving the adaptive advantage for individual dispersers in displaying plastic behavioral syndromes. Nonetheless, our result that simulated behaviorally plastic individuals best matched empirical patterns implies a need for more flexible definitions of connectivity that not only specifically emphasize the importance of behavior but also recognize that the influence of behavior can be dynamic and circumstance-specific. These trends may be particularly true for invasive species spreading from naturally dominated landscapes into human dominated landscapes, as was the situation in our Burmese python case study.

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**Table 2-1.** Simulation parameters coded into the vector-based movement map's attribute table and read by the individual-based model SEARCH. Movement parameters were based on land cover type and were parameterized based on field data from a radio telemetry study.

<b>Land cover type</b>	<b>Daily mean vector length (MVL)</b>	<b>Daily mean step length (MSL), in meters</b>	<b>Boundary crossing ranking</b>
Canal	0.9799	228	200
Agricultural lands	0.99	45	7
Low Intensity Urban	0.9999	32	4
High Intensity Urban	0.9999	32	2
Naturally-dominated habitat	0.9	19	5

**Table 2-2.** Simulation parameters coded into the vector-based risk map's attribute table and read by the individual-based model SEARCH. Risk parameters were parameterized based on 2014-2015 data from a radio telemetry field study.

<b>Land cover type</b>	<b>Description</b>	<b>Probability of mortality per timestep (12-hour)</b>
Human-dominated habitat	Correspond to the following land cover types defined by the movement map: agricultural lands, urban landscapes, and canals. These areas are heavily influenced by human activities.	0.0019
Naturally-dominated habitat	Correspond to the natural habitat cover type defined by the movement map. These areas have less anthropogenic influence in comparison to altered habitats.	0.0053

**Table 2-3.** Description of behavioral types on a shy-bold scale in relation to the model parameters corresponding to the probabilities of switching between safe/risky modes.

<b>Behavioral type</b>	<b>Probability of switching from risky to safe mode</b>	<b>Probability of switching from safe to risky mode</b>	<b>Description</b>
Most shy	0.1	0.001	Animals in risky mode are most likely to switch to safe mode; once in safe mode, animals are most likely to remain in safe mode.
Somewhat shy	0.1	0.01	Animals in risky mode are less likely to switch to safe mode compared to the “most shy” animals; once in safe mode, animals are just as likely to remain in safe mode as the “most shy” animals.
Behaviorally plastic	0.1	0.1	Animals switch back and forth between risky and safe mode with the same likelihood.
Overall intermediate	0.01	0.01	Animals switch back and forth between risky and safe mode with the same likelihood, but they switch less than “Behaviorally plastic” animals.
Somewhat bold	0.01	0.1	Animals in safe mode are less likely to switch to risky mode compared to the “most bold” animals; once in risky mode, animals are just as likely to remain in risky mode as the “most bold” animals.
Most bold	0.001	0.1	Animals in safe mode are most likely to switch to risky mode; once in risky mode, animals are most likely to remain in risky mode.

**Table 2-4.** Behavioral modifiers for virtual snakes while in risky and safe modes. The base parameter in the movement map for MSL (i.e., movement speed) and the base parameter in the risk map for per timestep risk of mortality are multiplied by the respective modifier corresponding to the current mode of an animal.

	Risky Mode		Safe Mode	
	Movement speed	Risk of mortality	Movement speed	Risk of mortality
Modifier	2.5	2.5	0.25	0.25

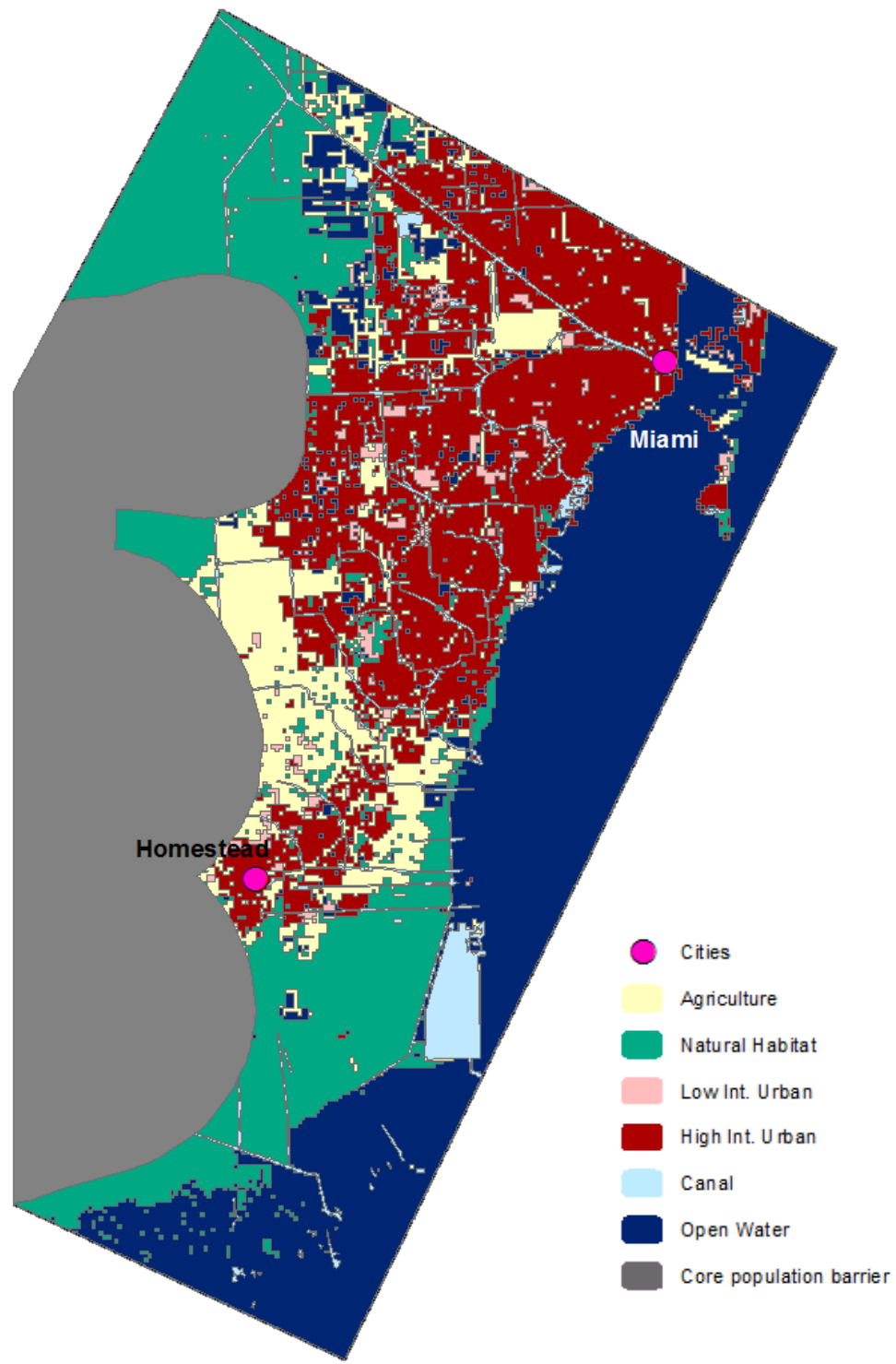
**Table 2-5.** Index of the annual rate of expansion of each behavioral scenario compared to the observed index of rate of expansion of the EDDMapS presence-only dataset.

	<b>Empirical Data</b>	<b>Most shy</b>	<b>Somewhat shy</b>	<b>Behaviorally Plastic</b>	<b>Overall Intermediate</b>	<b>Somewhat bold</b>	<b>Most bold</b>
<b>Annual rate of expansion (km • year<sup>-1</sup>)</b>	0.257	-0.306	0.912	0.757	-2.122	-1.624	-2.976
<b>Observed – Predicted (km • year<sup>-1</sup>)</b>	-	-0.563	0.655	0.499	-2.379	-1.881	-3.233

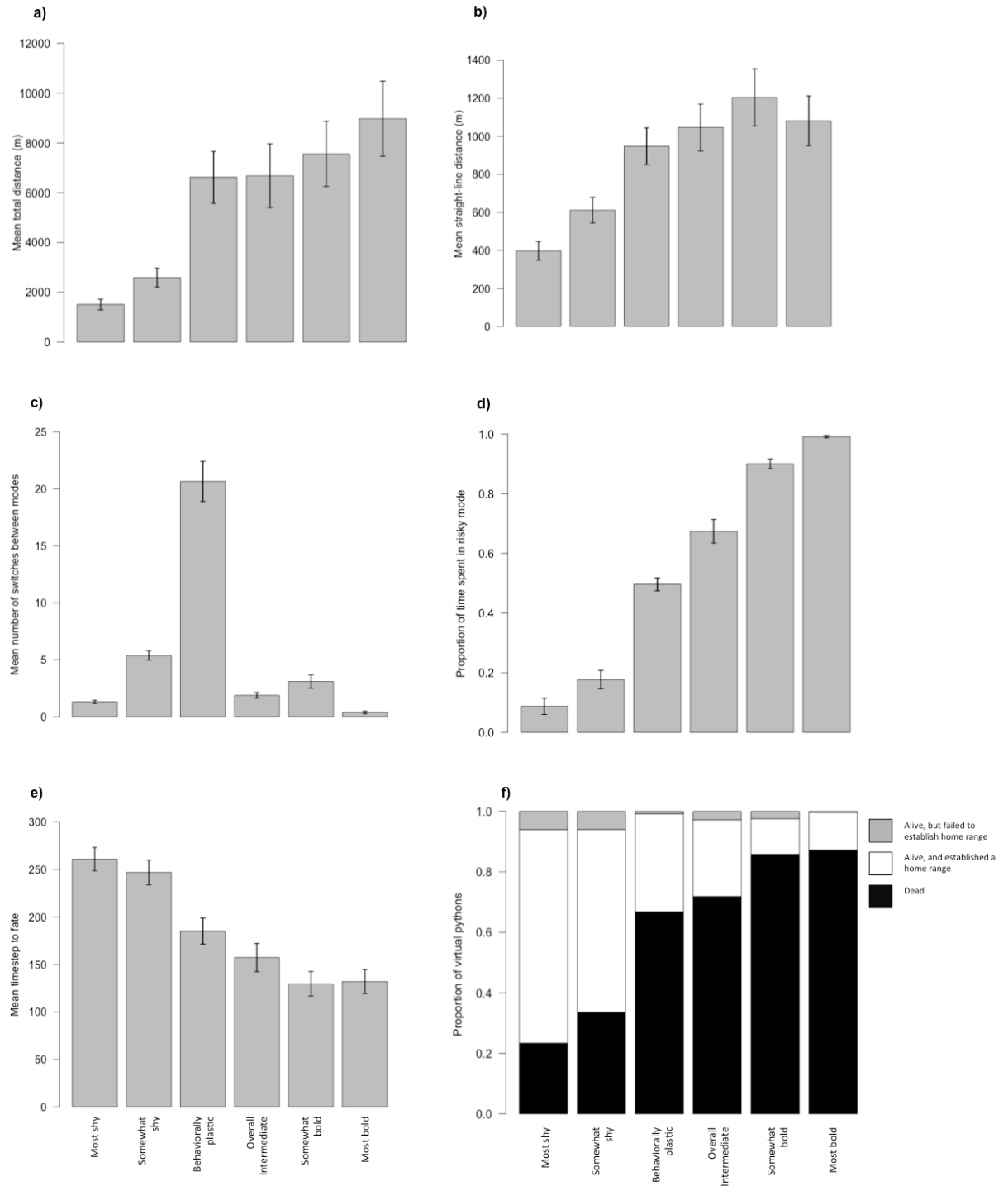
**Table 2-6.** Map agreement and omission and commission errors between the empirically derived geographical extent of the Burmese python population's range and the 6 simulated behavioral scenarios' ranges.

		Omission (% of domain)	Agreement (% of domain)	Commission (% of domain)
Non-invaded	Most shy	13	31	14
	Somewhat shy	16	28	11
	Behaviorally plastic	27	17	0
	Overall intermediate	35	9	0
	Somewhat bold	30	15	0
Phase 1 2004 – 2005	Most bold	28	17	0
	Most shy	7	22	12
	Somewhat shy	7	23	14
	Behaviorally plastic	6	23	16
	Overall intermediate	4	25	23
Phase 2 2008 – 2010	Somewhat bold	5	24	20
	Most bold	4	26	26
	Most shy	14	5	8
	Somewhat shy	15	4	7
	Behaviorally plastic	11	7	19
Phase 3 2011 – 2013	Overall intermediate	14	4	15
	Somewhat bold	12	7	23
	Most bold	16	3	11
	Most shy	7	1	7
	Somewhat shy	6	1	12
<b>Overall</b>	Behaviorally plastic	4	4	14
	Overall intermediate	4	3	20
	Somewhat bold	6	2	9
	Most bold	4	4	14
	Most shy	<b>42</b>	<b>58</b>	<b>42</b>
<b>Overall</b>	Somewhat shy	<b>44</b>	<b>56</b>	<b>44</b>
	Behaviorally plastic	<b>49</b>	<b>51</b>	<b>49</b>
	Overall intermediate	<b>58</b>	<b>42</b>	<b>58</b>
	Somewhat bold	<b>52</b>	<b>48</b>	<b>52</b>
	Most bold	<b>51</b>	<b>49</b>	<b>51</b>

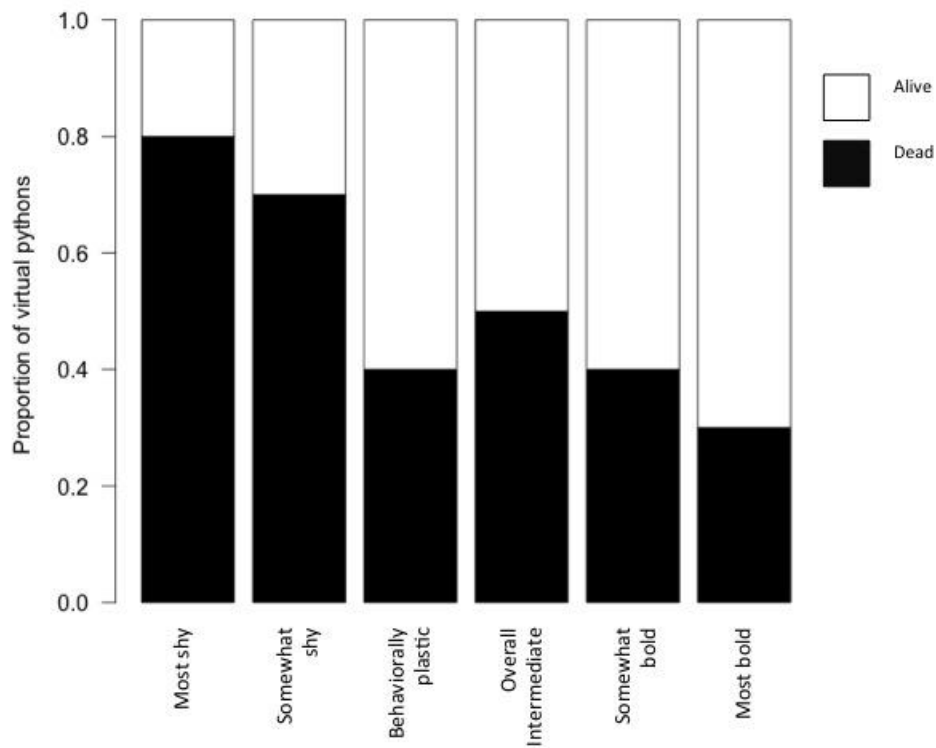




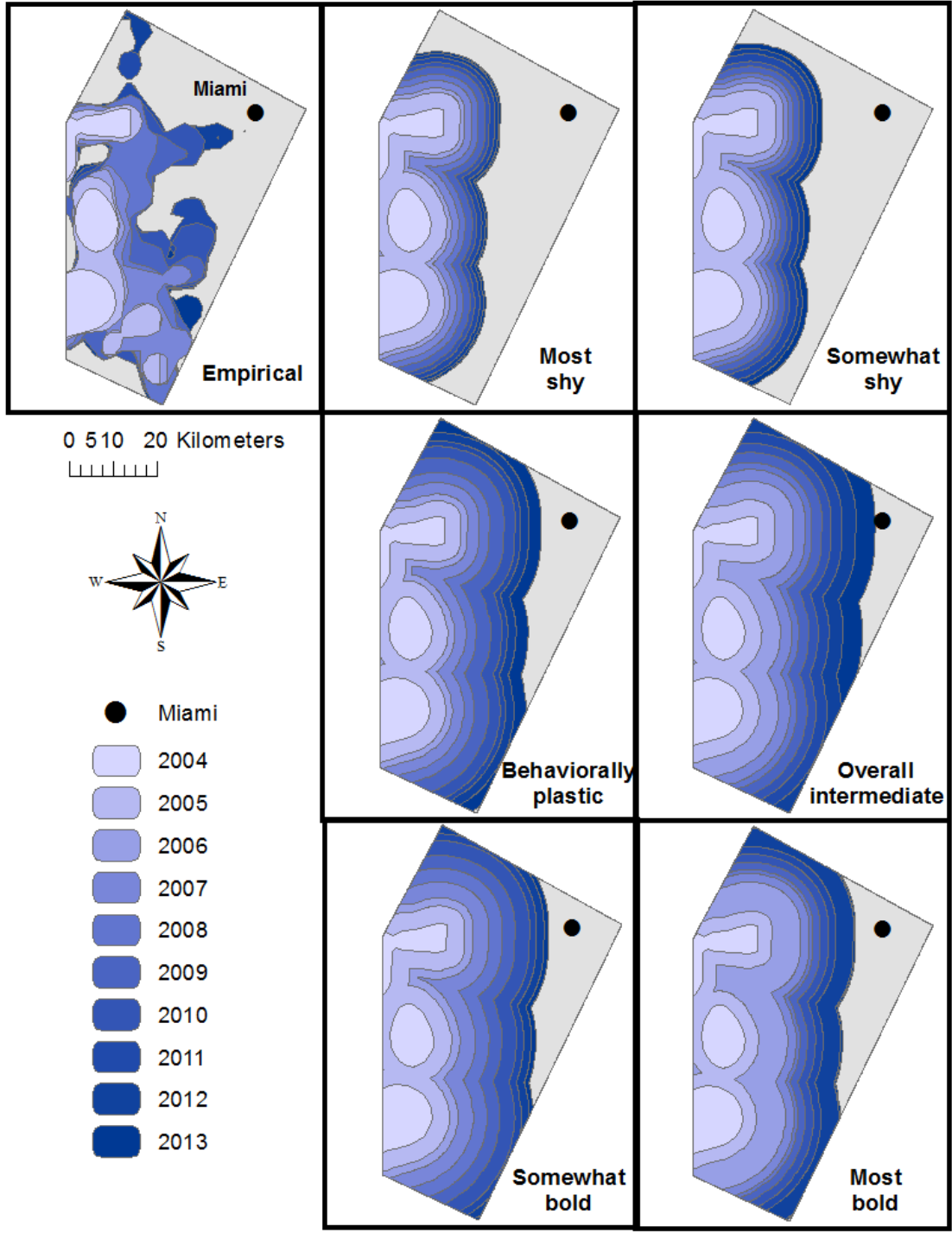
**Figure 2-1.** The Movement map input for SEARCH modeling showing land cover types and an example of a core-population barrier.



**Figure 2-2.** Summary of the (a) mean total distance traveled, (b) mean straight-line distance traveled, (c) mean number of switches between modes, (d) mean proportion of time spent in risky mode, (e) mean number of timesteps, and (f) proportion of fates, across all individuals within each behavioral scenario.



**Figure 2-3.** Fates of the virtual python that traveled the furthest straight-line distance from the previous year's leading edge across all 10 years for each behavioral scenario.



**Figure 2-4.** Geographical extent of population ranges by year from the empirical EDDMapS dataset and the 6 simulated behavioral scenarios.

## APPENDICES

**Appendix A.** Aggregated Florida Cooperative Land Cover Map (CLC) habitat classifications.

We used the CLC v. 3.0, developed by the Florida Fish and Wildlife Conservation Commission (FWC) and the Florida Natural Areas Inventory (FNAI). The CLC uses a hierarchical habitat classification system that is based on those currently used by the FWC, the FNAI, and Florida's water management districts.

We aggregated and reclassified land cover types into 18 categories as outlined in Table A-1. Land classes with the "Exotic Plants" categorization were cross-walked with the 2011 National Land Cover Database (NLCD) and we assigned the NLCD class the most related CLC cover type (Table A-2)

**Table A-1.** Aggregated CLC habit classifications.

<b>Final higher classification</b>	<b>Lower classifications</b>
Natural or Artificial Lakes & Ponds Estuarine	Natural Lakes and Ponds, Artificial Lakes and Ponds Keys Tidal Rock Barren, Saltwater Marsh, Mangrove Swamp
Hardwood Forested Uplands High Pine & Scrub Pine Flatwoods & Dry Prairie	Rockland Hammock Scrub, Sandhill Mesic Flatwoods, Scrubby Flatwoods, Pine Rockland, Dry Prairie
Mixed Hardwood-Coniferous Shrub & Brushland Coastal Uplands	Tree Plantations - Beach Dune, Coastal Berm, Coastal Strand, Maritime Hammock, Sand Beach
Barren Freshwater Non-Forested Wetland	Prairies and Bogs, Wet Prairie, Marl Prairie, Freshwater Marshes, Coastal Interdunal Swale, Floodplain Marsh, Glades Marsh
Freshwater Forested Wetland	Cypress/Tupelo, Strand Swamp, Other Coniferous Wetlands, Wet Flatwoods, Other Hardwood Wetlands, Hydric Hammock, Other Wetland Forested Mixed, Wet Coniferous Plantation
Freshwater Non-Vegetated Wetland Natural Rivers & Streams Canal/Ditch Low Intensity Urban High Intensity Urban	- - - - -
Rural Lands Agriculture	Improved Pasture, Unimproved/Woodland Pasture, Transportation, Communication, Utilities, Extractive -

**Table A-2.** New classification for “Exotic Plants” cover class, originally from the CLC. Grid cells classified as “Exotic Plants” were cross-walked with the NLCD, and based on the NLCD classification, they were assigned the most related CLC cover type.

<b>NLCD cover classification</b>	<b>Final CLC cover classification</b>
Open Water	Natural or Artificial Lakes & Ponds
Developed, Open Space	Rural Lands
Developed, Low Intensity	Low Intensity Urban
Developed, Medium Intensity	High Intensity Urban
Developed, High Intensity	High Intensity Urban
Barren Land	Barren
Deciduous Forest	Hardwood Forested Uplands
Evergreen Forest	Mixed Hardwood-Coniferous
Mixed Forest	Mixed Hardwood-Coniferous
Shrub/Scrub	Shrub & Brushland
Grassland/Herbaceous	Pine Flatwoods & Dry Prairie
Pasture/Hay	Agriculture
Cultivated Crops	Agriculture
Woody Wetlands	Freshwater Forested Wetland
Emergent Herbaceous Wetlands	Freshwater Non-Forested Wetland



**Appendix B.** Estimating sampling effort using a logistic regression model for Chapter 1 bias correction scenarios.

We estimated the sampling effort of the EDDMapS Burmese python dataset predicting occurrences of python using a logistic regression model. The predictor variables we selected are represented in Figure B-1.

The final logistic regression model was used to build the bias grids inputted into MaxEnt for the LOG and LOG-RD scenarios and to bias the randomly selected background points for the LOG-SWD and LOG-RD-SWD scenarios. We selected the best logistic regression model based on the log-likelihood (logLik), Akaike information criterion score ( $AIC_c$ ), the difference between models relative to the most parsimonious model ( $\Delta AIC_c$ ), and the Akaike weight ( $w$ ). Table B-1 shows the competing models. Figure B-2 shows (A) the final logistic regression bias grid and (B) the final logistic regression of roads bias grid.

**Table B-1.** Competing logistic regression models for the LOG and LOG-RD bias grids and background point selection for the LOG-SWD and LOG-RD-SWD scenarios.

<b>Model</b>	<b>df</b>	<b>logLik</b>	<b>AIC<sub>c</sub></b>	<b>ΔAIC<sub>c</sub></b>	<b>w</b>
Traffic + speed + rd + surv + pop	6	-1390.10	2792.22	0.00	1
Traffic + rd + surv + pop	5	-1401.67	2813.36	21.15	0
Speed + rd + surv + pop	5	-1467.36	2944.73	152.51	0
Rd + surv + pop	4	-1472.10	2952.21	159.99	0
Rd + surv	3	-1591.79	3189.58	397.36	0
Traffic + rd + pop	4	-2383.37	4774.76	1982.54	0
Traffic + rd	3	-2512.53	5031.07	2238.85	0
Speed + rd + pop	4	-2559.62	5127.24	2334.03	0
Speed + rd	3	-2779.53	5565.06	2772.84	0
Speed + rd	3	-2779.53	5565.06	2772.84	0
Intercept only	1	-2790.61	5583.22	2791.01	0

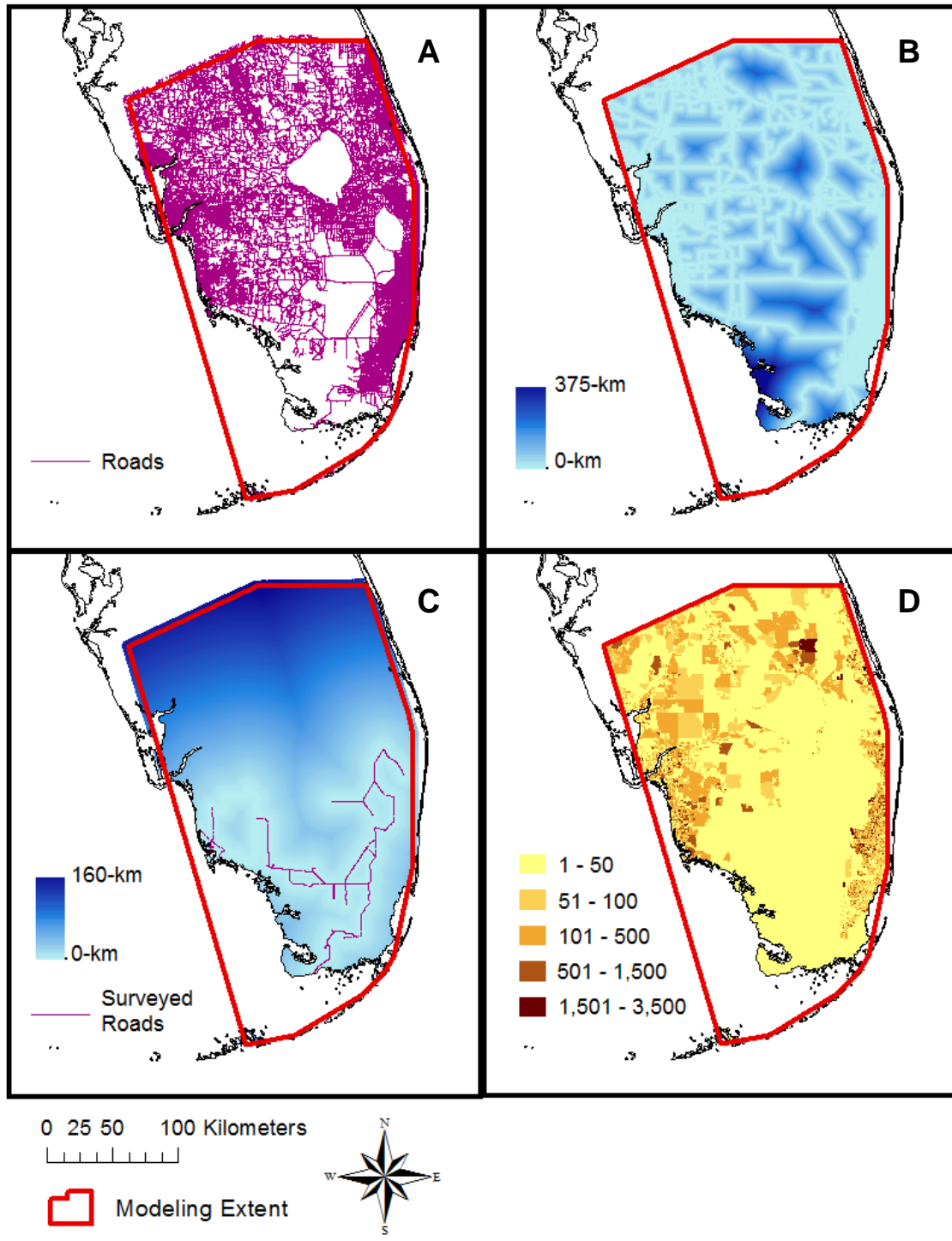
Traffic = average annual daily traffic of a road segment

Speed = speed limit of a road segment

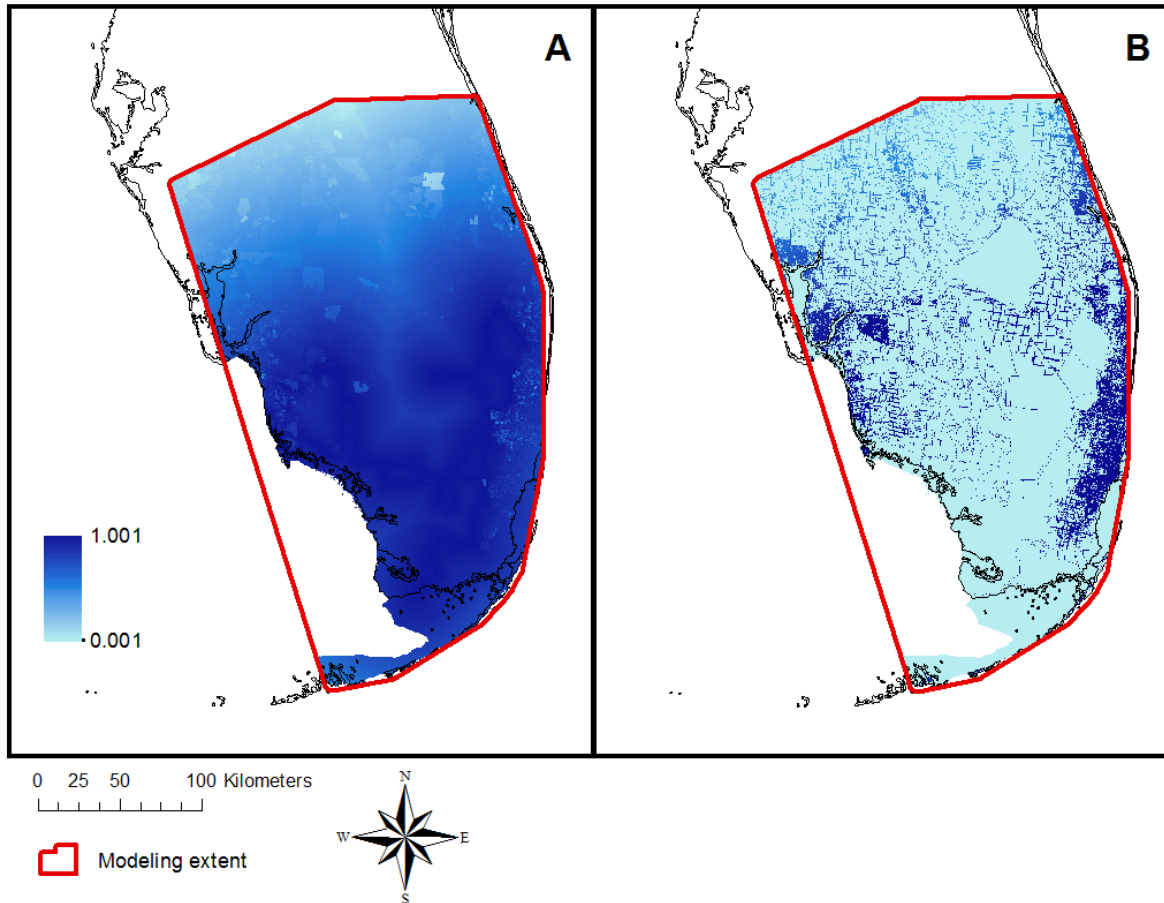
Rd = Euclidean distance to closest road

Surv = Euclidean distance to surveyed road

Pop = Human population density



**Figure B-1.** Predictor variables for the logistic regression model estimating sampling effort: (A) average annual daily traffic & speed limit of roads; (B) Euclidean distance to roads (m); (C) Euclidean distance to surveyed roads; and (D) population density.



**Figure B-2.** (A) Logistic regression of sampling effort bias grid and (B) logistic regression of sampling effort of roads bias grid.

**Appendix C.** Aggregated LULC classifications for movement map used in SEARCH models in Chapter 2.

In Chapter 1, we aggregated and reclassified the Florida Cooperative Land Cover Map (CLC) into 18 land cover types (see: Appendix A). In order to increase computer processing speed for our SEARCH simulations, we needed fewer land classifications to decrease the number of boundaries virtual animals would encounter. Table C-1 summarizes the reclassification of the CLC into 6 land cover types. Note that the movement map actually contains 7 land cover types, but the core-population barrier was an artificial cover type that we created as described in Chapter 2, section 2.2.6.2, Movement.

**Table C-1.** Aggregated land cover types.

<b>SEARCH movement map classification</b>	<b>CLC classification</b>
Open Water	Natural or Artificial Lakes & Ponds, Estuarine, Natural Rivers & Streams
Canal	Canal/Ditch
Agricultural Lands	Agriculture, Rural Lands
Low Intensity Urban	Low Intensity Urban
High Intensity Urban	High Intensity Urban
Naturally-dominated Habitat	Hardwood Forested Uplands, High Pine & Scrub, Pine Flatwoods & Dry Prairie, Mixed Hardwood-Coniferous, Shrub & Brushland, Coastal Uplands, Barren, Freshwater Non-Forested Wetland, Freshwater Forested Wetland, Freshwater Non- Vegetated Wetland

**Appendix D.** Visual representation of the calculated index to represent the annual expansion of the Burmese python population.

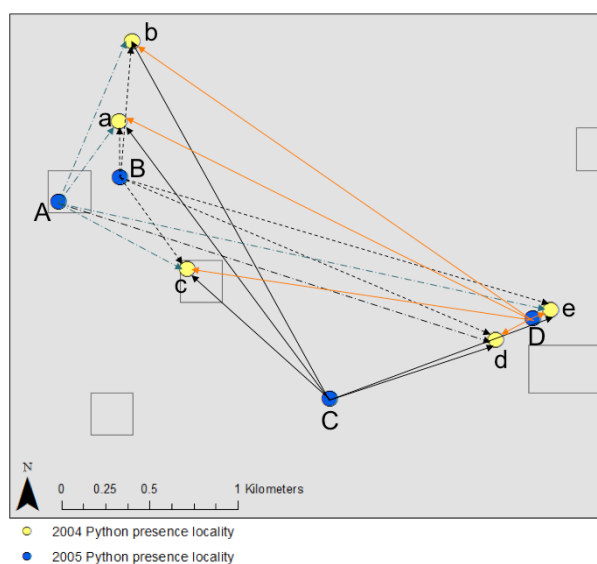
In this appendix, we visually demonstrate the calculation of the index we used for pattern matching the annual rate of expansion.

The examples in Tables D-1 and D-2 and Figure D-1 are a subset of the EDDMapS dataset for the years 2004 and 2005 for demonstration purposes. The remainder of the examples shows the results for the entire EDDMapS dataset examined.

First, we determined the distance between all presence points from each year compared to those in the subsequent year (Table D-1; Figure D-1).

**Table D-1.**

2005	2004	Distance (km)
A	a	0.571
	b	0.999
	c	0.821
	d	2.603
	e	2.865
B	a	0.278
	b	0.774
	c	0.641
	d	2.323
	e	2.561
C	a	1.978
	b	2.318
	c	1.098
	d	0.999
	e	1.356
D	a	2.604
	b	2.767
	c	1.986
	d	0.247
	e	0.114



**Figure D-1.**

Then we calculated the median of all the distances from the previous year for each point from the subsequent year (Table D-2).

**Table D-2.**

<b>2005</b>	<b>Median distance between 2004 points (km)</b>
A	1.572
B	1.315
C	1.550
D	1.544

These median distances were next averaged, representing the rate of expansion between two years (Table D-3).

**Table D-3.**

<b>Pairs of years</b>	<b>Rate of expansion (km)</b>
<b>2005-2004</b>	34.689
2006-2005	30.135
2007-2006	34.959
2008-2007	43.245
2009-2008	39.129
2010-2009	40.064
2011-2010	40.250
2012-2011	41.077
2013-2012	36.747



Next, we took the difference between successive values for each annual rate of expansion between years (Table D-4).

**Table D-4.**

<b>Pairs of pairs of years</b>	<b>Calculation (km – km)</b>	<b>Difference (km)</b>
[2006-2005] – [2005-2004]	30.135 – 34.689	- 4.554
[2007-2006] – [2006-2005]	34.959 – 30.135	4.824
[2008-2007] – [2007-2006]	43.245 – 34.959	8.286
[2009-2008] – [2008-2007]	39.129 – 43.245	- 4.116
[2010-2009] – [2009-2008]	40.064 – 39.129	0.935
[2011-2010] – [2010-2009]	40.250 – 40.064	0.186
[2012-2011] – [2011-2010]	41.077 – 40.250	0.827
[2013-2012] – [2012-2011]	36.747 – 41.077	- 4.330

Lastly, these differences were averaged and represented the overall average annual rate of expansion for the given simulation scenario, or in this example, the empirical dataset we compared against our simulation scenarios' outputs (Table D-5).

**Table D-5.**

<b>Scenario</b>	<b>Annual rate of expansion (km)</b>
Empirical dataset	0.257