Modeling Temperature-Dependent Range Limits for the Fire Ant *Solenopsis invicta* (Hymenoptera: Formicidae) in the United States

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ABSTRACT We predict the future range of the fire ant *Solenopsis invicta* Buren within the United States based on climate and its current extreme distributions. To reach that goal, a dynamic model of colony growth with two time steps per day was formulated that operates by colony area, *S*, and alate production, *a*. Colony growth rate depended on daily maximum and minimum soil temperatures. Temperature records at 4,537 meteorological stations within the current (near 1.5 million km^2) and potential range of *S. invicta* were obtained from NOAA's National Climatic Data Center. At each station, a colony was allowed to grow and lifetime female alate production was calculated. Estimated alate production was then examined at current extremes of the fire ant distribution at selected locations in Arkansas, Tennessee, and Oklahoma. Estimates from these locations were used to define four zones of colony proliferation success: certain, possible, undemonstrated, and improbable. An annual precipitation limit (510 mm) was selected to indicate regions where arid conditions may prohibit growth in areas without supplemental water sources. Results of the model predict that *S. invicta* will likely move 80–150 km north in Oklahoma and Arkansas. It will also likely continue expanding into portions of Virginia, Maryland, and Delaware in the east and New Mexico, Arizona, California, Oregon, Nevada, and maybe even Washington and Utah in the west.

KEY WORDS *Solenopsis invicta*, biogeographical range, modeling, distribution, United States, quarantine

THERE ARE TWO major reasons to model range limits of the fire ant *Solenopsis invicta* Buren. First, *S. invicta* is an important economic pest (Thompson et al. 1995) and knowledge of its potential range limits will indicate where quarantine efforts are most needed. The second reason is that fire ant biology and ecology are comparatively well known (Wojcik and Porter 2000) making the effort very interesting and tractable from a scientific standpoint. Imported fire ants are currently distributed across much of the southern United States where they occur across a wide range of temperature and precipitation.

The problem of determining the range limits of invading species is an issue that has attracted the attention of researchers working with many kinds of plants and animals throughout the world (Worner 1994, Sutherst et al. 1999, Baker et al. 2000). Several attempts have been made to predict the ultimate range of imported fire ants in the United States. The earliest estimates (Anonymous 1972, CAST 1976) were based on plant hardiness isolines (USDA 1941). Several other isoline predictions have also been published (Vinson and Sorensen 1986, Vinson 1997). To date, there are no worldwide estimates of the future range of *S. invicta* even though recent discoveries of this pest in Australia and New Zealand indicate that this information could greatly help target quarantine efforts.

Three attempts to model fire ant range limits in the United States 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) at a spatial resolution of one degree. The authors calculated fire ant propagation rate and applied it to the situation in Texas. They accurately predicted that fire ants were beginning to reach the northern limits of their range. However, they seriously overestimated the rate of western expansion (see Stoker et al. 1994 for a map of the 1993 distribution in Texas) apparently because dry conditions are a limiting factor, a possibility that Pimm and Bartell (1980) warned of in their paper.

Stoker et al. (1994) developed a mechanistic model to find a 'reproductive' border, which 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 a population of colonies and operates using seven ant developmental stages; it describes queen fecundity, mating flights, and dependence of developmental rates and mortality on air temperature. The model operated with daily air 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

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grew even up to the northern boundary of the Texas panhandle and probably beyond. We see two methodological deficiencies of the approach: first the application of a population-level model when a single colony model is sufficient and secondly no attempt was made to adjust the model to match reality. Additional problems were that the model did not deal with winter kill and did not use realistic estimates for worker mortality.

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 the growth of a single colony and operated using five ant developmental stages. It gave an approximate location for the fire ant geographical limit, but in very low resolution (three points along a Texas-Kansas-Wyoming transect and one point in Alabama). So, actually only one point on the fire ant range border was estimated. The model was fairly sophisticated and generally did a good job of simulating seasonal variability in colony growth, but prediction of thermal range limits were unreliable because the estimate of winter kill used in the model was not based on empirical data. A second problem was that workers in the model died too quickly at cool temperatures (see Calabi and Porter 1989).

From our point of view, the two last models were overly complicated and contained features which prevented realistic results. Many details about colony growth are known with low accuracy, and their incorporation into a model does not improve model quality because it makes the model less stable with respect to parameter variations. As we understand 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 that is just sufficient to solve the problem. While an ecologist usually tries to describe his object in detail in order not to loose the reality, a modeler tries to get the desired effects by minimum means. Our variant, offered below, was developed with a minimum of assumptions and with parameters fitted to provide a realistic outcome.

Materials and Methods

Soil temperature T_s is the key ecological factor which determines colony metabolism and activity (Markin et al. 1973; Porter and Tschinkel 1987, Tschinkel 1993; Porter 1988), therefore it was used below as the primary ecological factor.

The most biologically sound way to find a stable border would be to evaluate the "basic reproductive rate," R_0, equal to the average number of queen progeny surviving to adulthood, in the absence of intraspecific competition. Then, the needed border is found from the equation

$$R_0(T_s) = 1, \qquad [1]$$

(Birch 1948, May 1974, Cooksey et al. 1990, De Jong and Diekmann 1992, Hochburg et al. 1992). To find R_0, one needs to know with sufficient accuracy the rates for queen fecundity, colony alate production, and queen mortality. All three values need to be given as functions of colony size, and ecological factors like soil temperature, maybe precipitation, and competition with other species of ants. This seems to be too much for the current state of knowledge, so several assumptions were made to simplify the approach.

First, colonies were described by two dynamic variables—colony size as described by territory area, $S(t)$, and daily alate production, $a(t)$. Increases and decreases in colony size were governed by soil temperature. Instead of using equation 1 to find the border, we calibrated the model to adjust the calculated range to the furthermost points in the present distribution. Northward movement of this area has been very slow over the last 10 yr, indicating that the northern limits of the range are being reached, as predicted by Pimm and Bartell (1980). To calibrate the model, the total number of alates produced by a colony, $\alpha = \Sigma a(t)$ was considered a free parameter. In short, our model functions at two levels: the first is an ecophysiological model of the effects of temperature on colony growth and mortality; the second level is a geographic prediction of future range limits based on estimated lifetime alate production calibrated to current extreme limits of *S. invicta's* range. Amplification of this approach is given below.

Model Construction. We assumed that the number of workers in a colony is proportional to the area of its territory, S (see *Appendix*, Tschinkel et al. 1995, also please note that capital "S" is used to indicate territory size and should not be confused with subscript "$_s$" which is used to designate soil temperature). Consequently, the size of a colony at age t is given by colony area, $S(t)$ in m^2. From this we calculated colony alate production, $a(t)$, females per day. Because we had maximum and minimum temperature values for each day, we also used two time steps per day. Parts of this model grew out of a spatial model of fire ant territorial competition (Korzukhin and Porter 1994).

Colony Area Dynamics. Within our model, two processes determine dynamics of S, the production of workers and the death of workers. The rates of these processes depend on temperature and were determined from empirical laboratory observations (Porter 1988, Calabi and Porter 1989).

We distinguished two temperature intervals, each with its own specific colony dynamics (Fig. 1A). When $T_s > T_{s1}$, the balance of birth and death is positive, and $S(t)$ is growing with the specific growth rate $r(T_s)$ per day. When $T_s \le T_{s1}$, temperatures are too cold to grow (Porter 1988) and so the colony dies off with a rate $1/L(T_s)$, where $L(T_s)$, in days, is worker longevity given by the empirical curve shown in Fig. 1B. The curve indicates cold-stress or cold-coma mortality for $T_s < 4$°C (S.D.P. and T. Macom, unpublished data).

Colony Alate Production. After reaching the reproductive size, S_{rep}, m^2, a colony splits its growth re-

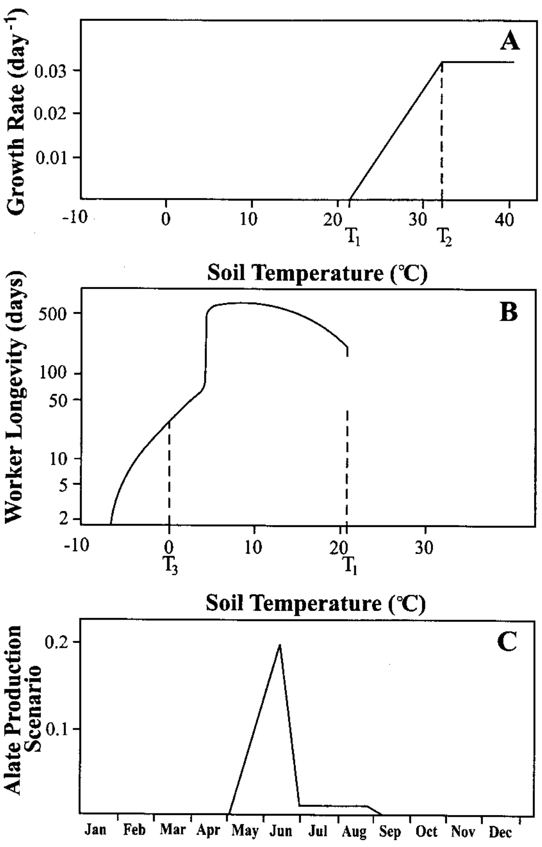

Fig. 1. Three empirical curves used in the model. (A) specific colony growth rate $r(T_s)$, 1/day (Porter 1988); (B) worker longevity $L(T_s)$, day (Porter 1988, Calabi and Porter 1989); (C) alate production scenario, $f(J) \leq 1$ (Tschinkel 1993). T_1, T_2, T_3 are temperature parameters (see text and *Appendix* for explanations).

sources between worker and alate production (Tschinkel 1993, Fig. 1C). The share of resources directed to alate production is given by a function $f(J)$ referred to later as the "alate production scenario," where J is Julian date. The share $f(J)$ is directed to alate production, while the rest $1 - f(J)$ is directed to worker production. The function $f(J)$ changes from 0 to 1; $f(J) = 1$ corresponds to zero worker production and 100% alate production, while $f(J) = 0$ corresponds to the opposite situation.

The above considerations were expressed formally in the system of equations for two dynamic variables for $T \geq T_1$ and $S < S_{rep}$:

$$S(T_s,t+1) = S(T_s,t) + r(T_s)S(T_s,t)[1 - S(T_s,t)/S^{max}]$$

$$\text{and } a(t+1) = 0 \qquad [2a]$$

for $T \geq T_1$ and $S \geq S_{rep}$:

$$S(T_s,t+1) = S(T_s,t) + [1 - f(t)]r(T_s)S(T_s,t) \cdot [1 - S(T_s,t)/S^{max}]$$

$$\text{and } a(t+1) = qf(t)r(T_s)S(T_s,t) \qquad [2b]$$

for $T < T_1$:

$$S(T_s,t+1) = S(T_s,t) - S(T_s,t)/L(T_s)$$

$$\text{and } a(t+1) = 0, \qquad [2c]$$

where t is colony age, in days, and $T_s = T_s(t)$ is current soil ($_s$) temperature (in °C); functions $r(T_s)$, $f(t)$, and $L(T_s)$ were described above; q is a parameter providing correspondence between colony size, S, measured in square meters, and alate production, a, measured in numbers. As one can see, colony area growth is restricted with the maximum colony area, S^{max}. (See *Appendix* for these and other parameter values.)

For the sake of simplicity, we assumed that S^{max} does not depend on temperature; this justifies the specific form of equation 2—under any positive $r(T_s)$, we have $S(T_s,t)$ going to S^{max} mandatory while in a case of the general equation like

$$S(T_s,t+1) = S(T_s,t) + r(T_s)S(T_s,t) - q(T_s)S^2(T_s,t)$$

we would get temperature dependent $S^{max}(T_s) = r(T_s)/q(T_s)$.

A queen establishes the nest at a given Julian date, J_0, with initial colony area $S_0 = S(J_0)$, and lives a maximum Λ days. A shrinking colony dies when it reaches some critical area S^{min} that can happen either after $t > \Lambda$ or after a long period of cold temperature.

The main output variable was the total number of alates produced, α, by a colony during its lifetime

$$\alpha = \Sigma a(t). \qquad [3]$$

Temperature Data. Data were taken from the National Ocean and Atmosphere Administration CD-ROMs (NOAA 1994); the last year available was 1993. Twenty-four states were selected including 15 where fire ant populations have been documented (Alabama, Arizona, Arkansas, California, Florida, Georgia, Louisiana, Mississippi, New Mexico, North Carolina, Oklahoma, South Carolina Tennessee, Texas, and Virginia), and nine adjacent states where fire ant infestations have not yet been reported (Delaware, New Jersey, Nevada, Oregon, Kansas, Kentucky, Maryland, Missouri, and Washington). After eliminating stations with heavily damaged data, 4,537 stations were left for model runs. Average interstation distances ranged between 26 and 38 km for the different states. Consequently, each station represented 660–1,440 km^2 (Virginia and Oregon, respectively). Two types of measurements were used:

(1) Direct soil daily maximum and minimum temperature values at 10 cm depth, T_s^{min}, T_s^{max}, were used (comprising ≈96% of the available soil temperature data). All soil temperature records started from 1982 or later. So, we had maximum soil temperature record length of 12 yr. Among 137 stations left for the analysis, 112 had 12 yr long records, whereas 25 others had intervals varying from 3 to 11 yr.

(2) Daily maximum and minimum air temperatures, T_a^{min}, T_a^{max}, 4,537 stations in total (including 137 'soil' stations). Missing values within the year (near 5% of total dates) were substituted by averages; missing years were not reconstructed.

Temperature values T_s^{min}, T_s^{max}, T_a^{min} and T_a^{max} from 137 'soil' stations were used for finding the regressions, $T_s^{min}(T_a^{min}, T_a^{max})$ and $T_s^{max}(T_a^{min}, T_a^{max})$ for the rest of 4,400 stations. We applied the formulas of Chang et al. (1994) and Kluender et al. (1993) to calculate soil from air temperatures. Our results are as follows:

$$\begin{aligned} T_s^{min}(J) &= 7.30 + 0.403T_a^{min}(J) + 0.193T_a^{max}(J) \\ &\quad - 1.98\sin(z) - 3.78\cos(z) \\ T_s^{max}(J) &= 7.63 + 0.154T_a^{min}(J) + 0.533T_a^{max}(J) \\ &\quad - 1.52\sin(z) - 4.50\cos(z) \end{aligned} \quad [4]$$

where $z = 2\pi(J/365)$, J is a Julian date. Statistical characteristics of the regressions are as follows: $R^2_{min} = 0.908$, standard deviation $s_{min} = 2.56$, number of empirical points $n_{min} = 511{,}832$; $R^2_{max} = 0.882$, $s_{max} = 3.40$, $n_{max} = 511{,}740$. n_{min}, n_{max} were less than possible maximum $N = 137 \times 12 \times 365.25 = 600{,}471$ because of trajectory incompleteness in 25 'soil' stations. For the 137 'soil' stations, we used the original soil measurements for model runs.

Soil temperature values for 10 cm were then corrected to mimic thermoregulatory movements of colony population that gave the model 'working' temperatures somewhat warmer than the original ones. Specifically, maximum temperatures at 10 cm (T_s^{max}) were increased to account for warmer mound temperatures during the day (T_{sm}^{max}) using the formula $T_{sm}^{max} = 0.092{+}1.28T_s^{max}$. This adjustment added 3–9°C to daily maximum temperatures based on observations that the degree of difference between mound and soil temperature increases with increasing soil temperature (S.D.P., unpublished data). 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 (S.D.P., unpublished). This was done by adding 1.4°C to T_s^{min} and subtracting 0.7°C from T_s^{max}. In north Florida, the majority of workers never move below 30 cm no matter how cold (S.D.P., unpublished data). We assume that this is the case in other parts of their range, but this needs to be verified along the northern limits of their range. Estimated minimum and maximum soil temperatures below 0°C were set equal to 0°C (see parameter T_3 on Fig. 1b) because plots of NOAA soil temperatures at 20 cm against air temperatures showed that soil temperatures at this depth never fall below 0°C even when air temperatures were extremely cold. Apparently the process of freezing almost always truncates soil temperatures at 0°C, at least, in regions along the northern boundary of the fire ant range.

Technically, for each station, we took the most recent trajectories, from $Y = 3$ to 12 yr long for T_s^{min} and T_s^{max} values. Then this original set was used to get a nine year long extension. One 9 yr long portion from the beginning was added to the end for $Y = 9$–12; two portions were added for $Y = 5$–8, and three portions for $Y = 3$–4. The first Y years were used in sequence to start the growth of Y colonies, while the remaining 9 yr served for continuation of the last colonies growth. Average lifetime female alate production, A, was the main output variable (α_k = individual colony production)

$$A = \Sigma\alpha_k / Y \quad [5]$$

Model Adjustment. Persistence of ants at a location requires that a queen produce, during her life, no less than some critical number of female alates, A_0, which results in precisely one queen surviving to the maturity, so the equality [1] will be satisfied. A_0 is determined by alate survivorship probability and by colony alate production during its lifetime; empirical values for these curves are poorly known. For example, field observations give a total female alate production range from several hundred to ten thousand (Markin et al. 1973, Morrill 1974). Because of this, we decided to find A_0 from the empirical fire ant distribution; in other words, the model was calibrated using the observed most northerly distributions. Five infested regions in Oklahoma (2), Arkansas (2), and Tennessee (1) were selected for this purpose ("calibration areas" are depicted as circles on Fig. 2).

The procedure consisted of the following. To account for considerable inter-station variability in alate production, we took five circles (radius = 58 km, corresponding to an average of 10 stations in the circle), and found the average alate production within each of them; number of covered stations varied from 10 to 11. The minimum value among these averages

$$A_{01} = \min(A_k), k = 1...5, \quad [6]$$

appeared in the Tennessee circle, $A_{01} = 3900$ (the other values were 4700 and 4600 for Arkansas, and 4300 and 5200 for Oklahoma). This number has an important ecological meaning. Being found for the infested area, it gives an estimate of the minimum alate production necessary for a queen to reproduce herself under field conditions. All currently noninfested areas that had greater alate production, that is

$$A > 3{,}900, \quad [7]$$

are the first candidates for infestation. So, we refer to this area as a zone of "certain" colony proliferation success. This is a conservative forecast because it is based on the current fire ant range and average alate production in the calibration area rather than extremes. We may need to repeat the adjustment procedure and zone of certain colony proliferation success if fire ants continue invading colder sites.

To reflect the uncertainty in infestation data, and inter-station temperature variations, we estimated another, more liberal, critical value of alate production, A_{02}, which gives a wider "possible" zone of future infestation. Among several conceivable ways to get this estimate, the following was used: We found the value of A_{02} equal to the average of minimum values found in each calibration area. With the exception of two very low values (in Arkansas $A = 25$, and in Oklahoma $A = 0$) that are naturally explained by mountain region heterogeneity, this procedure gave $A_{02} = 2{,}100$. So we take

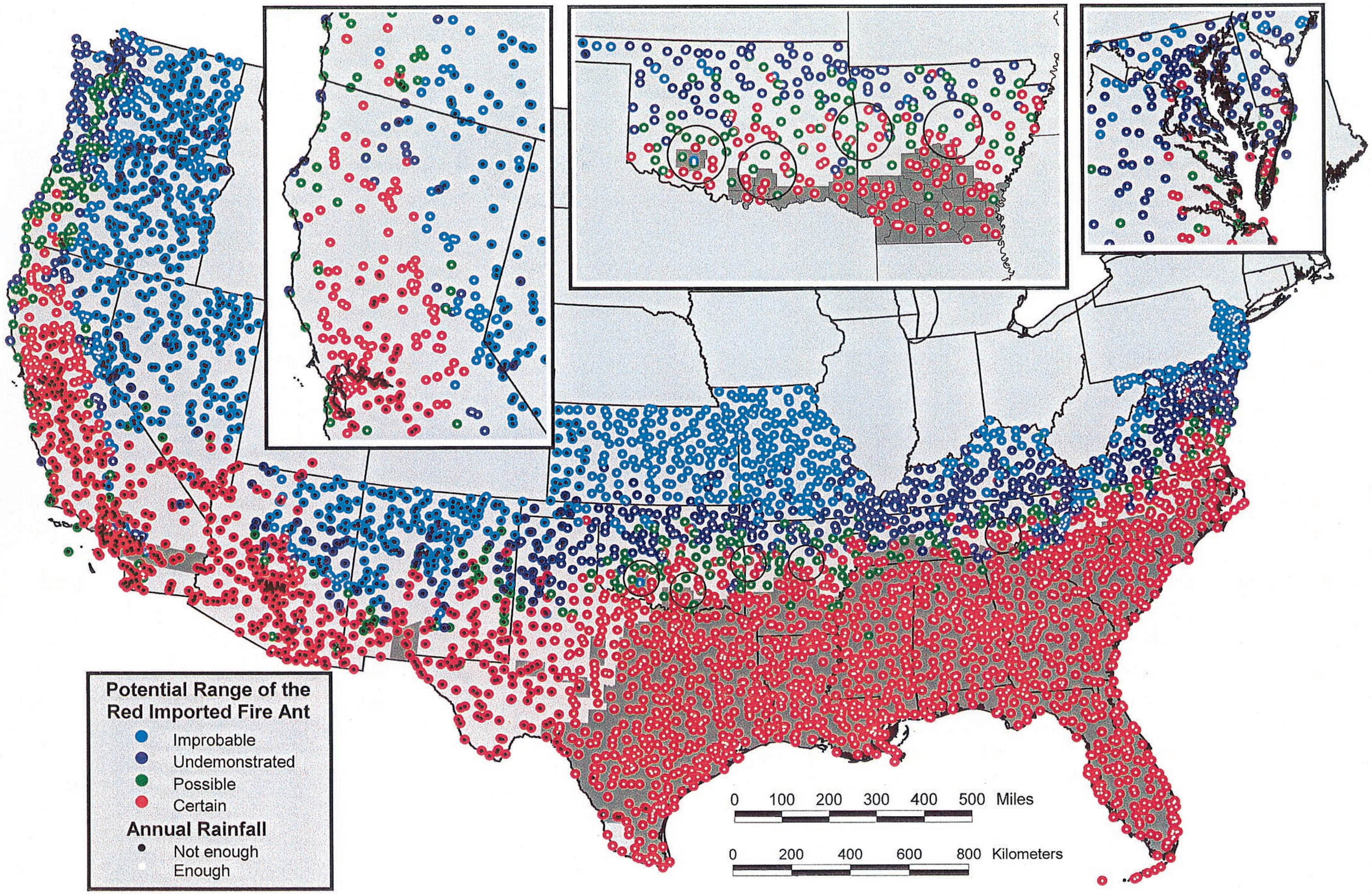

Fig. 2. Potential range of the red imported fire ant, *Solenopsis invicta*, in the United States. Red circles depict sites with "certain" reproductive success, $A > 3{,}900$ (A = female alate production); green circles—"possible" success, $2{,}100 < A \leq 3{,}900$; dark blue circles— "undemonstrated" or sites with weather conditions where *S. invictas* has no record of success, $0 < A \leq 2{,}100$; and light blue circles—"improbable" or sites where colonies did not survive to produce sexuals, $A = 0$. Quarantined counties are indicated by dark gray fill. White dots inside the colored circles correspond to sites with sufficient precipitation (estimated at >510 mm/yr) to sustain fire ants in the landscape, and black dots indicate arid sites which likely have insufficient rain. However, it is important to note that fire ants will survive in arid areas that are irrigated or have natural sources of water. The size and location of the fire ant calibration circles (black) are indicated for Oklahoma, Arkansas, and Tennessee (see text for details of calibration procedure).

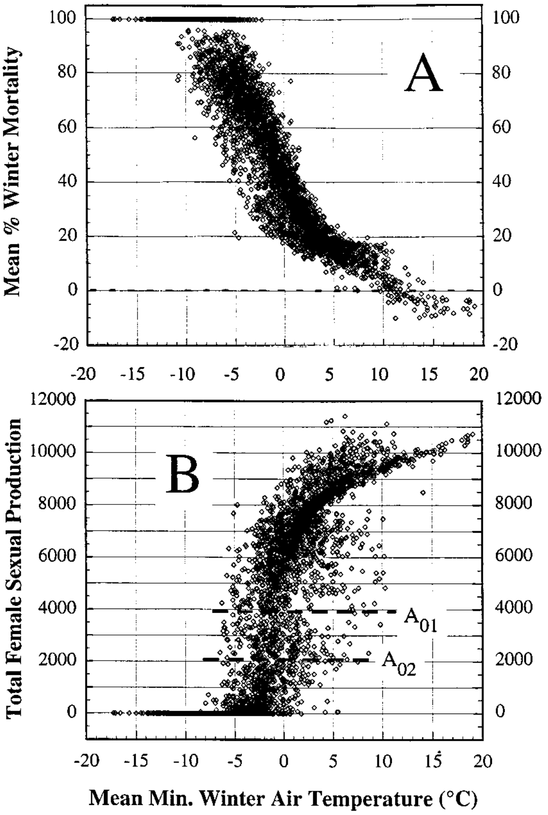

Fig. 3. (A) estimated percent winter kill of workers in *Solenopsis invicta* colonies at 4,537 sites plotted against mean minimum winter air temperatures (December–February). Each point is the yearly average of $Y = 3$–12 trial colony runs over the life of the colony. (B) Mean lifetime female alate production of trial colonies from 4,537 sites plotted against mean minimum winter air temperature (December–February). Each point is the average of $Y = 3$–12 trial colony runs.

$$A_{02} = 2{,}100 \qquad [8]$$

as another minimum estimate for alate production.

The last approach can be considered as an alternative to the one which leads to finding A_{01}. Obviously, usage of average circle alate production will always give greater critical values for A_0 than the value needed to infest all the individual locations, therefore the inequality

$$A_{01} > A_{02} \qquad [9]$$

is always true. This justifies the name liberal for A_{02} and "possible" for the corresponding infestation zone. Regions with alate production values less than A_{02} are referred to as "undemonstrated." If *S. invicta* have reached or are near their northern limits in Tennessee, then most or all of the "undemonstrated" sites will not be occupied by *S. invicta.*

It is important to note that fire ant colonies in this "undemonstrated" region, and even in the "possible" region, may not actually be able to produce the numbers of alates predicted if persistent winter kills reduce their ability to compete with native ants that are better adapted to cooler climates. Sites with zero alate production ($A = 0$) are obviously considered "improbable" locations for future invasion by the *S. invicta.* This designation, of course, depends on the accuracy of our estimates of cold coma mortality for the red imported fire ant, *S. invicta.* We do not yet have estimates for cold coma mortality of black imported fire ants (*Solenopsis richteri* Forel) or hybrid fire ants (*S. invicta* × *S. richteri*). Consequently, we did not use sites in Tennessee with black or hybrid fire ants for calibration of the model. If black or hybrid fire ants have a higher tolerance for cold temperatures, it seems likely that they will be able to move further north. However, the fact that infestations of black and hybrid fire ants are still not known from Kentucky suggests that these ants do not have a dramatically higher cold tolerance than the *S. invicta.*

Arid or semiarid conditions should also hamper the fire ant advance because of low habitat productivity and possible direct affects on colony founding. There are no reliable data of this kind, so we took a precipitation threshold of $P = 510$ mm/yr as a reasonable value limiting fire ant range. This value corresponds to a semiarid region in southern Texas (near Laredo) where fire ants have been reported to survive in natural mesquite scrub lands (L. E. and R.J.W. Patrock Gilbert, personal communication). However, fire ants are known to do well in arid areas that are irrigated or adjacent to natural water sources (Anonymous 1999, Frank 1988, MacKay and Fagerlund 1997).

Results and Discussion

Potential Fire Ant Range. The model was run in all 4,537 station locations and average alate production [5] was calculated for each point. Fig. 2 shows the total theoretical range with several insets for regions of particular interest. The red circles indicate sites of "certain" infestation. The green circles are sites of "possible" infestation. The dark blue circles depict sites in the model with cold temperatures at which fire ants have not demonstrated their ability to survive (beyond our "certain" and "possible" estimates for survival). Light blue circles correspond to sites with no alate production where success is very "improbable".

What can be seen first, is a full coverage of the current fire ant quarantine zone with red circles that confirms our selection of a calibration area in the most extreme limit of the current range.

Green circles occur primarily in a transitional zone where red, green, and blue stations are mixed. The reason for this "fuzzy border" is the spatial heterogeneity of weather (temperature). At what degree it is caused by the intrinsic temperature spatial variability, and at what by the heterogeneity of the habitat (vegetation, attitude, aspect) is another question. The existence of the fuzzy border is also the reason for the "certain" and "possible" estimates discussed above.

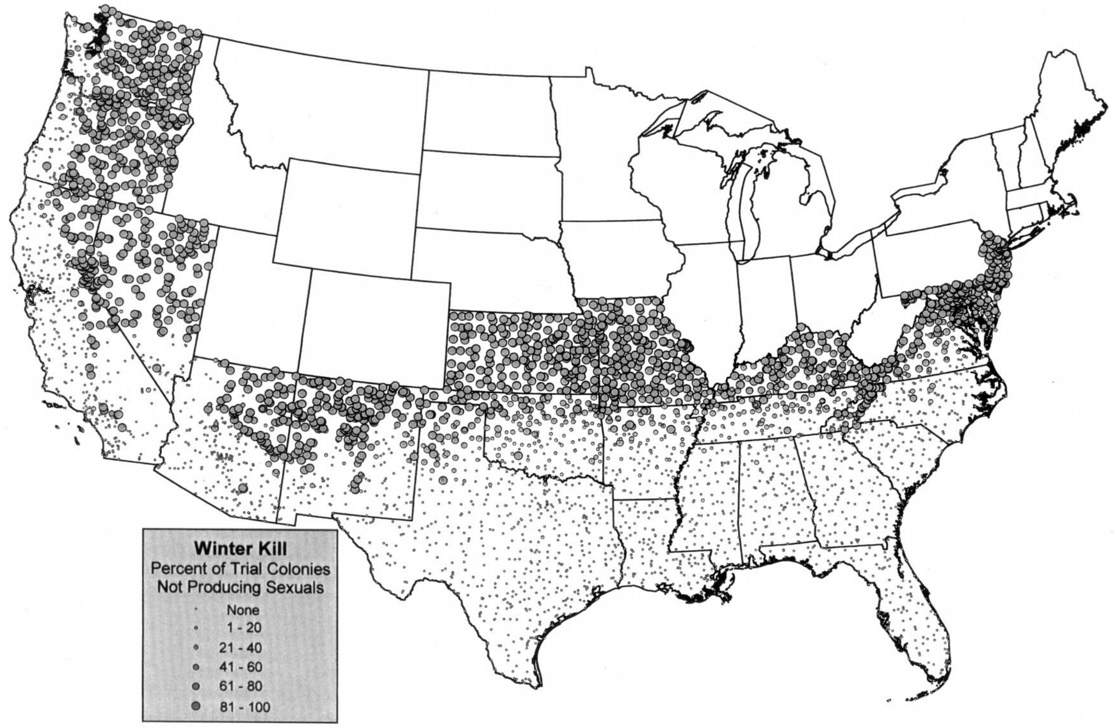

Fig. 4. Geographic distribution of colony winter kill predicted by the model. Each dot indicates the percentage of trial colonies at each site that did not grow large enough to produce sexuals during their lifetime because of winter kill. Trial colonies were run sequentially each year for 3–12 yr, depending on the length of weather data (maximum/minimum air or soil temperatures).

For the *S. invicta*, the "certain" estimate is best if the current distribution has reached or nearly reached its maximum limits. The "possible" estimate is better if fire ants have only just invaded the most southerly locations along this fuzzy border at which they can survive. Red imported fire ants still appear to be moving northward at a slow rate in Oklahoma, Arkansas, and probably Tennessee; consequently, the "possible" estimate may provide a better estimate of the ultimate fire ant distribution.

With the "certain" success zone, our model predicts large range extensions of the *S. invicta* in several regions of the United States (Fig. 2). The model predicts a 120–150 km northern extension in Oklahoma, the same size extension in Arkansas, and 80–100 km northern extension for Tennessee, except most of Tennessee is occupied by black or hybrid fire ants so the model may not apply well to this state. The CAST (1976) report used the −12.2°C (10°F) mean annual minimum air temperature isoline (USDA 1941) to predict the potential imported fire ant range in the United States based on their northern expansion until 1976. Our results (Fig. 2), adjusted to the 1999 distribution of imported fire ants, indicates that the −15°C (5°F) isoline (see USDA 1941, Vinson 1997) would be more accurate in the southeastern United States. However, mean annual minimum temperature isolines may not work well in the Pacific Northwest, because cool summer temperatures limited the ability of colonies in our model to produce sexuals (Fig. 2). Range estimates using the −17.8°C (0°F) isoline (Killion and Grant 1995, Anonymous 1972) were not based on empirical data and currently appear overly liberal. In any case, any attempts to apply "temperature isoline-based" range predictions will be essentially correlative so generally one cannot expect that they will work successfully for the whole range.

For the whole fire ant range (Fig. 2), the model predicts considerable expansion of the current range to the northeast and to the west, mainly in maritime parts of Virginia, western parts of Texas, and wide regions of New Mexico, Arizona, California, and Oregon. Even Washington, Delaware, Maryland, Nevada, and Utah may be able to support fire ant populations at some sites. Areas around San Francisco and Sacramento, CA, appear to be especially good habitat because of moderate temperatures and adequate precipitation. Low precipitation values will almost certainly restrict fire ant propagation in most unirrigated sites between western Texas and eastern California (Fig. 2). However, areas along water courses and hundreds of thousands of hectares of irrigated land in urban and agricultural areas are susceptible.

Mechanics of Range Limit. As detailed earlier, our estimates of future range limits are based on a core ecophysiological model of alate production. Alate production and population survival is, of course, a balance between the effects of cold kill in the winter and colony growth in the warmer months. Our estimates of winter kill caused by extended periods of cold induced immobility or cold coma (temperatures < 4°C; S.D.P. and T. Macom, unpublished data) was the principle factor limiting colony survival in the model.

Figure 3A plots the predicted percent reduction in colony size during the winter months (December–February) against the mean minimum air temperature for those months. Colony size at sites with mean minimum temperatures between ≈2°C and 10°C declined 10–20% during the winter months, mainly due to low natural mortality when brood was not produced. Colonies at sites with mean minimum temperatures above 10°C actually grew during the winter months as indicated by the negative percent reductions. However, as mean minimum temperatures declined from 2 to −8°C, the percent reduction in colony size increased rapidly to 100%, due to the estimated effects of prolonged periods of cold coma. Below about −8°C most sites showed 100% winter kill. Although not clear from Fig. 3A, colonies at 423 sites suffered 100% winter mortality in the first year of all 12 trial runs.

Total lifetime female alate production was strongly correlated with mean minimum winter temperatures (Fig. 3B). From 18°C to ≈2°C, alate production declined gradually. But below 2°C, alate production dropped dramatically, generally reaching zero at mean minimum temperatures between −3 and −7°C. Colonies at 1,155 of the 4,537 sites never grew large enough to produce sexuals. Below −3 to −7°C, colonies were generally killed outright (Fig. 3A), so sexual production was zero. The scatter of 50–70 points to the right of the main cluster was mainly (>90%) west coast sites (California, Oregon, Washington) that are apparently unusually warm in the winter but cooler than normal in the summer; consequently these sites suffered little or no winter kill but lower than expected sexual production during the warmer months. A comparison of Fig. 3A and Fig. 3B indicates that average winter mortality of 50–70% is required to drive sexual production down below the critical level (A_{01} or A_{02}) for sustaining a population.

Fig. 4 shows the percentage of trial colonies at each site that were unable to grow to maturity and produce alate queens. Without winter kill, almost all colonies would have been capable of growing to maturity at almost all sites. The distribution of winter-kill limited colonies (Fig. 4) is reasonably consistent with the available empirical data. Winter kill of exposed colonies has been reported from north central Georgia (80–100%, winter 1976–1977; Morrill et al. 1978) and Lubbock, TX (60%, winter 1986–1987; Thorvilson et al. 1992). However, little or no winter kill occurred at these same times for other years. Diffie et al. (1996) followed colonies for 5 yr (1985–1990) in north and north central Georgia without finding clear evidence of winter mortality, so it seems likely that the winter kill reported for 1976–1977 (Morrill et al. 1978) may have been a fairly rare event. Callcott et al. (2000) at a site in southeastern Tennessee reported high winter kills for the winters of 1993–1994 (88% of colonies), 1994–1995 (61%), and 1995–1996 (79%). They further reported that these kills were best correlated to the number of consecutive days with maximum temperatures below 1.1°C, a measure that is congruent with our method of estimating cold coma mortality. Hopefully, future studies will be able to directly test our predictions of winter kill (Fig. 4) by linking direct measurements of soil temperatures with colony survival at specific sites.

The slow northerly expansion of *S. invicta* along their northern border (Callcott and Collins 1996) combined with evidence of strong and frequent winter kill in Tennessee (Callcott et al. 2000) strongly indicates that *S. invicta* is reaching the northern limits of its potential range (Pimm and Bartell 1980). Red imported fire ants will probably require 30–40 yr to complete their invasion of sites within the city of Gainesville, FL (Wojcik 1994). If the invasion process is so slow in an area with prime thermal conditions, then it may require fire ants several hundred years to fill in all of the marginal sites where fire ants can survive along a fuzzy (heterogeneous) northern border.

This model was calibrated to the most northern locations where fire ants are known to survive in rural environments. Fire ants will likely survive in colder climates in urban environments and other areas with solar heat sinks and artificial heat sources (Thorvilson et al. 1992). In these areas fire ants will generally not be landscape pests; however, they may be able to temporarily infest the landscape during warm years from nearby refugia. Our range estimates were primarily based on 1982–1992 weather data. Global warming could also cause fire ants to expand further north than expected (Patz et al. 1998).

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Appendix. Primary model parameters and standard values

Standard model parameters, units (source)	Parameter values
Colony size	
Max territory area, S^{max}, m^2 (Markin et al. 1975)	100
Territory area at which worker mortality causes colony death, S^{min}, m^2 [a]	0.01
Initial territory area, S_0, m^2 [b]	0.02
Minimum area for colony production, S_{rep}, m^2 [c]	10
Max colony growth rate, r^{max}, 1/d (Markin and Dillier 1971, Porter 1988)	0.03286
Temp when colony growth begins, T_1 (Porter 1988)	21°C
Temp for maximum growth rate, T_2 (Porter 1988)	32°C
Lower limit for effective soil temperature, T_3	0°C
Queen longevity, Λ, days (Tschinkel 1987)[d]	3000
Colony proliferation parameter, q[e]	89
Julian date of colony founding, J_0	165

[a] Corresponds to ≈15 workers.

[b] Estimated from mean worker density (1/m^2), Wilson et al. 1971, and the number of workers in new postclaustral colonies (Porter and Tschinkel 1986).

[c] Estimated from average empirical colony age when proliferation begins.

[d] We chose this value because it is somewhat larger than that estimated by Tschinkel (1987) on the assumption that rates of sperm depletion would be a bit less in cooler climates.

[e] Estimated from Markin et al. 1973, Morrill 1974, and our adjustment of alate production model (unpublished data).