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Gordon H. Rodda

*USGS Fort Collins Science Center*

Robert N. Reed

*USGS Fort Collins Science Center, reedr@usgs.gov*

Catherine S. Jarnevich

*USGS Fort Collins Science Center*

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# CLIMATE MATCHING AS A TOOL FOR PREDICTING POTENTIAL NORTH AMERICAN SPREAD OF BROWN TREESNAKES

GORDON H. RODDA, ROBERT N. REED, AND CATHERINE S. JARNEVICH, USGS Fort Collins Science Center, Fort Collins Colorado, USA

**Abstract:** Climate matching identifies extralimital destinations that could be colonized by a potential invasive species on the basis of similarity to climates found in the species' native range. Climate is a proxy for the factors that determine whether a population will reproduce enough to offset mortality. Previous climate matching models (e.g., Genetic Algorithm for Rule-set Prediction [GARP]) for brown treesnakes (*Boiga irregularis*) were unsatisfactory, perhaps because the models failed to allow different combinations of climate attributes to influence a species' range limits in different parts of the range. Therefore, we explored the climate space described by bivariate parameters of native range temperature and rainfall, allowing up to two months of aestivation in the warmer portions of the range, or four months of hibernation in temperate climates. We found colonization area to be minimally sensitive to assumptions regarding hibernation temperature thresholds. Although brown treesnakes appear to be limited by dry weather in the interior of Australia, aridity rarely limits potential distribution in most of the world. Potential colonization area in North America is limited primarily by cold. Climatically suitable portions of the United States (US) mainland include the Central Valley of California, mesic patches in the Southwest, and the southeastern coastal plain from Texas to Virginia.

**Key Words:** *Boiga irregularis*, brown treesnake, climate match, GARP, invasive species, native range, United States.

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## INTRODUCTION

The brown treesnake (*Boiga irregularis*) is native to northern and eastern Australia, eastern Indonesia, Papua New Guinea, and most of the Solomon Islands. Following World War II, the brown treesnake was accidentally translocated in cargo to the formerly snake-free island of Guam, with devastating consequences for native birds, bats, and lizards (Savidge 1987, Fritts and Rodda 1998). The US Department of Agriculture (USDA) Wildlife Services (WS) now conducts a cargo inspection program to keep the snake from spreading from Guam to other areas.

In invasive species management, climate matching is used primarily for two purposes: to assess overall invasion risk and prioritize destination-specific management actions. An example of the former is Australia's algorithm for assessing the risk of importing exotic reptile species (Bomford et al. 2005), which attributes a higher risk to species that could colonize a larger proportion of the destination country. An example of the latter is WS's risk management of cargo outbound from the island of Guam (D. S. Vice,

personal communication), which concentrates interdiction effort (dog-aided searches, etc.) on shipments bound for destinations most likely to support colonization by brown treesnakes. To date, the climatic division of destinations into high- and low-risk categories has been qualitative. While it is clear that Honolulu is at greater risk than Anchorage, uncertainty surrounds intermediate climates such as that experienced by Los Angeles.

A vast literature exists on climate matching not only for the purposes cited above, but also for predicting species occurrences within unsurveyed native range sites (Scott et al. 2002), and projecting range shifts in response to global climate change (Araujo and New 2007). Within the invasive species field, a continuum of approaches is recognizable, one end of which emphasizes the focal species' physiological tolerances as determined in the lab and the other end relying on automated searching for statistical correlations between site occupancy and climate values. An example of the former is the software package CLIMEX (and its predecessors, including BIOCLIM), which has been used extensively for

insects and plants, but also terrestrial vertebrates (Nix 1986, Pheloung 1996, Sutherst et al. 1996, Elith et al. 2006). Mapped range limits are associated with climate values, but the program also seeks physiological data of relevance such as minimum temperature tolerated, diapause duration, temperature threshold for emergence, and so forth. CLIMEX has default climate-matching algorithms that it will use to predict limiting conditions based on broad ecological categories that the investigator assigns (e.g., tropical versus temperate setting).

An example of the latter are programs such as Genetic Algorithm for Rule-set Prediction (GARP) and WhereWhy (Stockwell and Noble 1992, Stockwell 1999, Stockwell and Peters 1999, Stockwell et al. 2005), which automate the exploration of statistical association between occupied sites and climate values (other types of values could be included, for example soil type, but those geographic information system [GIS] layers must be provided by the user). GARP is genetic in the sense that in each generation (of the model) a climate variable (e.g., mean maximum July temperature) is randomly added to the model, as if it were a genetic mutation. The program then compares the goodness of model fit of the descendant model to that of the progenitor and retains the “mutation” if the fit improves. This process continues iteratively until no further improvements are obtained from a specified number of mutations. Like evolution, the mutations are not directed, so there is no guarantee that the resultant model will be optimal. Furthermore, although climate variables are inherently relevant to identifying range limits, the specific variables are chosen on statistical rather than biological grounds. In a statistical sense, the GARP algorithm is “fishing,” with attendant risks of identifying a correlated but non-causal link. The successor program to GARP is WhereWhy, which adds some look-ahead capability so that the better models are discovered more expeditiously (Stockwell et al. 2005). Nevertheless, GARP and WhereWhy produce a large number of models whose outcomes are tabulated spatially to provide the proportion of colonization “successes” for each map pixel.

These programs have been criticized on a number of grounds (O’Connor 2002, Guisan et al. 2006), including lack of statistical protection against fishing and overfitting, lack of independence in the source data set, lack of independence between fitting and testing data sets, climatic irrelevance of localities that are in the

interior of a species’ range, assumption that a single suite of climate variables is responsible for diverse range limits, and the assumption that climate as a proxy for niche will apply to a novel environment in the same manner as it applies in the native range (Broennimann et al. 2007).

These problems are evident in the GARP map prepared by Stockwell et al. (2005) for the brown treesnake. The source data for that work were Australian National Museum specimen localities. Overfitting was evident in the highest probability of colonization assigned to the two sites (vicinities of Sydney and Brisbane) from which most of the specimens were obtained. Occupied but infrequently-collected sites midway between Sydney and Brisbane, or north of Brisbane were scored as low probability of colonization (the same rating as improbable sites such as Tasmania, Colorado or northern China). Because the same data set (though different points) were used for both training and testing the GARP algorithm, Stockwell et al. (2005) claimed an accuracy score of 80%, even though the GARP models failed to identify most of the Australian native range as having high probability of colonization.

The assumption that climate delineates niche and does so in the same way in native and introduced ranges is difficult to fully test. Ideally, one would like to have a prediction well documented prior to a colonization, and retrospectively compare the equilibrium distribution of the colonized area to that which was *a priori* predicted. Brown treesnake colonization of North America has not yet occurred, fortunately, but if it does, the GARP map produced by Stockwell et al. (2005) will provide a useful basis for comparison. In our opinion it is notable that the highest probability of colonization was not associated with southern Florida (which we judge to be highly vulnerable), but with the arid southern part of Texas. Southern Florida was judged much less vulnerable than northern Florida, and all of the Northeastern and upper Midwestern states (to the map’s truncation at 40°N) were mapped in the same risk class as peninsular Florida and most of the occupied parts of Australia. We believe that this erroneous assessment is based on GARP choosing variability in temperature (rather than temperature) as the key association with the climatically-variable areas from which most of the Australian National Museum specimens were collected (notably the Blue Mountains west of Sydney). This illustrates a hazard of automated searches for climatic correlates.

We preferred to investigate the brown treesnake's climate envelope by starting with biological first principles. We recognized that climate is a proxy, and may be a poor proxy, for the ecological conditions that permit a population to reproduce faster than mortality. Rodda et al. (1999b) demonstrated that prey availability is a key parameter limiting brown treesnake success in the native range and in the Mariana Islands, and prey availability is likely to be a factor in ability to colonize North America. Prey availability is likely to be loosely and positively correlated with both temperature and rainfall, but the brown treesnake can transcend excessively cold or dry seasons by hibernation and aestivation, respectively. Hibernation and aestivation are exhibited by brown treesnakes in Australia (Ehmann 1992, Ehmann 1993, Greer 1997), but the durations are not known. Unless the unfortunate colonization of the mainland US occurs, we can not know whether the temperature limits that apply to the brown treesnake in its native range will apply equally in North America. Proceeding on the basis that they may, we delineated the monthly mean temperature and rainfall limits to determine which areas of the mainland US are at greatest risk of brown treesnake colonization.

## METHODS

We used the range map in Rodda et al. (1999a) to distinguish occupied from unoccupied localities. We pooled localities within each 1 degree latitude/longitude (lat/long) cell. These localities were matched to the closest choice from among the 85,000 stations reported in the World Climate (2007) data set. When elevation data were available (i.e., most cells) we made sure that weather station elevations matched snake localities. The World Climate stations were grouped into lat/long cells of 1 degree. Although the World Climate dataset was large, mean monthly temperature figures were unavailable for many of the cells in the brown treesnake's native range. When possible, we used single stations that reported mean monthly values for both rainfall and temperature. In a few cases, we combined data from two stations in the same cell to obtain both climate data types. In the vast majority of cases for which both climate data types were available, we were able to match snake presence records with weather stations located in the same 1-degree lat/long cell, but for a few important localities we could find weather records only for an adjacent cell

(only weather stations with equivalent elevations were considered). World Climate has no stations appreciably above sea level for New Guinea, yet montane locations are occupied by the brown treesnake (Rodda et al. 1999a). We were able to obtain two useful upper montane New Guinea climate records from Hyndman and Menzies (1990).

To analyze rainfall on a logarithmic scale and include weather stations that had not recorded rainfall during particular months, we coded zero rainfall means as 0.01 mm/mo. We were able to match one Guam and 38 native range localities with appropriate climate data: Australia (21), Indonesia (7), Papua New Guinea (8), Guam (1) and the Solomon Islands (2).

We plotted each of the 39 climate records as 12-sided polygons, each vertex representing the mean conditions for one month of the year. We anticipated that the aggregate climate space occupied by the 39 polygons would be reasonably well defined in relation to maximum heat and rainfall, but would have irregular excursions into climate space of extreme cold and aridity, representing months of hibernation and aestivation, respectively.

By progressively flagging the 1-3 months of greatest aridity against the graphical background of the 39 climate polygons, we observed that only the first- and second-most arid months were confined to sparsely-occupied climate space. From this, we inferred that the brown treesnake generally avoids extreme aridity, but is probably capable of up to 2 months of aestivation. We conducted a similar analysis for hibernation periods of 2-5 months, and concluded that brown treesnakes can probably hibernate for 4 months.

We fit the closest convex polygon that included all points believed to represent climatic conditions experienced by active brown treesnakes, and checked this climate envelope hypothesis against field observations reported in the literature.

Finally, we applied our hypothesized climate envelope implied by the 39 climate polygons from native range weather station data to climates recorded in the mainland US. We obtained average monthly precipitation (cm) and average monthly temperature ( $^{\circ}$ C) data from the on-line Daymet database for the US (<http://www.daymet.org>; Thornton et al. 1997). Thornton et al. (1997) used daily observations from over 6,000 stations across the US collected from 1980 to 1997 to create the surfaces at a 1 km<sup>2</sup> resolution. The equations defining the climate space of the convex polygon

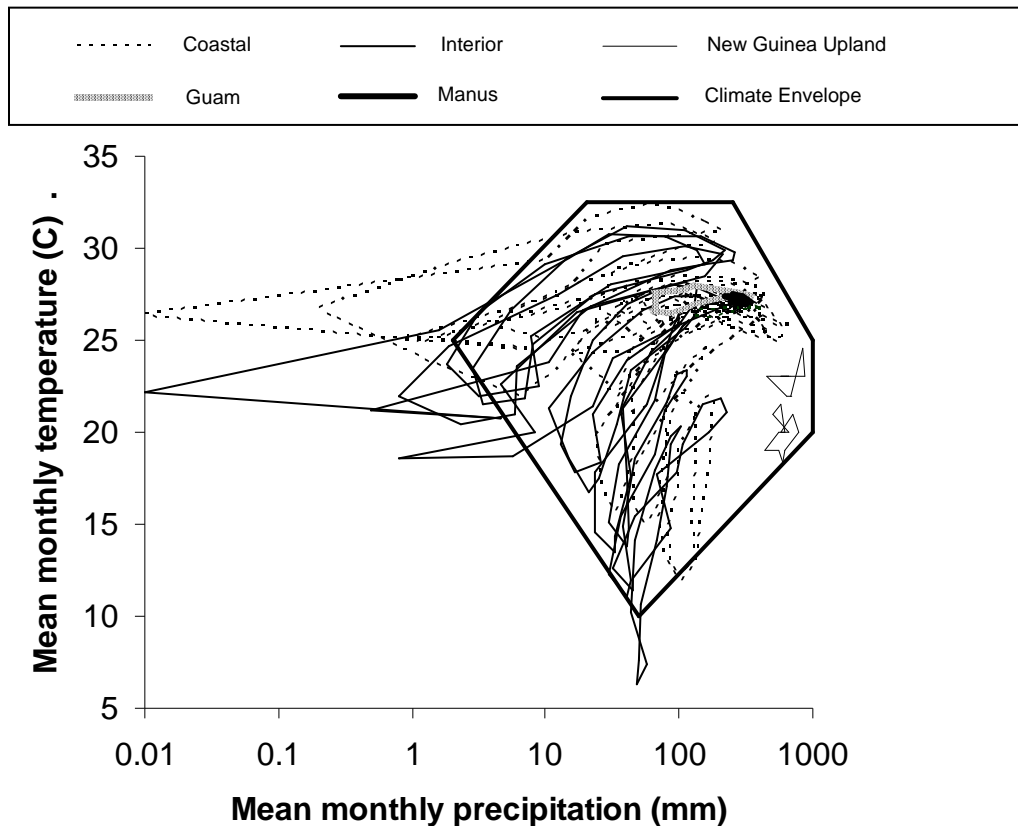
occupied by the 39 climate polygons were implemented using Visual Basic for Applications with ESRI's ArcGIS 9.0 ArcObjects to produce the US map of habitat suitability for the brown treesnake.

## RESULTS

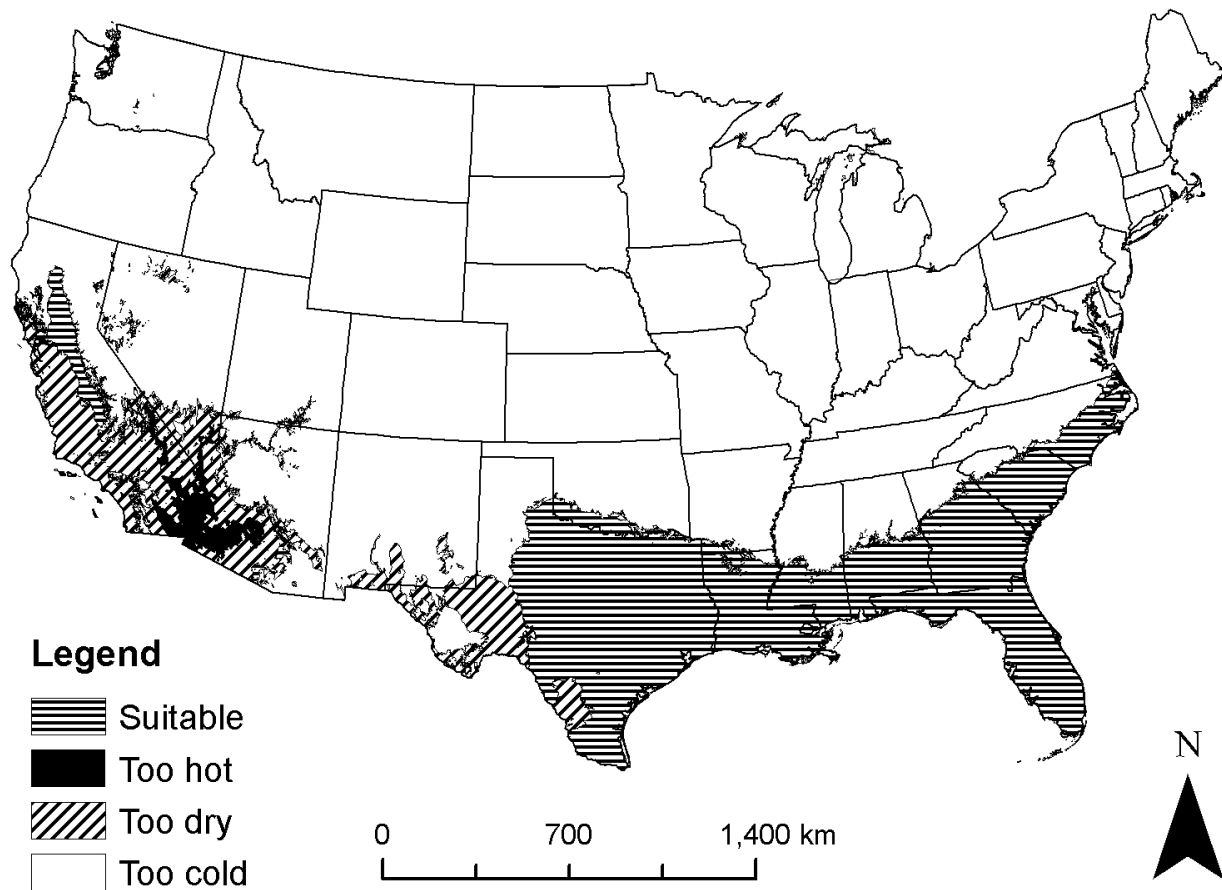
The 12-sided climate polygons for the 39 sites occupied by brown treesnakes exhibited a fairly definite upper temperature limit corresponding to a mean monthly temperature of 32.5 C (Figure 1). Similarly, the upper rainfall limit was decisive; we obtained no evidence of brown treesnake occupancy of sites with mean monthly precipitation of > 1000 mm (Figure 1). The two high elevation sites from Papua New Guinea exhibited cool, wet conditions that did not overlap with the conditions reported from climatically adjacent sites (all of which were at or near sea level).

In contrast to the relatively compact climate polygons on the warm and wet sides of the brown treesnake climate space, the arid and cold sides exhibited short excursions into very dry and fairly cold conditions. If one excludes the arid excursions from the climate space that the brown treesnake can occupy and remain active, the range of monthly rainfall ranges from 2-1,000 mm.

Our climate envelope hypothesis outlined in Figure 1 indicates an active monthly mean temperature range 10-32.5 °C. This range of conditions is much broader than that experienced on Guam (Figure 1), which itself is a substantially wider range of conditions than is present on Manus, the island believed to be the source of the Guam population (Rodda et al. 1992). Manus has equable rainfall (monthly means 218-346 mm) and practically invariant temperature (monthly means 27.0-27.4 °C).



**Figure 1.** Climate envelope for the native range of the brown treesnake as delimited by mean monthly precipitation and temperature. All of the 12-sided polygons represent native range sites except Guam, where the snake is introduced but very successful. Manus is believed to be the origin of the population on Guam.



**Figure 2.** Potential brown treesnake range in the continental US, as delimited by the climate envelope shown in Figure 1.

Based on climate match, much of the continental US was deemed too cold for brown treesnakes (Figure 2). Nonetheless, a broad swath of the southeastern US coastal plain has a suitable climate, including most of (west to east) Texas, Louisiana, Florida, Georgia, and South Carolina, and substantial parts of (west to east) California (Central Valley), Mississippi, Alabama, and North Carolina. Desert areas of the Southwest were generally too dry (Mojave, Sonoran, and Chihuahuan deserts), and the lower Colorado River basin was seasonally hotter than the prescribed 32.5 °C. Nonetheless, scattered throughout and surrounding these zones of excess heat and aridity were slightly higher elevation sites that were acceptably mesic.

## DISCUSSION

Although weather data from the brown treesnake's native range exist for most coastal localities, upland weather records were conspicuously underrepresented. For example, if we had not obtained the two upland Papua New Guinea records, we would have missed a substantial portion of the occupied climate space. The disjunct location of those upper montane records on the climate space diagram (Figure 1) indicates that lower montane weather records are missing, despite the ample field evidence that brown treesnakes are not only present, but exceptionally abundant in lower montane sites (Parker 1982, O'Shea 1996, Rodda et al. 1999b). We note that even the wetter coastal localities were undocumented in the World Climate data set (e.g., the southern or "weather" coast of Guadalcanal Island had no stations and no European settlements), perhaps reflecting a preference of

European settlers for drier colony sites within Melanesia. If such sites were climatically documented, we expect that the upper acceptable rainfall limit for brown treesnakes would be expanded substantially beyond the 1000 mm/month we recorded. Such an expansion would not affect the identification of suitable areas of the mainland US, but would increase the range of sites deemed suitable in Asia and South America.

The range of sites deemed suitable in North America uniformly includes all sea ports from the Mexican border of Texas to Norfolk, Virginia (Figure 2), and most destinations within the Southeastern coastal plain. The situation on the West Coast is complicated by the interdigitation of acceptable and unacceptable sites in southern California, though the Central Valley possesses a uniformly suitable climate. Thus shipments into or via San Francisco would be at higher risk than those destined for Los Angeles or Phoenix. Shipments destined for montane sites in southern California or Arizona might be at risk if the elevation is moderate (Figure 2). Furthermore, assignment of “too dry” to areas in the Southwest is sensitive to uncertainty about the permissible duration of aestivation in brown treesnakes. Direct evidence of the duration of aestivation in Australia would be useful for refining area boundaries in the American Southwest. Rocky Mountain, Northwest, North Central, and Northeastern states appear to be uniformly too cold for brown treesnakes. According to 2000 census figures, about 80 million people live in US counties where all or part of the county was classified as having a suitable climate.

Although the northern states are outside of the climate space inferred from the brown treesnake native range, the full scope of the snake’s climate tolerances may not be reflected in the native range. The high latitude limit of the brown treesnake’s native range is on a narrow front around Sydney, Australia, a relatively arid location wedged between saltwater and mountains. There are no cool high-rainfall sites at the high-latitude periphery of the brown treesnake’s native range; thus caution should be applied in inferring the snake’s cold-mesic tolerances.

The success of any invader is set by the population’s ability to reproduce fast enough to offset mortality. Climate influences both reproduction and mortality, but the linkage is often indirect. None of the extant climate-matching programs goes much beyond basic climate statistics, and none measures recruitment or mortality rates. Although climate is an important

correlated factor in invasion success, brown treesnakes have a variety of behavioral mechanisms (aestivation, hibernation, restricting activity to suitable microenvironments) for buffering themselves from physiologically-stressful environments. However, if insufficient prey resources are available, no amount of physiological tolerance will provide the energy required for reproduction. We do not adequately understand the operation of the complex interaction between a population and its environment, in particular that of brown treesnakes, nor are we able to predict how the interaction might change in a new locality or for a new population.

New colonizations often pass through a genetic bottleneck that alters the population’s genetic makeup and potentially the population’s realizable niche. The lineage of brown treesnake that occurs on Guam may have passed through genetic bottlenecks during the colonization of Guam and during the earlier colonization of Manus, which has a very restricted climate space (Figure 1). Laboratory tests of survival (Christy et al. 2007) indicate that Guam brown treesnakes possess a short-term temperature tolerance that is substantially wider than the range of monthly means shown in Figure 1 for all occupied sites; thus despite any putative genetic bottlenecks Guam snakes can survive the full range of conditions. Nonetheless, short-term survival may not be a good indicator of the environmental conditions required for invasion success.

Thus, there are a multitude of mechanisms that might allow brown treesnakes to occupy more or less of North America than suggested by this climate matching model. Based on climatic conditions, a substantial portion of the southern US is at risk of brown treesnake colonization. We did not investigate climate matching of Mexico and Neotropical sites, but our climate match indicates that the brown treesnake should be able to colonize areas immediately south of the Rio Grande river.

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