Spatial Model of Territorial Competition and Population Dynamics in the Fire Ant *Solenopsis invicta* (Hymenoptera: Formicidae)

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ABSTRACT We developed a simulation model of monogyne red imported fire ant, *Solenopsis invicta*, populations that operates by competitive interactions of individual colony territories. This model describes six major aspects of colony life history: nest founding, brood raiding, territory expansion, queen death, possible requeening, and colony death. Individual colony territories are represented by rectangles, whose sides change independently depending upon the presence and size of neighboring colonies. Growing colonies try to occupy free space, while retaining square territorial dimensions whenever possible. The growth of fire ant populations in the model compared well with available field data. The model predicted that competitive exclusion caused by territorial interactions should occur when areas reach 70–90% territory coverage. Several computer experiments were conducted with the model to examine the importance of colony growth rate, brood raiding activity, and other parameters on the relative success of sequentially founding colony cohorts. A 1-wk advantage in founding generally increased the long-term survival of young colonies by 40–80%. We also examined the factors affecting average coverage of an area by colony territories. Maximum coverage was achieved under a continuous influx of 50 queens/(ha·wk) or a single settlement of 1000 queens/ha; both values were much less than actual magnitudes of queen influx observed in the field.

KEY WORDS territory growth, brood raiding, colony founding

WE CAN DISTINGUISH two main types of spatial interactions among colonies of the red imported fire ant, *Solenopsis invicta* Buren. For young colonies, spatial interaction occurs by means of brood raiding (Tschinkel 1992a, b). After ≈2 mo, however, monogyne fire ant colonies apparently become strictly territorial (Tschinkel 1992a, b), and spatial interactions generally occur along nonoverlapping territorial borders (Wilson et al. 1971). A number of studies indicate that within 1–2 yr (Markin et al. 1973, Lofgren & Williams 1985, Callcott & Collins 1992, Collins et al. 1992) fire ant colonies occupy almost all of the available territory (Wilson et al. 1971). Other observations show that whole territories have irregular shapes, but their maximum to minimum dimension ratio does not deviate strongly from one (Wilson et al. 1971, Markin et al. 1975, Showler et al. 1990).

The main problem with modeling fire ant territories is describing the joint growth of touching but nonoverlapping figures of different sizes that can completely cover the study area. The idealization needs to be computer-tractable in the sense of realistic run time and memory. All other biological features (alate dispersal, colony growth, colony mortality) can be modeled in some manner depending on the needed degree of detail.

We are not aware of any spatial model that satisfies our central requirements. In forestry, the approach to partitioning space between irregularly located trees is well known. This procedure calculates the polygon-form area around every tree depending on its size and competitive power (e.g., Adlard 1974, Czaran & Bartha 1992). The resulting polygons do cover the area completely, but the approach is not easily adopted to the description of an intermediate situation when the plane is not totally covered. The single work devoted to spatial modeling of ant territories (Ryti & Case 1992) examined interactions of colonies by means of interaction of points (nest locations) rather than actual colony territories.

We have constructed a spatial model of fire ant territories that operates by competitive interactions of rectangular territories. This model generally assumes a constant environment and a homogeneous habitat, although some aspects of spatial and temporal heterogeneity are simulated.

The primary objective was to produce a model that can be used to study the interrelationship of major fire ant population parameters. This model is not the final word on fire ant population biology; rather, it is intended as a first effort that provides a number of interesting insights and hopefully sets a base for future efforts.

Model Description

Search for Territory Geometry. We initially tried circles and squares in a search for an appropriate shape to represent colony territories. These shapes were rejected after preliminary computer experiments with single-aged populations resulting from one mating flight. At time zero ($t = 0$), we distributed Q points representing postclaustral colonies randomly over a plot of area A, and let the figure (circle or square) grow from every point according to the usual logistic equation

$$S_i(t + 1) = S_i(t) + r[1 - S_i(t)/S_{\max}] \quad (1)$$

where S_i is individual colony area, $S_{\max}$ is the maximum territory area for a colony, and r is the initial growth rate per unit time which is taken to be one week for all further calculations. The second type of trial population was multi-aged; that is, we distributed Q new colonies (points) at every time step. In both cases, the colony in one of two contacting territories (number 1 or 2) died with the probability M depending on the territory area ratio,

$$M_2 = (S_1/S_2)/[1 + (S_1/S_2)], \quad M_1 = 1 - M_2 \quad (2)$$

(We omit here some technical details of the interaction algorithm connected with possibility of simultaneous intersection of more than two figures owing to a discrete time step of the model.) This type of spatial system, usually consisting of circles, is well known in the literature (e.g. Slatkin & Anderson 1984), therefore, we will not describe the resulting spatial patterns and dynamics in detail but present only a few system features.

Experimental trials were conducted with the following parameters: plot area (A) of 100 by 100 m (1 ha), maximum territory area ($S_{\max}$) of 100 m^2, initial colony growth rates (r) of 0.23 (or 23% weekly growth rate for young colonies), and an initial colony area (S_0) of 0.2 m^2. First, we tried a single-aged system with initial nest densities that were potentially large enough to reach unit territory coverage of plot area. Changing initial colony number, Q_0, from 100 to 4,000, changed territory coverage from 24 to 32% for circles and from 27 to 32% for squares.

Next, a multi-aged case was tried in which new colonies were added at each time step. The number of time steps was large enough for reliable time average estimations. The results for squares and circles were very close so we present only the circle case. Under weekly queen influxes changing from 3 to 400, the territory coverage changed from 39 to 42%, with equilibrium colony number changing from 120 to 1,400.

The most important feature of the observed patterns in both cases is that the maximum share of area covered by the figures did not exceed 50%, a value far below the 90–100% coverage generally observed for fire ant territories. It is unlikely that triangles or hexagons would give much better results. The main conclusion from these experiments is that fire ant territories cannot be simulated with rigid geometrical figures as described above.

Final Spatial Algorithm. It was desirable to develop an algorithm that represented a free growing colony territory as some simple figure (e.g., square or circle) and which also prescribed some simple rules for figure shape change when territories contact. Suppose we begin from small circles growing from points randomly distributed over a plane. When two circles contact, we can cut them along the chord to receive nonoverlapping figures, but the picture becomes rather sophisticated when three or more circles intersect. Also, from the computational point of view, this algorithm demands the use of sine and cosine functions, which would be very time-consuming for large populations.

We offer an alternative idealization, which describes a colony's territory as a square when it grows free and as a rectangle with sides independently changing according to certain rules when it contacts with neighbors. This approach is a four-sided approximation to an arbitrary shaped territory with flexible borders.

The algorithm consists of two main parts—one relates to mature colonies interacting only along territorial boundaries; the other relates to juvenile colonies that can expand by brood raiding activity. Please note that all references to queen influx refer to postclaustral queens with incipient colonies and not to newly mated queens. This was done because we were interested primarily in colonies that are capable of interacting with their neighbors. A second consideration was that this modification substantially reduced the volume of model calculations. Influx rates of newly mated queens are generally about 10 times greater than the number that actually survive through to the postclaustral stage of colony founding (Morrill 1974, Tschinkel 1992a). We will begin with the mature colonies.

Territorial Interactions of Mature Colonies. For every time period, colony territory growth was calculated in two substeps: *attempted growth* and *territorial interactions*. The primary condition for every time step is some spatial pattern of nonoverlapping colony territories.

Attempted Growth. The maximum possible area increment for each territory was taken, according to the logistic growth equation 1, but the direction of growth was determined by a territory's *touch status*. The rule was that colonies with larger territories could grow in the direction of its smaller neighbor as if there was free space but

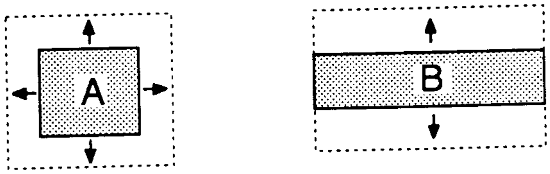

Fig. 1. Colony territory growth scenarios. (A) Free-growing square. (B) Free-growing rectangle.

the latter could not. Also, we proposed that a square is the form of a rectangle which is optimal from an energetic point of view.

If a territory had no neighbors, it stayed a square (Fig. 1A); formulae for size change are obvious. If a territory was a free rectangle, it increased its shorter dimension in two directions symmetrically (Fig. 1B). All principal combinations of growth for a colony having one, two, or three larger neighbors are shown in Fig. 2. (The algorithm deals with an arbitrary number of larger neighbors.) As can be seen, a colony tries to optimize its shape if the neighborhood allows it and grows in a free direction if shape optimization is not possible.

Territorial Interactions. The second growth step consisted of colony interactions after intersection of territory increments. Trimming of overlapping territories was determined by the following rules. In the *corner-type* intersection (Fig. 3A), the larger colony cut down the smaller colony, leaving the larger of two possible rectangles. In the *side-type* intersection (Fig. 3B and C), the smaller target colony was trimmed along the side of its larger neighbor. Completely overlapped territories were eliminated as well as territories that declined below a specified minimum area after being squeezed by its neighbors.

We have described the core algorithm for pair interactions. When smaller target colonies were intersected by more than one larger neighbor, or when intersecting colonies displayed a chain pattern, the result depended on the sequence of colony interaction searches. Colonies squeezed by larger neighbors from two opposite sides (e.g., colony SN4; Fig. 2) could reach a very long dimension in one direction. To avoid this unrealistic behavior, we restricted colony length by some constant. The borders of the study plot were taken as unpenetrable for individual colony territories; that is, each border was considered a larger neighbor (LN).

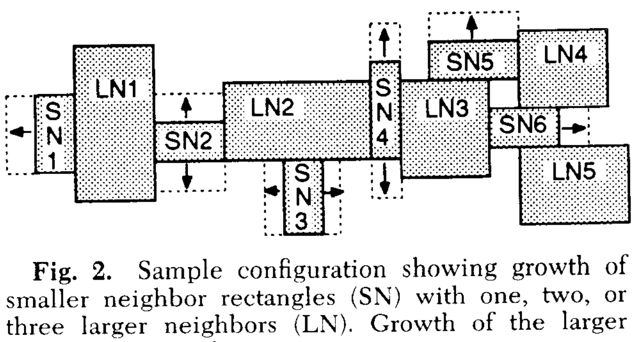

Fig. 2. Sample configuration showing growth of smaller neighbor rectangles (SN) with one, two, or three larger neighbors (LN). Growth of the larger neighbors is not shown.

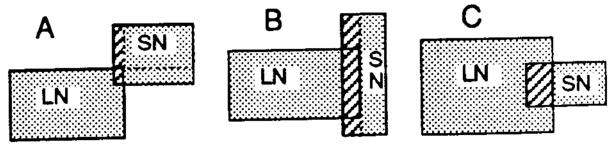

Fig. 3. Trimming algorithm for overlapping territories. (A) The larger of two possible rectangles is left in corner-type overlap. (B, C) Two types of side-type overlap. In all cases, the diagonal lined portion of the smaller neighbor is cut out.

Colonies having one or both of their longer sides touch-free (including free rectangles) were subjected to a reshaping process toward the energetically optimal square form of their territories. Under this transformation, taken at every time step, colony area was constant. Namely, for the variable

$$Z = \text{vertical length/horizontal length}$$

we took the linear law of change,

$$Z(t + 1) = Z(t) + c_1[1 - Z(t)]$$

where the reshaping constant ($0 \leq c_1 \leq 1$) determined the rate of Z going to 1. For the purpose of this study $c_1 = 0.5$.

Complete Coverage Test. Numerical trials were used to determine whether the model algorithm satisfied our demand of complete or almost complete coverage of the study area by colony territories. Results showed that the algorithm was very effective from this point of view. A multi-aged system with continuous queen founding influx was not a proper test because it would inevitably reach complete coverage. So, we tracked a single-aged situation with densities of initial nests, Q_0, large enough to reach unit coverage under a given S_{max}; that is, for $Q_0 \times S_{max} \gg A$ (A = 100 × 100 m, $Q_0 >$ 500/ha, S_{max} = 100 m^2). A colony squeezed to territory S_{min} = 0.1 m^2 was considered dead. Repeated trials showed that territorial coverage of the study area averaged almost 97% (95–99%), with the mean number of surviving colonies equal to 160 (145–175) at 50 wk.

Idealizations and Assumptions of Algorithm. Rectangular territories are the most obvious idealization of this algorithm; real territories are of course irregularly shaped. This model also assumes that territory area is proportional to colony size. Clearly, this will not always be the case, but the relationship should hold when averaged over time within homogeneous habitats. It should also be noted that until territories become close-packed, their boundaries are probably best viewed as approximations representing effective territory size because it is unknown how much, if any, competition with neighboring colonies compresses territory size. Another limitation is that

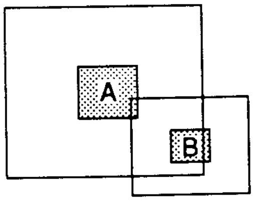

Fig. 4. Overlapped brood raiding zones (empty rectangles). Shaded areas indicate foraging territories. Colony A will incorporate colony B in the course of brood raiding.

the model does not allow a smaller colony to defeat a larger colony in territorial competition. Generally, a larger colony should be the winner, but occasionally a smaller colony might be able to successfully defend a territory against a larger but distant colony. Obviously, there is ample room to expand on the sophistication of this algorithm; nevertheless the current algorithm should provide a reasonable approximation at least until the interactional dynamics of fire ant territories are better understood.

Brood Raiding. In addition to the main part of spatial interaction algorithm, juvenile colonies could also engage in brood raiding activity. Actual brood raiding probably occurs in a dendritic or net-like fashion. For the internal consistency of this model, however, brood raiding was simulated with overlapping rectangular zones of interaction which represented the *effective* area for brood raiding. Every colony could engage in brood raiding activity or could be subjected to brood raiding if it was less than a set maximum age or size. Larger colonies brood raided and incorporated, with some probability, all the contents of smaller colonies if their brood raiding zone covered the center of the smaller colony (Fig. 4). This condition reflected observations that the winners of raids are usually the colonies with more workers (Stamps & Vinson 1991, Tschinkel 1992a).

The variable, brood raiding zone, was taken as a square with the area proportional to colony area:

$$\text{brood raiding zone} = B\ (\text{colony area}) \tag{3}$$

where $B > 1$ is a constant which we termed the "brood raiding ratio."

Colony Growth. As before, colony growth was described by one variable—individual colony territory area (S) changing, if a colony can grow free, in accordance with the logistic growth equation 1. We intentionally avoided subdividing stages of brood development in our model (e.g., Brian et al. 1981), because our primary aim was to simulate colony spatial interactions proper.

Data by Markin & Dillier (1971) for young colonies give a growth rate constant of $r = 0.23$/wk, and Markin et al. (1973) data give $r = 0.30$/wk for colonies with maximum and minimum worker population number. Laboratory populations under optimal conditions can realize values of about 0.35/wk (Porter 1988). For a long-term growth trajectories (up to 5.5 yr), Tschinkel (1988) gives a much lower value of $r = 0.024$/wk, but it should be noted that this value is averaged across season.

Queen and Colony Mortality. Realistic descriptions of fire ant population dynamics must include colony death. This can be described in two steps—the queen's death and the subsequent death of colony workers.

Queen Mortality. Queens can die because of two density-independent causes of mortality: random mortality and old-age mortality. For our simplified model of colony life, we restricted ourselves to one argument governing random or unexplained queen mortality (M)

$$M = M_S$$

where S = colony area. Random mortality (M) was applied to each queen in the model as a stochastic variable by using a random number generator. The form and parameters of this function were roughly estimated from field data. In Tschinkel's work (1992a) for incipient colonies (colony age ≤7 wk), the number of surviving colonies in a semilog plot closely follows a straight line giving a total mortality rate of $M_{tot} \approx$ 0.36/wk. Field observations allowed Tschinkel to distinguish between random and brood raiding factors of colony death. We used this information to estimate both components of death averaged for the first 7 wk of colony life. Brood raiding mortality (M_{BR}) was ≈0.25/wk and random mortality (M_1) was ≈0.17/wk. For colonies with ages between 7 and 18 wk, the same work gives a random mortality rate (M_2) of ≈0.04/wk. This can be attributed to a medium colony age of 13 wk. Random mortality of mature colonies (M_3) is very low but actual values are not yet available. We estimated M_3 as 0.001/wk, but field data is greatly needed.

According to Wilson et al. (1971), the density of worker ants for young colonies is ≈1,500 ants/m^2. The initial population of incipient colonies is about 30 worker ants (Porter & Tschinkel 1986). This gives an initial colony territory area of $S_0 \approx$ 0.02 m^2, a size that corresponds to M_1 (Fig. 5). Under a colony growth rate equal to 0.23, with the initial area estimated above, an exponentially growing colony at 13 weeks reaches an area of $S_{13} \approx 0.2$ m^2 corresponding to M_2. A mature colony has a maximum territory area $S_{max} \approx 100$ m^2 (Markin et al. 1975, Wilson et al. 1971), a size that corresponds to M_3.

These estimations give us three values of mortality within the whole span of colony territory area (S). Fig. 5 shows that the dependence is rather close to linear in log-log scale, with parameters

$$M_S = 0.011\ S^{-0.53} \tag{4}$$

It is interesting to note that death rate was very close to an inverse dependence on the average

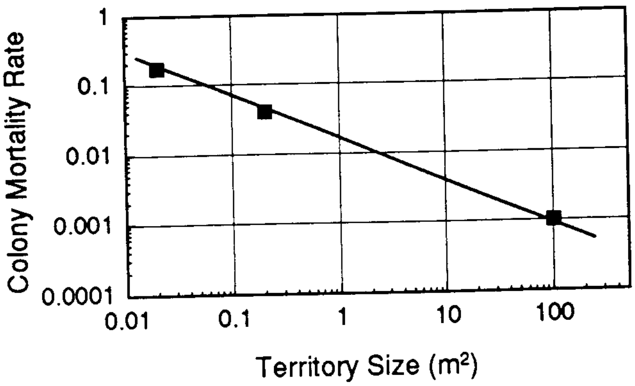

Fig. 5. Approximate dependence of weekly colony mortality on estimated territory area (points correspond to M_1, M_2, and M_3; see text).

perimeter of colony territory (exact dependence on the perimeter would demand $M_S \approx 1/S^{0.5}$).

For every queen, maximum longevity was considered as normally distributed with some standard deviation and the mean value equal to 300 wk (Tschinkel 1987).

Colony Mortality. After the queen died, the death of colony workers was described by a simple power function

$$P_t = P_0\exp(-c_2\,t) \qquad (5)$$

where P_0 is colony population size at the moment of queen death, t is the time since queen death, and c_2 is a constant rate of worker death which is close to the inverse of worker ant longevity in summer (Calabi & Porter 1989), $c_2 \approx 1/13$ wk.

In our spatially-oriented model, it was proposed that worker population, P, is proportional to the colony area (f is some parameter),

$$P = fS$$

so the area of a queen-deprived colony also changed following equation 5 (besides possible changes induced by spatial interactions with neighbors). The colony was considered dead after its territory decreased below a minimum value.

Requeening. A new queen landing in a queen-right colony territory was considered dead, but if a colony did not have a queen, it could adopt a new one (Tschinkel & Howard 1978) according to a specified probability.

Natural Variability. Population parameters are rarely fixed in time or space. To better imitate natural conditions, the model was designed so that standard deviations could be selected for the following parameters (see *Appendix*): queen influx, initial territory area, maximum queen longevity, and colony growth rate. For the latter, the model allows selection of both temporal growth variability and a fixed genetic (or spatial) variability. Large temporal variability could result in negative growth rates for some colonies, but large genetic variability resulted in the immediate death of all founding colonies with negative growth rates.

In summary, the model includes more than twenty parameters (see *Appendix*), a number that appears more intimidating than it really is. The core of this model is an algorithm for fire ant territorial interactions that is linked to colony growth. Queen influx rates and queen mortality rates are also essential components of the model. The remaining 15 subsidiary parameters can be turned off to simplify the model or modulated to assess their relative impacts on different aspects of fire ant population biology. The model was programmed in PASCAL 6.0. It requires at least 640K of RAM and a math coprocessor. One kilobyte of memory contained about five colonies, so the conventional operative memory could support ≈2,500 colonies. Computation time was proportional to the square of total colony number. For 1,000 colonies, one time step with an 80486DX2/50 Mz microprocessor and a math coprocessor took 30 s. Copies of the model and several additional variants can be obtained by writing the authors.

Quantitative Evaluations of Model

General Dynamics. Below we modeled a series of fire ant populations that originated after 8 wk of constant queen influx, a period that corresponds to intensive May-June queen production: $Q(t) = Q_0$ when $t = 0, \ldots, 7$, and $Q(t) = 0$ when $t > 7$, where Q_0 is constant intensity of influx. Major model parameters for these runs are listed in the Appendix except that variability parameters were set to zero in the initial evaluations. Because estimates of colony growth rates and the parameters of queen mortality were based on summer data, our model operated by *summer weeks*; consequently, one calendar year corresponded to 30–40 model steps (depending on latitude) rather than the expected 52 (Porter 1988).

The process of territory expansion and plot occupation show several stages, which correspond to specific spatial patterns and territorial dynamics (Fig. 6). During initial settlement (stage A), the number of new colonies rose sharply as more and more colonies were founded, even though many colonies died as a result of brood raiding and random mortality factors. After the cessation of queen influx (stage B, t = 8 wk), total colony numbers began to decrease rapidly because of high mortality associated with young colonies. Nevertheless, territories of surviving colonies continued to increase exponentially. This stage is also characterized by minimal territorial interactions because of small territory size. Following equation 4, mortality rate decreased by 12% every week: $M[S(t)] \approx \exp(-0.53 \times 0.23\,t) = \exp(-0.12\,t)$.

During the period of early territorial interactions (stage C), mortality reached a minimum value. When the coverage ≈70%, larger colonies

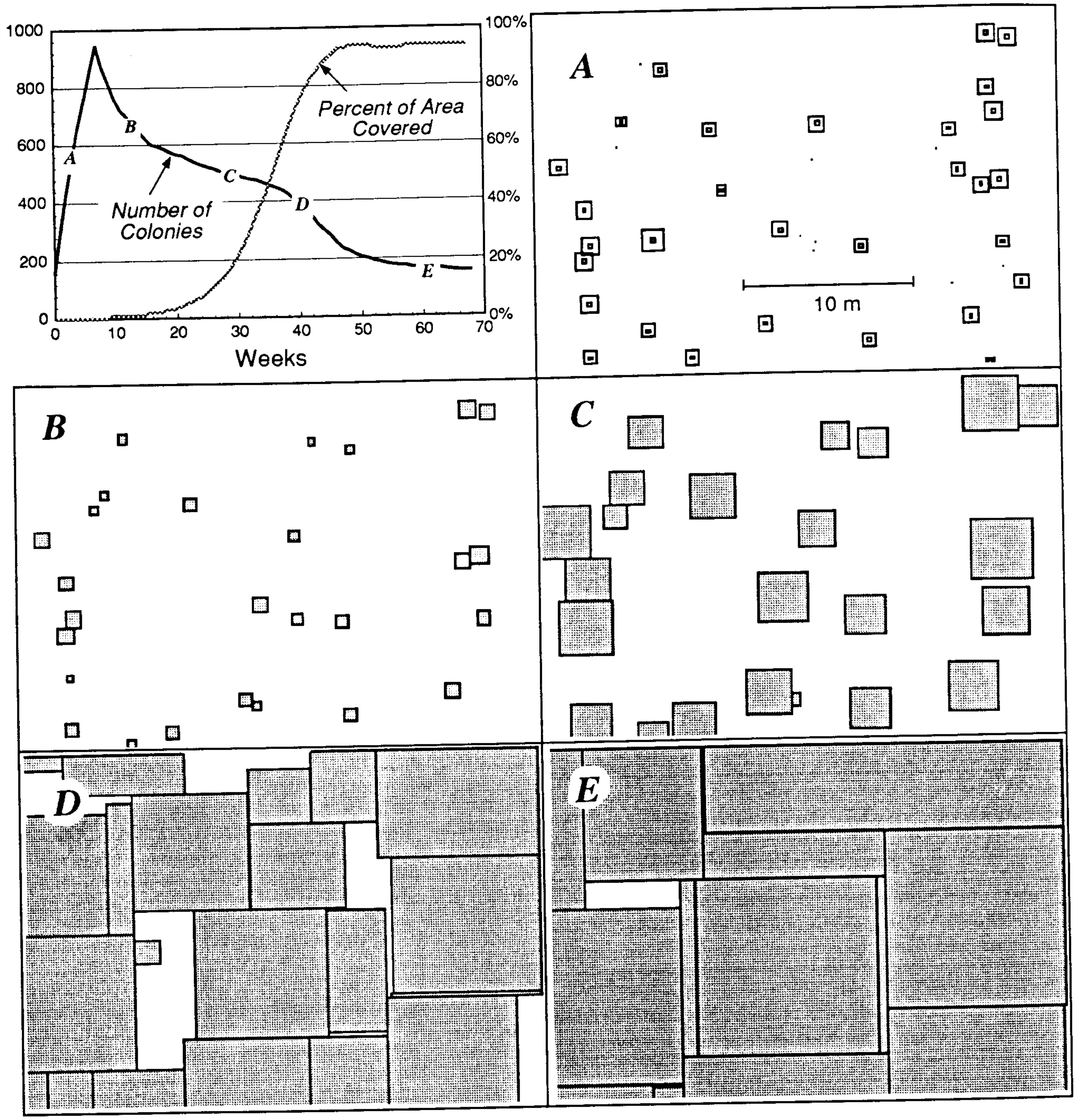

Fig. 6. Total colony number and territory coverage during fire ant invasion of an unoccupied habitat. Letters A–E correspond to the following stages, respectively: initial settlement and brood raiding, free growth, early territorial interactions, competitive exclusion, and mature. The outer squares in stage A represent zones of brood raiding.

began competitive exclusion of smaller ones (stage D). This stage was characterized by strong spatial interactions and intensive competitive mortality. It was interesting to observe that the survival advantages associated with earlier founding and increased growth rates did not become apparent until after the intense competition associated with stage D. At the end of this short stage, the territorial coverage reached its maximum value (≈96%). Territories of individual colonies were about 60–70% of their maximum potential (S_{max} = 100 m^2). In the mature stage (stage E), mortality rate was again low, and spatial interaction was again rather weak. Mean territory size of surviving colonies gradually increased as mature colonies died and the surrounding colonies expanded to fill the voids. Trials with continuous queen influx were almost exactly the same as those described above because long-term survivorship of queens that attempted to found colonies more than 8 wk after the initial cohort was essentially zero.

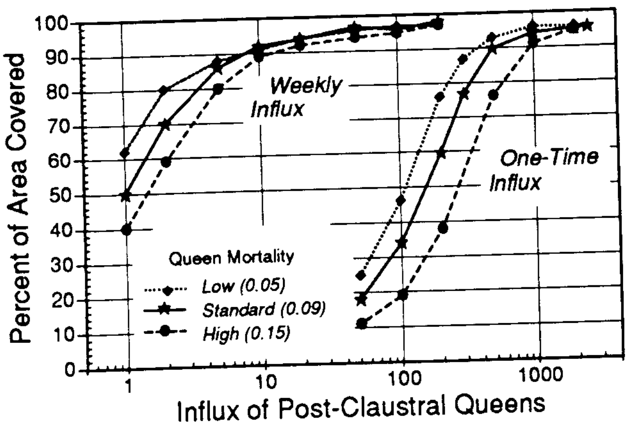

Fig. 7. Final percentage of area covered by colony territories under weekly and one-time influxes of postclaustral founding queens (number per hectare), for three values of young colony mortality. Each point is the mean of 10 model runs.

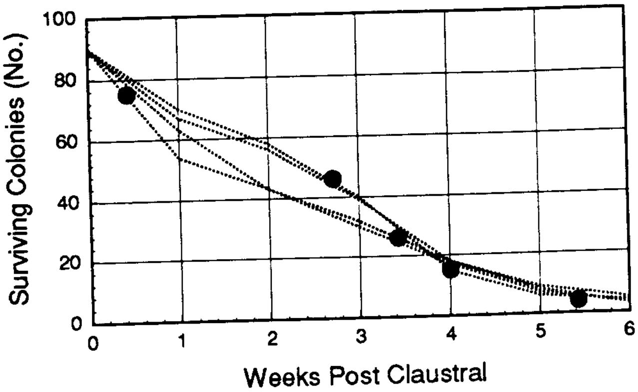

Fig. 8. Simulation of postclaustral colony number dynamics with brood raiding ratios (B) of 12–18, and temporal colony growth rate deviations of 10–20% of the mean (dashed lines). Large dots are the empirical values reported by Tschinkel (1992b).

Queen Influx Rate. Fire ant populations vary considerably from area to area. The following tests were run to evaluate how sensitive territorial coverage, C, is to the influx rate of postclaustral founding queens (Fig. 7). We examined this territory saturation problem under standard parameter values. Two influx scenarios were selected. The first consisted of a one-cohort package where $Q_t = Q_0$ when $t = 0$, and $Q_t = 0$ when $t > 0$, with the intensities taken within interval $50/\text{ha} \le Q_0 \le 2{,}500/\text{ha}$ and registration time $t = 80$ wk. The second was continuous influx $Q_t = Q_0$ for all t, with the intensities $1/(\text{ha}\cdot\text{wk}) \le Q_0 \le 200/(\text{ha}\cdot\text{wk})$ and registration time $t = 300$ wk.

For a one-cohort queen influx total, territory coverage reached maximum values ($C \approx 95\%$) when influx rates Q_0 were greater then 900 incipient nests per hectare. For trials with continuous influx, total coverage was reached when influx rates were greater than 50 incipient nests per hectare. These results indicate that *S. invicta* can reach its maximum population densities with queen influx rates far below those reported for the United States (Morrill 1974).

Brood Raiding Test. We undertook a quantitative comparison of our model to Tschinkel's (1992b) field data concerning the brood raiding dynamics of postclaustral founding colonies. With some simplifications, the system examined was a rectangular plot (38 by 22 m) populated by ≈80 incipient colonies (of approximately one age), subjected to brood raiding and random mortality (Fig. 8). After estimation of the mortality function (equation 4), the central parameter, which remained unknown, was the brood raiding ratio B in equation 3. Founded nests were scattered over the plot randomly.

Numerical experiments with the model showed that the survivorship of colonies during brood raiding depended very strongly on B. This should be expected, taking into account the autocatalytic nature of the brood raiding process (Tschinkel 1992b). Maximum brood raiding age was equal to 6 wk (Tschinkel 1992b). Maximum colony area for brood raiding was set equal to 3 m^2; although, colonies rarely reached this size in 6 wk. The best imitation of colony number dynamics took place under brood raiding ratios of 14–18 (Fig. 8). The relative accuracy of description by all four points (the first point with colony number = 80 was fixed) was within 14–30% of Tschinkel's data; values that look satisfactory taking into account the simplicity of the model and the uniqueness of the field data. We should also note that brood raiding ratios for pastures are probably much lower because Tschinkel's tests were conducted on newly cleared land that was almost completely bare.

Relative Survival Advantages of Early Cohorts. One of the central assumptions of this model is that larger colonies will out-compete smaller ones for foraging territory. Because colony size is a function of age, older cohorts of founding colonies should have a considerable and cumulative advantage over younger ones.

To compare the relative survival advantage of early cohorts, we undertook a number of computer experiments with our model by changing its major population parameters. Standard parameter values are marked below with an asterisk. In any given run, we changed only one of the parameters in the standard set, to see its effect on survival success. Initial output data concerned the percent survival, $V(w)$, for each cohort, $w = 0, 1, \ldots 7$. We generally analyzed these values at time $t = 52$ wk. As before, we used 8 wk of constant queen influx. The seven parameters under change were

(1) queen influx (Q) = (100; 300*; 1,000; 2,000 1/wk),
(2) brood raiding ratio (B) = (1, 4*, 12),

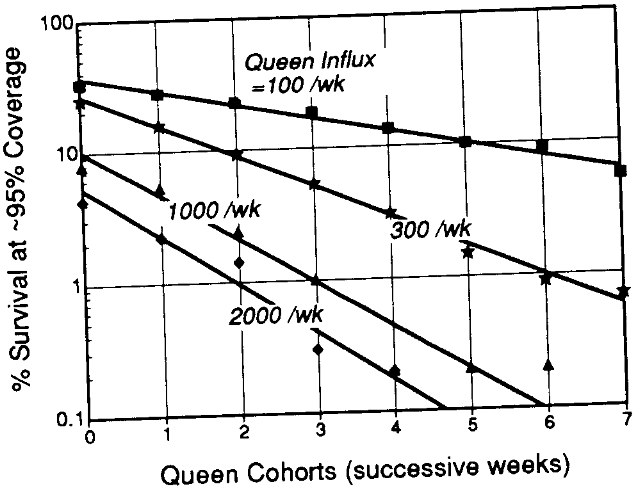

Fig. 9. Percentage of colonies surviving to 52 wk as a function of cohort order. Each line represents survival under different weekly rates of queen influx per hectare. Points for each line are the means of 10 trials.

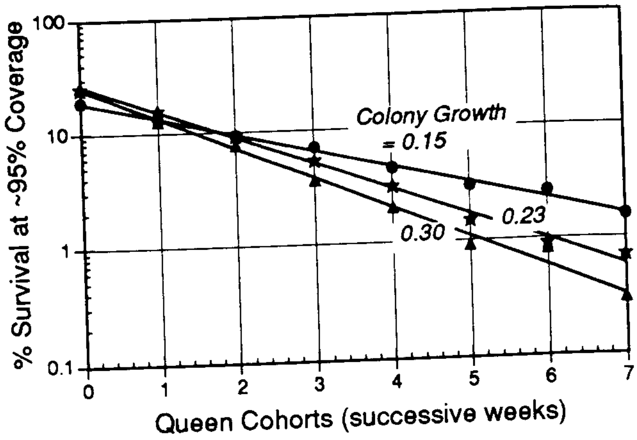

Fig. 10. Percentage of cohorts surviving to 52 wk as a function of cohort order, under different colony growth rates. Points for each line are the means of 10 trials.

(3) colony growth rate (r) = (0.15, 0.23*, 0.30 1/wk),
(4) random mortality of young colonies (M_y) = (0.15, 0.09* 1/wk),
(5) maximum territory size (S_{max}) = (33, 100*, 300 m^2),
(6) genetic growth rate variability (D_{ri} = 5%*, 10%, 50%, 100% of the mean population growth rate), and
(7) temporal growth rate variability (D_{rt} = 5%*, 10%, 50%, 100% of the mean individual colony growth rate).

For all experiments, the percentage of surviving colonies, V, in each weekly cohort decreased exponentially as a function of time (linearly in semi-log coordinates), in other words

$$V(0):V(1):\ldots:V(7) = v \approx \text{constant slope}$$

Therefore, any earlier cohort had a constant relative survival advantage, R, compared with the next cohort:

$$R = [V(w) - V(w+1)]/V(w+1) = 1/v - 1 \approx \text{constant.}$$

This result seems not to be trivial, taking into consideration the essentially nonlinear nature of the model.

Fig. 9 shows the dependence of cohort survival on cohort order for different values of queen influx. (All curves in Figs. 9–11 present the average of 10 independent runs each with different initial random numbers.) As one can see, the slopes of the lines became more pronounced as the rate of queen influx increased. The relative weekly survival advantage between neighboring cohorts increased from 28% for Q = 100 to 117% for Q = 2,000. As explained above, these values were determined from the slope by calculating the percentage of drop in survival from one weekly cohort to the next). Note that the percentage of drop appears less than it really is because of the semilog plot. Total survivability for colonies also decreased when queen influx increased; this was because the number of surviving colonies remained constant.

Increases in maximum territory size produced effects that were similar to those just reported for queen influx rates. The survival advantage for starting a colony a week earlier increased from 32% for S_{max} = 33 to 133% for S_{max} = 300. Apparently, this was because larger territory size allowed earlier cohorts occupy larger portions of available territory.

Increasing colony growth rate increased the relative survival advantage from 41% for r = 0.15 to 85% for r = 0.30 (Fig. 10). Note that only the slope of the lines in Fig. 10 changed in contrast to Fig. 9 where the y-intercepts of the lines also changed substantially. Decreasing young colony mortality (M_I) had effects that were very similar to those observed for growth rates. The relative survival advantage increased from 43% for M_I = 0.15 to 72% for M_I = 0.09.

Surprisingly, varying the brood raiding ratio and maximum brood raiding age did not affect either the relative survival advantage or the absolute cohort survivability.

Variability associated with growth rates reduced the survival advantage of earlier cohorts; however, survival advantages calculated with initial and temporal colony growth variability showed different patterns (Fig. 11). An increase in temporal variability lead to a gradual decrease of R because small differences averaged out over time. On the other hand, small increases in genetic variability caused a sharp fall of R because small fixed differences in growth rates were compounded and accumulated from week to week. The combination of both genetic and temporal

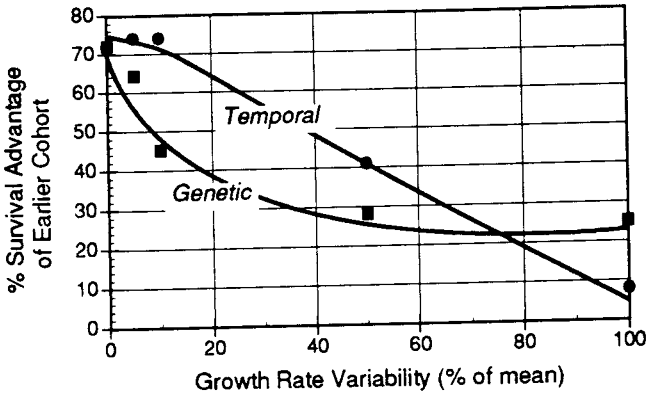

Fig. 11. Effects of temporal and genetic growth-rate variability on the percent survival advantage of being in an earlier cohort. Percent survival advantages were calculated from the slopes of plots like those used in Figs. 9–10. Growth variability is plotted as a percentage of the mean (r_o = 0.23) and ranged from ±0.0115 for 5% variability to ±0.23 for 100% variability. Points for each line are the means of 10 trials.

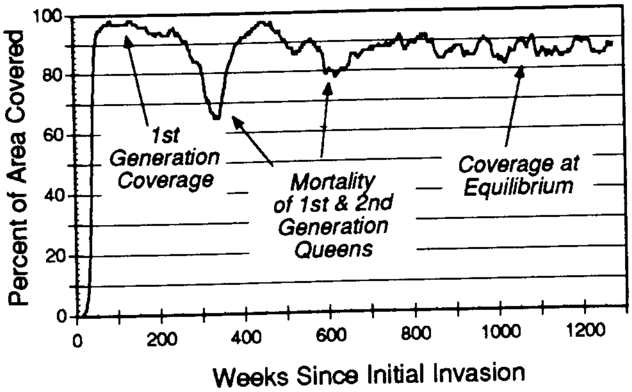

Fig. 12. Long-term dynamics of territory coverage as affected by the old-age mortality of colony queens at 300 ± 30 wk. This run used a continuous influx of 50 queens/(ha · wk) to maintain coverage (see Fig. 8) with no requeening of colonies.

variability produced results that were equivalent to genetic variability alone.

The general conclusion from these experiments is that individual colony parameters of growth rate (r), maximum territory area (S_{max}), and young colony viability, ($1 - M_y$), acted in the expected manner; that is, their increase improved the success of colonies in earlier cohorts. Explaining why brood raiding did not affect the relative survival of different cohorts is not so easy. Apparently, the magnitude of standard queen founding influx is too small for changes in brood raiding intensity to affect survival.

Long-Term Patterns of Territory Coverage. We examined long-term colony dynamics on a 1-ha territory during time periods of up to 1,200 wk. Queen founding influx in those tests was continuous and constant (Q = 50/(ha·wk)). Maximum queen longevity was set at L = 300 ± 30 wk. Parameters under change were (1) requeening probability of a founding queen landing in the territory of a dying colony (c_1) = (0*, 0.25, 0.50, 1.0) and 2) mature colony mortality (M_3) = (0.0001, 0.0005, 0.001*, 0.002, 0.005; see Fig. 5), where $M_3 = M(S_{max})$. Standard values are starred.

Fig. 12 illustrates how territory coverage changed with time when the adoption probability was zero and the mortality of mature colonies was 0.001/wk. One can observe two distinct drops of coverage corresponding to maximum-age mortality of queens from the first and second generations. After the second drop, the age distribution of the population became so wide that the third generation drop did not emerge. Colonies of the first queen generation, which invaded unoccupied territory, achieved an average coverage of 97%, whereas the average coverage reached after $t \approx 800$ wk was only 87%. The initial maximum was higher than the long-term mean because queens did not begin dying of old age until ≈300 wk.

As expected, an increase in adoption probability lead to increased average coverage; the relationship was close to linear with long-term coverage changing from 87% for c_1 = 0 to 94% for c_1 = 1. An inverse dependence was found with mature colony mortality; long term coverage changed from 89% for M_m = 0.0001 to 80% for M_m = 0.005. Long term coverage values could reach 99% when high adoption rates were combined with high queen influx rates; however, under natural conditions, adoption probabilities are apparently fairly low because 25% or less of field colonies are eventually requeened (Tschinkel & Howard 1978).

Summary. This model simulates growth and competitive interactions of fire ant territories. As desired, the model's rectangular approximations of growing fire ant territories filled almost all available space on our computer test plots. The time-course of territory occupation was similar to that reported in the literature (Markin et al. 1973, Lofgren & Williams 1985, Callcott & Collins 1992, Collins et al. 1992). Computer simulations of brood raiding produced results that were equivalent to those observed in the field (Tschinkel 1992b) with brood raiding ratios of 14–18. We were able to base most of the variables used in the model on field data (see *Appendix*); however, further information is especially needed for the survivorship of mature colonies. Several parameters were based on only one study or interpolated from laboratory data; additional studies would, of course, improve the reliability of these values and allow us to better assess natural variability.

Results of this model raise a number of interesting predictions. For example, the model predicts that competitive exclusion of smaller colonies will occur primarily over a 10-wk period beginning when 70% of the available area is covered by fire ant territories. Long-term runs of the model predict that newly infested areas should experience substantial population drops at time intervals corresponding to the old-age death of the first and second generation queens (≈6 and 12 yr). Another, prediction is that fire ant populations (as reflected by territorial coverage) should be ≈10% higher in recently infested areas (1–5 yr) than in areas that have been infested for many years (>15 yr). This should occur because queens do not die of old age in recently infested areas. The model also predicts that a 1-wk advantage in colony founding will improve a colony's chances of survival to maturity by 40–80% or more depending on conditions.

This model includes many aspects of fire ant biology, but it has several important limitations that should be considered in future models. Specifically, this model does not link colony growth and worker death to seasonal changes in temperature. The inclusion of thermal information (Porter 1988) would allow the model to operate on a realistic time scale that could be adjusted to match different climatic conditions. An algorithm that allows irregularly shaped territories would improve the visual realism of the model and perhaps the accuracy of its predictions. Another modification might be to index the probability of a larger colony defeating a smaller one to the size of the smaller colony and its distance from the larger colony. Similarly, territorial expansion or compression probably causes temporary fluctuations in worker densities within the territories; consequently, another adjustment might be to link the outcome of territorial interactions to worker densities in those territories. These modifications would permit larger colonies to occasionally loose territorial conflicts with smaller colonies. Cyclic population changes associated with sexual production (Tschinkel 1988) are another phenomenon that deserves further attention because it may have substantial effects on territorial dynamics. For example, territories might expand and contract in direct proportion to seasonal changes in colony size. Alternatively, fewer workers may simply defend the same territory or colonies might allocate a higher proportion of colony workers to maintain territories during the summer when populations are normally lowest. A spacial model of polygyne fire ant populations could also be very interesting, but this model would differ considerably for the one we have developed because it would lack territorial interactions and most new colonies would be formed by colony budding rather than claustral founding of newly mated queens (Porter 1991).

Note that trial versions of the model are now available that adjust colony growth rates according to seasonal differences in temperature, run competitive territorial simulations of several genetic strains or species of fire ants at once, and model spatial heterogeneity of fire ant reinvasions after control treatments.

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Appendix

Primary model parameters and standard values

Model parameters (units); source	Standard values
Brood raiding	
Probability	1
Ratio(B);[a]	4
Maximum age (wk); Tschinkel 1992b	6
Maximum territory area (m^2);[b]	3
Colony dimensions	
Maximum territory area, S_{max}, (m^2); Markin et al. 1975[c]	100
Maximum colony length (m); estimated	20
Territory area at which squeezing causes colony death (m^2);[d]	0.1
Initial territory area, S_0, (m^2);[e]	0.02
Initial territory area standard deviation, D_s (m^2);[f]	0.002
Colony growth	
Initial rate, r, (1/wk); Markin & Dillier 1971[g]	0.23
Fixed genetic standard deviation of rate, D_{ri}, (1/wk); turned off	0
Temporal standard deviation of rate, D_{rt}, (1/wk); turned off	0
Queen mortality	
Maximum rate, M_y (1/wk); Tschinkel 1992a	0.09
Minimum rate, M_m (1/wk); estimated	0.001
Mean maximum longevity, L, (wk); Tschinkel 1987	300
Standard deviation of maximum longevity (wk); Tschinkel 1987	44
Queen influx (postclausal)	
Duration (wk); early summer peak, Morrill 1974	8
Density, Q, (1/(ha·wk));[h]	300
Standard deviation of density, D_Q, [1/(ha·wk)]; turned off	0
Other parameters	
Adoption probability, Req; turned off	0
Territory reshaping rate, c_1, (1/wk) (estimated)	0.5
Rate of orphaned colony death, c_2 (1/wk) (Calabi & Porter 1989)	0.08
Plot dimension by x (m)	100
Plot dimension by y (m)	100

[a] Set low on the assumption that brood raiding ratios through grass in pastures are much less than the 14–18 that we estimated for bare ground (Tschinckel 1992b).

[b] In the absence of information about how large founding colonies can become before brood raiding ceases, this parameter was set too high to function in the model.

[c] This is for a fairly dense population; other sources suggest maximum areas of 200 m^2 or more (e.g., Wilson et al. 1971).

[d] Equal to ≈150 workers; probably sould have been set to 0.02, but very small colonies rarely interact so this change would have very little effect on tests.

[e] Estimated from mean worker density per square meter (Wilson et al. 1971) and the number of workers in new postclaustral colonies (Porter & Tschinkel 1986).

[f] Estimated from variability in the number of initial workers (Porter & Tschinkel 1986).

[g] Markin et al. (1973) data gives 0.30/wk and Porter (1988) gives about 0.35/wk in lab tests.

[h] Set low to speed runs. Approximately, 1/2–1/4 of rates reported by (Morrill 1974) assuming 10% of queens survive to the postclaustral stage (Tschinkel 1992a).

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