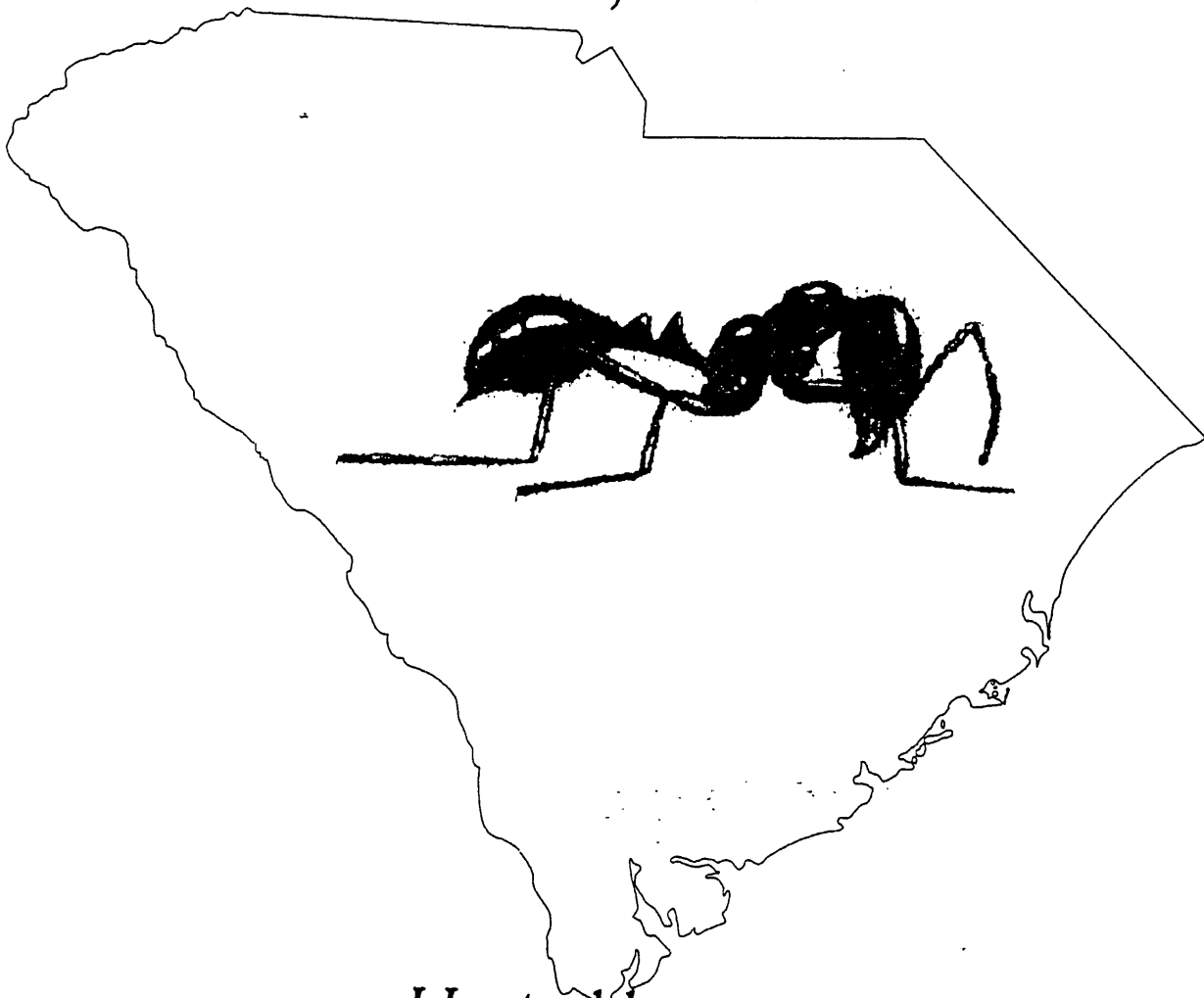# *1999 Imported Fire Ant Conference*

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Modeling Range Expansion of the Red Imported Fire Ant in the United States

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There are two major reasons to model red imported fire ant (*Solenopsis invicta*) populations. The first is its economic importance (e.g., estimated total losses for nine heavily infested southern states are about $2.77 billion annually [Thompson et al. 1995]). The second is a technical one: fire ant biology and ecology are comparatively well known (Wojcik and Porter 1997). Consequently fire ants are a good target for using ecological mechanisms to explain their geographic distribution. The current fire ant distribution is shown in Figure 1 and can be found on the WWW (http://www.aphis.usda.gov/oa/antmap.html).

Three attempts to model this biogeographical problem are reported in the literature. A statistical-based work by Pimm and Bartell (1980) used three monthly mean climatic variables (rainfall and number of cold and hot days) in a one-degree latitude x longitude spatial resolution. The authors calculated fire ant propagation rate and applied it to the situation in Texas. A comparison with actual expansion rates over the years showed that the rates were seriously overestimated (see Stoker et al. 1994 for the map of 1993 distribution in Texas).

Stoker et al. (1994) developed a mechanistic model to find a 'reproductive' border that is a point in space where a queen during its life produces exactly one queen surviving to maturity. This mechanistic model describes the joint dynamics of population of colonies and operates using 7 ant developmental stages; it describes queen fecundity, detailed dependence of the developmental rates and mortality on air temperature, and mating flights. The temperature scenario was presented using daily temperatures normally distributed around monthly means. The model was applied to a transect in northern Texas and did not show a distribution limit that matched reality. Mating flights took place and colonies could grow everywhere. As a conclusion, authors suggested that their already complicated model should be complicated further. The central methodical deficiency of their approach is the application of a population-level model (with inter-colony competition) to a problem that likely needs a single colony model.

The third work (Killion and Grant 1995) tried to find a 'growth' border that is a point in space where a fire ant colony ceases to grow. The temperature scenario used was similar to that taken by Stoker et al. (1994). The mechanistic model described single colony development and operated by 5 ant developmental stages. It gave a reasonable location for the fire ant geographical limit, but in very low resolution (three points along a Texas-Kansas-Wyoming transect and one location in Alabama). So, actually only one point on the fire ant range border was determined.

From our point of view, the last two models were overly complicated and contained some features which prevented realistic results. Many details about colony growth are known with low accuracy, and their incorporation into some model does not improve model quality because it makes the model less stable with respect to parameter variations. As we see the problem, model development needs to rely not on the

description of a 'real' colony, with more and more details, but on a search for an idealized case which is just sufficient to solve the problem. While an ecologist usually tries to describe his object in detail in order not to lose the reality, a modeler tries to get the desired effects by minimum means. Reality is infinite, so nobody knows *a priori* which necessary and sufficient features one needs to incorporate to reach realistic results. Our variant is offered below.

Soil temperature, T, is the main ecological factor which determines colony metabolism and activity (Markin et al. 1973, Vinson and Sorensen 1986, Porter 1988, Tschinkel 1993).

The most biologically sound way to find a stable border would be to evaluate the "basic reproductive rate," R, making it equal to the average number of queen progeny surviving to adulthood in the absence of intra-specific competition. Then, the needed border is found from the equation

$$R(T) = 1 \qquad (1)$$

(Birch 1948, May 1974, Cooksey et al. 1990, Hochburg et al. 1992, De Jong and Diekmann 1992). To find the basic reproductive rate, one needs to know with sufficient accuracy queen fecundity, colony alate production, and queen mortality rate. All three values need to be given as functions of colony size, and ecological factors like soil temperature, and maybe precipitation and competition. This seems to be too much for the current state of knowledge, so several assumptions were made to simplify the description.

First, colonies were described by two dynamic variables - colony area and colony daily alate production. Increases and decreases in colony area are governed by soil temperature. Then, instead of using equation (1) to find the border, we calibrated the model to adjust the calculated range to the extreme points in the insect's present distribution. To do this, total number of alates produced by a colony over its lifetime was considered as a free parameter.

Model construction

The condition or state of a colony at any given age is provided by colony area (Korzukhin and Porter 1994), and by colony alate production per day. Because we have two temperature values for each day, we made two time steps per day. We assumed that the number of workers in a colony is proportional to colony area.

Colony area dynamics. Within our model, two opposite processes determine dynamics of colony area, the production and death of workers. The rates of these processes depend on soil temperature and were determined from laboratory observations (Porter 1988, Calabi and Porter 1989). The details of this modeling process will be presented elsewhere.

Colony alate production. It is supposed that after reaching the reproductive stage, a colony splits its growth resources between worker and alate production. The share of resources directed to alate production is given by a function we call the 'alate production scenario' (Tschinkel 1993). The model assumes that all alates produced fly out of the nest immediately. The details of this modeling process will be presented elsewhere.

A queen establishes the nest at a given Julian date, with initial colony area and lives a given maximum number of days. A shrinking colony dies when it reaches a critical area, which can happen either when it reaches old age or after a sufficiently long period of cold temperature. The main output variable of the model is total number of alates

produced by a colony during its lifetime

Temperature data

Data were taken from National Ocean and Atmosphere Administration CD-ROMs; the last year available was 1993. Seventeen states were selected including 12 where fire ant populations are documented (Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, and Virginia), and 5 states where fire ant infestation are likely (Arizona, California, Kentucky, New Mexico, and Oregon). After eliminating stations with very fragmented data, 3,528 stations were left for model runs. Two types of measurements were used.

1. Direct soil daily maximum and minimum temperature values at 10 cm depth, for 132 stations were used. All soil temperature records started from 1982 or later. Among the stations, 110 had 12 year-long records and 22 others had intervals varying from 4 to 11 years.

2. Daily maximum and minimum air temperatures were available for 3,528 total stations (including 132 'soil' stations). Missing values for the days within a month were reconstructed by interpolation; missing months within a year – by averages; missing years were not reconstructed.

Temperature values from the 132 'soil' stations were used for finding the regressions for the other stations. With few modifications, we applied the formulas of Chang et al. (1994) and Kluender et al. (1993) to calculate soil from air temperatures. The details of this modeling process will be presented elsewhere. For the 132 'soil' stations, the original measurements were used.

Soil temperature values for 10 cm were then corrected to mimic movements of colony population that gave our model 'working' temperatures somewhat warmer than the original ones. Specifically, maximum temperatures were increased to account for warmer mound temperatures during the day. Also, soil temperatures below 4°C were adjusted to soil temperatures at 30 cm to account for movement of the workers to this depth during periods of cold weather.

Model adjustment

To reproduce itself, a queen must produce, during its life, some critical number of alates, which results in precisely one queen surviving to maturity, so the equality of equation (1) will be satisfied. Alate production is determined by alate survivorship probability from birth to maturity, and its real value is known with low accuracy. Field observations give a range from 200 to 10,000 (Markin et al., 1973; Vinson and Sorensen, 1986). Because of this, we decided to find alate production from the empirical fire ant distribution; in other words, the model was calibrated using the observed distribution.

The procedure was intuitive, using observation, our model, and logic. The model was run on all 3,528 weather station locations to get average alate production for each site. We then sorted the data to find sites fitting two criteria: infested with RIFA for several years and having low alate production. The site best fitting this description was in eastern Tennessee, and it had been studied for several years by CMAVE scientists. It showed continued RIFA population survival but winter mortality had been observed. This site set the minimum alate production level for successful colonization, 8,300. This number bears important ecological meaning. Being found for the infested area, it gives the minimum alate production necessary for a queen to reproduce itself. All areas which have alate production greater than 8,300 are likely candidates for infestation. So, we can refer to this

area as a zone of 'certain' colony proliferation. This is a 'conservative' forecast because it uses the current range for the fire ant.

If our logic is in error, then perhaps an alate production of 8,300 is too high. What might be an alternative value? To generate another value we selected five sites on the northern border of RIFA range expansion. These infested areas are in Oklahoma, Arkansas, and Tennessee (Figure 2). We generated five circles, with radius equal to about 58 km, to provide about 10 stations per circle. Our logic for doing it went something like this. We know from observation that populations can grow at the center of each circle. Thus, we would expect colonies to survive to the south and maybe to the north. To get a more 'liberal' estimate we then calculated the alate production for each weather station within each circle and selected the site with the lowest "reasonable" alate production, which was 4,500. We tossed out two of the 53 sites because they produced very low values (50 alates in Arkansas and 1,013 alates in Tennessee). This became our second level of range expansion. A third level are stations that generated less than 4,500 total alates. Fire ant populations are not likely to be maintained there.

When and if fire ants reach the areas and sites with projected lower alate production, we will need to repeat the adjustment procedure and the zone of certain colony proliferation success will need to be increased.

Arid or semiarid conditions should hamper fire ant advance because of restricted habitat productivity and possible direct effects to the fire ant's life cycle (e.g., increasing difficulties in nest finding). There are no reliable data of this kind, so we took a precipitation threshold of 510 mm/yr, as a reasonable value limiting fire ant range; it corresponds to a semiarid region in southern Texas with reported spotty fire ant findings (personal communication). However, fire ants should do just fine in arid areas that are irrigated or adjacent to natural water courses.

Results and Discussion

Figure 2 shows the predictions generated for Arkansas, Oklahoma and Tennessee, while Figure 3 shows it for the 17 states analyzed. Plus signs indicate stations fitting our conservative estimate (YES), and the dark squares the liberal estimate (MAYBE). Open triangles depict sites with cold temperatures that probably limit fire ant survival (NO).

Mixed symbols represent the transitional zone where YES, MAYBE, and NO stations are mixed. The apparent reason for this "fuzzy border" is the spatial heterogeneity of weather (temperature) data. At what degree survival is caused by the intrinsic temperature spatial variability, and at what by the heterogeneity of the habitat (e.g., soil cover and relief) is another question. The existence of the fuzzy border is also the reason for the liberal and conservative estimates discussed above.

Some features of the predicted distribution can be noted. In a smaller scale (Figure 2), the liberal zone considerably exceeds the current range. The model predicts 120-150 km northern extension in Oklahoma, the same size northeast extension in Arkansas, and 80-100 km northern extension for Tennessee.

The conservative estimate is best if the current distribution in these three states has reached or nearly reached its maximum limits. The liberal estimate is probably better if fire ants have only just invaded the most southerly locations along this fuzzy border at which they can survive. Fire ants still appear to be moving northward at a slow rate in Oklahoma, Arkansas, and probably Tennessee; consequently, the liberal estimate may

provide a better estimate of sites at which fire ants have demonstrated their survival ability.

For the whole fire ant range (Figure 3), the model predicts considerable broadening of the current range, mainly in maritime areas of Virginia, western areas of Texas, and wide regions of California and Oregon. Low precipitation will likely seriously restrict fire ant propagation in the area between western Texas and eastern California, with exception of irrigated areas.

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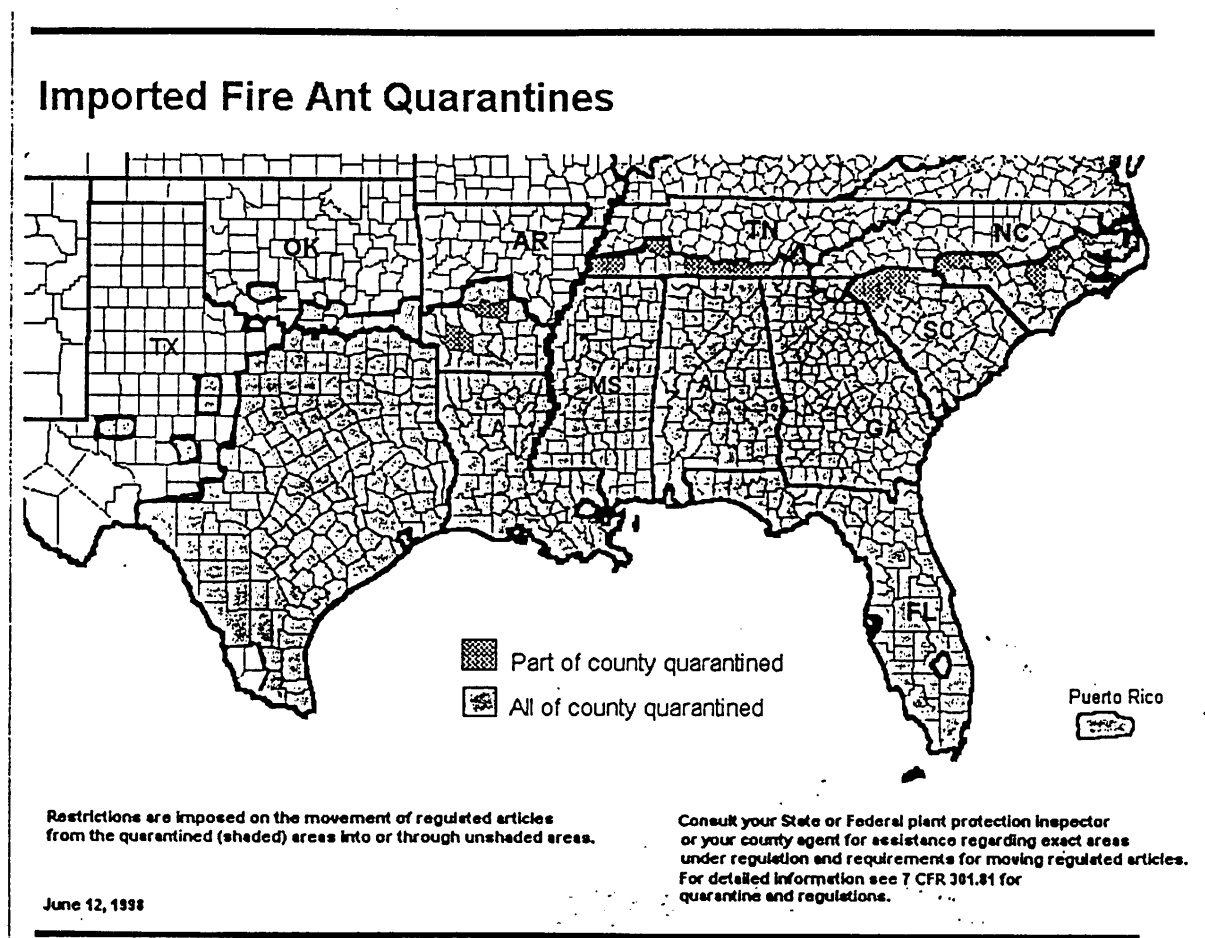   Florida.

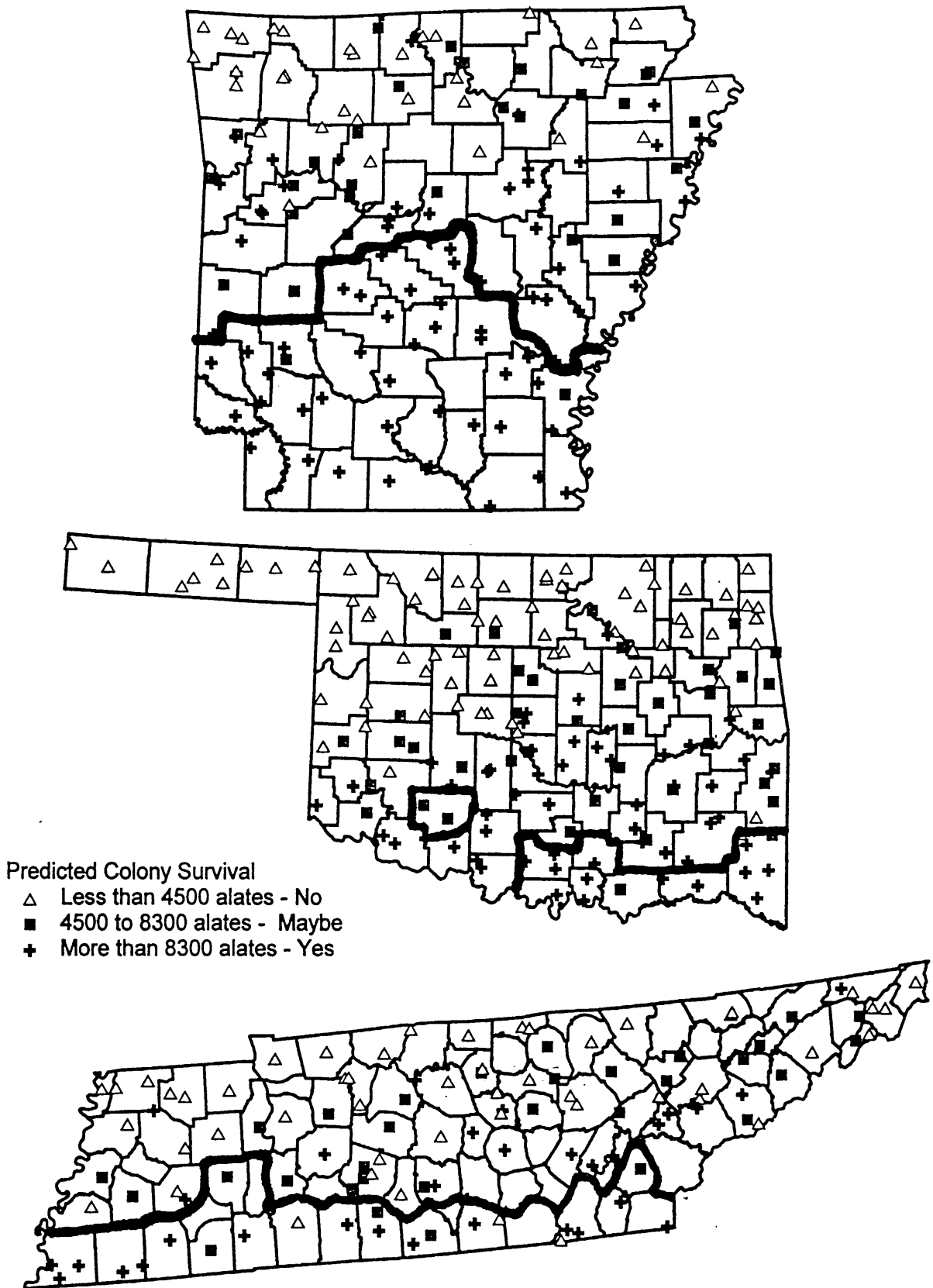Fig. 1. Imported fire ant quarantine map - 1998.

Predicted Colony Survival
△ Less than 4500 alates - No
■ 4500 to 8300 alates - Maybe
+ More than 8300 alates - Yes

Fig. 2. Three partly infested states selected for model calibration.
Currently infested areas are below the thick lines.

Predicted Colony Survival
△ Less than 4500 alates – No
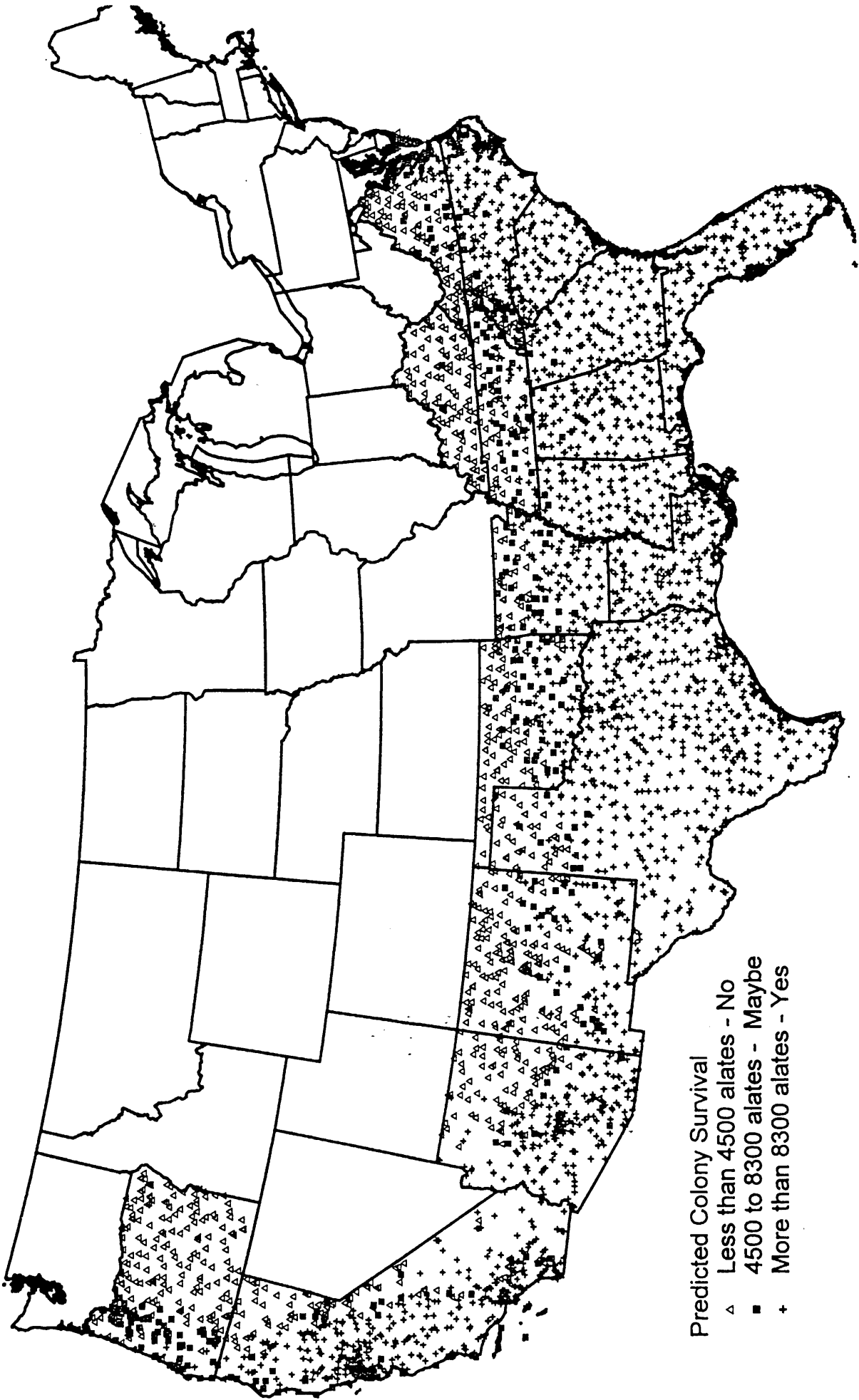■ 4500 to 8300 alates – Maybe
+ More than 8300 alates – Yes

Fig. 3. Predicted RIFA colony survival across the United States.