Distribution of the red imported fire ant, *Solenopsis invicta*, in road and powerline habitats

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**Abstract**

For early-successional species, road and powerline cuts through forests provide refugia and source populations for invading adjacent forest gaps. Within an 800 km² forest matrix in South Carolina, we determined if width, disturbance frequency or linear features of road and powerline cuts influenced the mound distribution of the red imported fire ant, *Solenopsis invicta* Buren. For each of five linear habitat types, differing in width and disturbance frequency, we mapped all mounds located within ten 500 m segments. Mean mound density was lowest in narrow, infrequently-disturbed closed-canopy dirt road habitats (8.8 mounds/ha). For types with an opening in the forest canopy (i.e., open dirt road, gravel road, paved road and powerline cut), mean mound density was highest in narrow habitats where disturbance was intermediate (open dirt roads, 86.5 mounds/ha). It was lowest in wide habitats where disturbance was infrequent (powerline cuts, 27.6 mounds/ha). Mean mound size was greater in infrequently-disturbed powerline cuts than in frequently-disturbed paved roads. Mounds were located significantly closer to road or forest edges than expected by random. In all types except dirt roads, mounds were more common toward northern edges, and more so as the orientation of the linear habitat changed from north/south to east/west. These data suggest that narrow, disturbed habitats are more suitable for fire ant establishment and success than wider ones, and that the distribution of fire ants in linear habitats is not as uniform as it has been shown to be in pastures. A decrease in roadside disturbance and an increase in shade, especially along the northern edge, may result in lower fire ant mound density in these linear habitats.

**Introduction**

Linear habitats, such as road and powerline cuts, embedded within a forest matrix may provide suitable habitat for early-successional or disturbance-oriented plants and animals amidst an otherwise uninhabitable landscape (Bennett 1991; Forman 1995; DeMers 1993; Warner 1992). They may also serve as barriers (Merriam et al. 1989; Mader 1984), dispersal corridors (DeMers 1993; Vermeulen 1994; Geitz et al. 1978), and invasion routes (Lewis 1991; Amor and Stephens 1976) for many species. For the red imported fire ant, *Solenopsis invicta* Buren, road and powerline cuts may provide not only primary habitat but also a refugia or source population for dispersal into adjacent forest gaps.

Southeastern U.S. forests are fragmented by a shifting mosaic of early-successional forest gaps caused by logging practices and by a reticulate pattern of linear, early-successional habitat, or corridors (Forman 1995; Rich et al. 1994; Kroodsma 1982), in the form of road and powerline cuts. Unlike forest gaps, these linear habitats are maintained in an early-successional stage by anthropogenic disturbance such as mowing or burning. Additionally, they are typified by higher degrees of edge environments and shading than non-linear gaps (Reed et al. 1996, Kroodsma 1982). *Solenopsis invicta* frequently colonizes both logged gaps and road and powerline habitats. In
logged gaps, populations persist for the first five to ten years of reforestation (personal observations). The prevalence of the more permanent road and powerline habitats ensures that few logged gaps lack nearby refugia or source populations of fire ants. However, if some road and powerline cuts provide better fire ant habitat than others, then the structure of the linear habitat network may determine the rate and degree of fire ant invasion into forest gaps.

Solenopsis invicta is a notorious pest species that has strong effects on other organisms. Native ants are frequently displaced through competition (Tschinkel 1987; Porter and Savignano 1990; Camilo and Phillips 1990; Morris and Steigman 1993; Porter et al. 1988), and total arthropod diversity and abundance are often reduced when S. invicta is abundant (Tedders et al. 1990; Reagan 1986). Fire ants are also predators of the young of birds, small mammals, and reptiles (Allen et al. 1994).

The potential impacts of S. invicta are exacerbated in areas where mounds are abundant (W.R. Tschinkel, personal communication). Because mound volume is positively related to the number and biomass of ants in a mound (Tschinkel 1993), the impacts are also stronger where mounds are large. Fire ants have been shown to be abundant in open habitats where the soil has been disturbed by agricultural practices, logging, or vehicles (Tschinkel 1986; Porter and Savignano 1990) and where direct sunlight can reach the soil surface (Brown 1980). They are rare in shaded or undisturbed habitats such as forests (Tschinkel 1987; Summerlin 1976; Maxwell 1982).

The objectives of our study were to determine whether the abundance, size, or spatial distribution of S. invicta mounds varied among five linear habitat types. We hypothesized that mound density and volume are related to habitat width and to the frequency of direct mound disturbance, and we predicted that mound density and volume would increase with width but would decrease with decreasing disturbance frequency. We also hypothesized that the spatial distribution of mounds is related to linear features of the habitat such as edges and would therefore be less uniform than the mound distribution in pastures.

Wide road and powerline cuts may be preferred by fire ants for two reasons. First, wide habitats have a larger area that is not shaded by the adjacent forest canopy. Secondly, dispersing alates respond to reflectance and vegetation cues from the ground (Maxwell 1982). Therefore, wide habitats may be easier to locate than narrow ones.

Although initial large-scale disturbances such as logging, burning, mowing or till ing often precede fire ant establishment, extremely frequent and direct disturbance to the mound as a result of continued burning or mowing may limit the size and abundance of mounds. For this reason, early-successional habitat with low levels of direct disturbance to the mounds may have higher mound density and volume than those that are mowed or burned more often.

Studies of the spatial distribution of S. invicta mounds are few and have been performed mainly in pastures, where mature mounds have an approximately uniform distribution due to intraspecific competition (Adams and Tschinkel 1995; Baroni Urbani and Kannowski 1974). Edges, which predominate in linear habitats, are often areas where levels of light, temperature, litter moisture, humidity, and species diversity change abruptly (Matlack 1993; Yahner 1988; Wales 1972). Fire ants may be attracted to or repelled by the edge environment and either target it for mound construction or avoid it. For this reason, the spatial distribution of mounds within linear habitats may be related to the presence or orientation of edges and be less uniform than it is in pastures. Furthermore, like mound density and mound volume, mound distribution may vary with habitat width and disturbance frequency.

**Methods**

This study was conducted at the Savannah River Site (SRS) in the coastal plain of South Carolina. SRS is an 800 km² national environmental research park forested primarily by longleaf (Pinus palustris), slash (Pinus elliottii), and loblolly (Pinus taeda) pines. The area was probably invaded by S. invicta in the early 1970's (Bure et al. 1974; Wojcik 1983). A network of several linear habitat types fragments the forest matrix. In this study, we examined five types distinguished by width and disturbance frequency: powerline cuts, paved roads, gravel roads, open dirt roads (i.e., the forest canopy did not extend into the center of the road), and closed-canopy dirt roads. The roadsides (i.e., the vegetated strip between the road edge and the forest edge) of the paved, gravel and open dirt roads were predominantly grassy. The roadsides of the closed-canopy dirt roads were sparsely vegetated and were covered with pine needles or leaves, and the powerline cuts were vegetated primarily by tall herbaceous species.
Disturbance regimes in each habitat type were obtained from the USDA Forest Service Savannah River Forest Station and verified by observation. In powerline cuts, vegetation was burned or sprayed with herbicide once every five years. Vegetation in the paved roadsides was mowed as needed (usually three or more times per year). Gravel and open dirt roadsides were mowed approximately twice per year. Closed-canopy dirt road habitats were disturbed only by occasional vehicular traffic. Because of the disturbance regimes, the height of the vegetation in October 1996 averaged 12 cm in the paved roadsides. 30 cm in the gravel roadsides, 30 cm in the open dirt and closed-canopy dirt roadsides, and 100 cm in the powerline cuts.

The habitat types varied in their suitability for fire ant establishment. The powerline cuts used in this study did not contain service roads. Therefore, the entire cut was equally available for fire ant colonization. In paved and gravel road habitats, fire ants were not able to colonize the asphalt or gravel and were therefore restricted to the roadsides. The roads in the dirt road habitats consisted of two compacted tire tracks interrupted by a less-compact, vegetated median. Fire ants could colonize the roadsides and the median but not the tire tracks.

For each habitat type, we randomly chose ten vectors radiating from the center point of the roughly circular SRS and located the 500 m road or powerline segment closest to the end of each vector. Segments that intersected or were adjacent to forest stands younger than fifteen years or other early-successional habitats were disqualified and new segments were chosen. All chosen segments were located in upland, sandy soils dominated by Fuquay and Blanton sands (USDA 1990).

During October 1996, we surveyed each of the fifty segments (ten segments per type) for all active S. invicta mounds greater than 10 cm in diameter. We excluded smaller mounds because their size suggested recent establishment. New colonies experience high rates of attrition (Lofgren et al. 1975; W.R. Tschinkel, personal communication), and we chose to exclude mounds that might not persist through the year. Mound activity was determined by observing loose dirt on the mound and by digging into the mound and noting the presence of ants. Temperatures during sampling were moderate (20°-30°C), and ants were active and near the surface of the mounds. We measured the dimensions of each mound surveyed, and we estimated mound volume using the formula for half of a sphere (Porter et al. 1992. v=(2/3)πr³abc) where a = length of the mound’s long axis/2, b = length of the mound’s short axis/2 and c = mound height). We also measured the distance of each mound (to the nearest 0.1 m) from three points: the forest edge, the road edge, and the starting point of each 500 m segment. Powerline cuts did not contain road edges so distances were measured from the forest edge and from the starting point of the 500 m segment only.

Forest edges were defined as borders where soil disturbance from the original construction of the road or powerline cut ended. In almost all cases, this border was clearly denoted by a small ridge of soil. In cases where a distinct ridge was not present, the forest edge was delineated at the trunks of trees in the treeline. The treeline always almost coincided with a visible shift in vegetation and was easily identified. Some mounds were located just inside the forest, and we included these in our study if their distance into the forest from the forest edge did not exceed two meters. These mounds received insolation similar to mounds opposite the edge, and their proximity suggested a relationship between their presence and that of the adjacent open habitat. Road edges were defined as the border where the vegetation in the roadside abutted the asphalt, gravel or compacted tire track.

The width of each segment was measured at 50 m intervals. In the four road habitat types, we measured the width of the road, the width of each roadside, and the width of the dirt road median. There were no roads in powerline cuts, so we measured the total width only. In addition to width, the orientation of the long axis of each segment was measured using a compass. Some small dirt roads curved moderately, and their orientation was considered the average compass heading.

Analysis. We estimated the area of each site in two ways. The ‘total area’ was defined as the area of the entire segment, and the ‘inhabitable area’ was defined as the area assumed to be available for S. invicta colonization (i.e., total area minus the area of the asphalt, gravel, or tire tracks). Mound density for each segment was calculated per total area and per inhabitable area before analysis.

Differences in mound density among linear habitat types were compared using a one-way ANOVA and Tukey’s HSD (Sokal and Rohlf 1995). Differences in mound volume were analyzed using a nested ANOVA where mounds were nested within segments and Tukey’s HSD.
We examined the spatial patterns of mounds perpendicular to the long axis of a habitat in two ways. For both these analyses, we excluded all mounds located in the median of the dirt roads. We first determined whether mounds were distributed randomly throughout the inhabitable area by calculating the distance of each mound to the nearest edge (i.e., road edge or forest edge). We compared the distances observed with those expected by a random distribution using a one-sample Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf 1995).

Second, we determined whether mound density or volume were greater in some regions than others. We divided each roadside into two linear strips of equal width parallel to the long axis, for a total of four strips per segment (Figure 1a). In powerline cuts, we divided each segment into four linear strips of equal width parallel to the long axis (Figure 1b). All strips were designated A, B, C and D from north to south respectively. We compared the densities among strips by fitting the data to a Poisson distribution using SAS Proc Genmod with a model for overdispersion since our variances were large (SAS Institute 1996). The number of mounds within most areas was large so we were also able to analyze our results using a one-way ANOVA and Tukey's HSD. These results did not differ greatly from those generated using the Poisson distribution. Since the ANOVA was the more conservative test, we will report only the ANOVA results. We compared mound volume among strips using a nested ANOVA and Tukey's HSD. We determined whether the orientation of the road or powerline cut (i.e., degrees from 0° N) was related to the difference in mound density between the northern and southern roadsides (or halves in powerline cuts) using a weighted regression analysis where segments were weighted according to total mound density.

To examine the spatial patterns parallel to the long axis of a segment, we used the Kolmogorov-Smirnov test to determine whether mounds were distributed randomly along the 500 m length. We divided the 500 m distance into 10 m sections and compared the densities observed in each section with those expected by a random distribution.

Results

Comparison of habitat types

Results of our analyses were similar using either total or inhabitable area; therefore, we report only those for inhabitable area. Habitat types differed significantly in width: powerline cuts were widest, followed by paved and gravel, then open dirt, and closed-canopy dirt roads (Figure 2). Mound density differed among habitat types, but not as predicted. Density was relatively low in the narrowest type (closed-canopy dirt roads) as predicted. However, for the four open canopy types, density was higher in the narrowest type (open dirt roads) than in the widest type (powerline cuts), and there was a trend for decreasing mean density as width increased (Figure 3a). Furthermore, mound density was greater in habitat types with intermediate to frequent disturbance (open dirt and paved roads) than...
types with infrequent disturbance (powerline cuts and closed-canopy dirt roads; Figure 3b). Mound density was most variable (i.e., largest standard error) in open dirt road habitats (Figure 3).

Mound volume was not clearly related to habitat width (Figure 3c), but mounds were largest in the unmowed powerline cuts and smallest in the frequently-mowed paved roadsides (Figure 3d). The trend (not significant) in mound volume may indicate an inverse relationship with disturbance frequency. Mound volume was most variable in closed-canopy dirt road habitats (Figure 3).

**Spatial distribution within habitats**

**Distributions perpendicular to the long axis of the habitat.** Within four habitat types, mounds were closer to either the forest edge or the road edge than expected by a random distribution (Figure 4). Closed-canopy dirt road habitats were not included in this analysis because the number of mounds (n=20) was too low. Most mounds (26%) were located within 2 m of the forest edge in powerline cuts and within 1 m of either edge in paved and gravel roadsides (49% and 64% respectively). Along the road edge, mounds were commonly located so close to the edge that a portion of the mound actually spilled over on to the asphalt or gravel. More mounds were located close to the forest edge than the road edge in gravel (204 vs. 114 mounds), open dirt (206 vs. 80), and closed-canopy dirt (25 vs. 3) roadsides. In paved roadsides, more mounds were located close to the road edge (318 vs. 259).

*Solenopsis invicta* preferred some linear strips of the habitat for colonization over others. In all fifty segments combined, mound density was greater in strip A than D (Figure 5). This trend was evident in all habitat types except open dirt roads, but the differences were significant in gravel roads only. In all fifty segments combined, mound volume was higher in strip A than in strips B and C (Figure 6). Within each habitat type, however, differences in mound volume among strips were not significant.

A wide and frequently traveled road may act as a barrier to colony movement. If fire ants cannot move the colony across the asphalt or gravel expanse, then each roadside may have a functional northern region (i.e., strips A and C). We combined the mound density in strips A and C and compared it with the combined density in strips B and D. The density in A+C was larger than the density in B+D in paved (74.2 mounds/ha, SE=10.2 vs. 43.9 mounds/ha, SE=7.8, p<0.05) and gravel roadsides (66.3, SE=11.6 vs. 29.3, SE=10.4, p<0.05). The density in A+C was not different from the density in B+D in powerline cuts (35.2, SE=9.3 vs. 14.8, SE=4.6, p>0.05), open dirt (57.3, SE=14.7 vs. 62.4, SE=17.8, p>0.05) or closed-canopy dirt roadsides (7.4, SE=2.4 vs. 4.4 mounds/ha, SE=2.4, p>0.05).

The difference between the mound density in the northern and southern roadsides (or halves in powerline cuts) was related to the orientation of the habitat (Figure 7). The difference between the mound density in the northern and southern roadsides (or halves) was negative or small in roads or cuts oriented more north/south. This difference increased as the orientation of the road or cut shifted from north/south to east/west ($R^2=0.19$, $p=0.003$). Most of the high-density habitats, however, had orientations within 40° of north (Figure 7).

**Distributions parallel to the long axis of the habitat.** Along the 500 m axis of the segments, mounds in the roadsides or powerline cuts were not randomly distributed. Mounds in the ten closed-canopy dirt road segments were not analyzed because of low numbers. For the remaining forty segments surveyed, mound density in each of the fifty 10 m sections was similar across the entire 500 m in only four segments: one gravel and three paved road habitats. In the other thirty-six cases, mound density differed more among 10 m sections than would be expected by a random distribution ($p<0.05$).

**Discussion**

**Effects of linear habitat type**

Fire ant mound density differed among habitat types; however, the density was not related to habitat width or disturbance frequency in the ways that we predicted. The narrowest habitat type (closed-canopy dirt roads) did indeed have the fewest mounds, as predicted, but among the four open-canopy types, density was highest in the narrowest type (open dirt roads) and lowest in the widest type (powerline cuts; Figure 3a). Our results suggest that direct sunlight is a requirement for fire ant colonization. Mound densities were non-existent in five of the ten closed-canopy dirt road segments and extremely low in the other five. Thus, our original prediction that greater width
leads to greater density is correct; however, once the habitat exceeds a critical width (i.e., one that allows for some direct sunlight at the soil surface) other factors are more important. Our evidence suggests that disturbance is one of those key factors. Frequent direct disturbance seems to increase rather than decrease fire ant mound density. Mowing or burning decreases vegetative height and exposes or disturbs soil. The increased insolation and soil disturbance may stimulate fire ant colonization or population growth more than the decrease in growth we expected from direct, physical disruption of the existing mounds. Other key factors that may determine differences in mound density among habitat types include the availability of resources and the abundance of predators of fire ant queens, but our data cannot provide information about these hypotheses.

The differences in fire ant densities suggested by our mound density data may be partly offset by a different trend in mound volume. Mounds were smaller in habitats that were disturbed more frequently, and the difference between the extreme disturbance regimes in open habitats (i.e., powerline cuts vs. paved roadsides) was significant (Figure 3d). Mounds in paved roadsides may be run over by mowing machinery several times a year. Colonies may be forced to move or rebuild each time, and thus, their smaller size may reflect a transition phase. Abandoned mounds, many marked by tire tracks, were often seen within 2–4 m of active mounds. Mean mound volume
in powerline cuts, however, may have been larger because mounds may escape physical destruction for up to five years. We observed more evidence of mound relocation in paved and gravel roadsides than in powerline cuts. The demonstrated relationship between mound volume and ant abundance (Tschinkel 1993) may not be as strong for frequently-disturbed mounds as it is for infrequently-disturbed mounds; however, our results suggest that powerline cuts have more fire ants per mound than paved roadsides. The impact of fire ants on their community depends on both mound density and volume because both contribute to ant abundance. However, differences in mound volume among habitat types are not nearly as large as differences in mound density. Therefore, it is likely that mound density plays a larger role in determining the impact of fire ant invasion.

**Spatial distribution within habitats**

Fire ant mounds were more abundant near the northern side of linear habitats (i.e., strip A), and the disparity between the density in the northern and southern roadsides (or halves) increased in roads or cuts oriented more east/west. Mounds near the northern side may receive more insolation than those near the southern side, especially during winter months. In winter, the area close to the southern edge of a linear habitat (i.e., strip D) is shaded for at least part of the day. Optimal temperatures for colony growth of *S. invicta* are between 24° and 32°C (Porter 1988, Lof-
Figure 5. Mound distribution perpendicular to the long axis of the linear habitat by density in all segments combined (n=50) and in each habitat type (n=10 for each, ± standard errors). A, B, C, and D denote linear strips located in the northernmost to southernmost sides of the habitat respectively. Bars with different letters are significantly different (p<0.05) using Tukey’s HSD.

gren et al. 1975), and the location of the mound may influence thermoregulation. Individual mounds are often oriented so that the long axis of the mound runs north/south for more effective thermoregulation (Hubbard and Cunningham 1977). It is likely that the location of the mound would serve this same purpose.

Fire ants usually move their mounds at least once per year for reasons that are not apparent (Hays et al. 1982). We sampled all segments in October and did not replicate our study in other seasons. Therefore, we do not know whether ants move their mounds northward as the southern roadside becomes more shaded or whether colonies that initially established near the northern side experience lower attrition.

The structure of the linear habitat type affects the north/south mound distribution (Figure 5). In paved and gravel roadsides, mound density was higher in strips A+C than strips B+D. For fire ants, the road constitutes a wide, uninhabitable expanse. Colonies in the southern roadside may not be able to establish mounds further northward than strip C. The mound densities in strips A and B were different in gravel roadsides, but they were the same in paved roadsides. Since paved road habitats are wider, a larger area may receive more sunlight. Colonies in the northern roadside may not need to be close to the northern edge to receive sufficient insolation. Open dirt road habitats, which had the same mound density in all strips, may not be wide enough to provide insolation along any
consistent edge. This does not help explain the high mound density in this habitat type, but it may help explain the high variability in mound density among segments. In powerline cuts, fire ants favored the strips near the forest edges (i.e., A and D). Mound density was low in strips B and C even though the adjacent forest never shades these regions.

Mounds were largest towards the northern side of the linear habitats (Figure 6). However, they were not significantly different from those near the opposite forest edge (i.e., strip D). Colonies in strip A may grow larger as a result of more effective thermoregulation, or when close to edges, or both. Additionally, mounds near the forest may escape direct physical disturbance from mowing machinery.

Our results suggest that ants prefer edges in general regardless of orientation and that the spatial distribution of mounds cannot be explained primarily in terms of thermoregulation (Figure 4). Mounds located in any strip were frequently built close to the road or forest edge. Several hypotheses may explain this distribution. For example, fire ants may be responding to the distribution of other species, or the soil structure near edges may be important. Soil near forest edges contains more tree roots and decomposing wood; soil near paved and gravel roads contains more gravel. Both edge soils may be easier to excavate. Banks et al. (1990) documented numerous potholes resulting from the tunneling of *S. invicta* under highways in Florida and North Carolina. Edges may also provide
Figure 7. Difference between the mound density in the northern (N) and southern (S) roadides (or halves in powerline cuts) as a function of road or cut orientation ($R^2 = 0.19, p < 0.003$) using a weighted regression. Larger symbols denote segments with greater total mound density.

microsites where humidity, temperature, foraging efficiency, vegetative cover, or the frequency of direct disturbance changes.

The spatial distributions of mounds differ between linear and non-linear early-successional patches. Mature mounds in pastures with high mound density are regularly distributed (Adams and Tschinkel 1995). Baroni Urbani and Kasowski (1974) found that mounds were somewhat aggregated at a small scale, but over an entire pasture, mounds were roughly uniform. Similarly, we have observed that mounds in forest gaps are not associated with edges. The spatial distribution of mounds within pastures, agricultural fields, and forest gaps may reflect a response to small-scale environmental heterogeneity such as tree stumps, fence posts (Hays et al. 1982), slight variation in topography (Maxwell 1982), or other mounds (Adams and Tschinkel, 1995). In contrast, the spatial distribution of mounds within linear habitats (Figures 4 and 5) may reflect a response to large-scale environmental heterogeneity such as the level of inscription, soil compaction, or temperature found along a consistent edge.

Solenopsis invicta is an exotic species whose effects on native ants and other arthropods are detrimental. Furthermore, its abundance and distribution throughout the southeastern U.S. is growing (Vinson 1994, Porter et al. 1988). In order to prevent or slow further invasion into newly-disturbed areas, the spatial distributions of mounds and the use of different linear habitat types by S. invicta need to be considered. To limit the suitability of road and powerline cuts as primary habitat for the red imported fire ant, our study suggests that a reduction in roadside disturbance (i.e., less mowing) and an increase in the amount of forest canopy allowed to shade roadides, especially towards northern edges, may result in lower fire ant mound density.

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