Biol Invasions
DOI 10.1007/s10530-008-9254-x

ORIGINAL PAPER

A case study of human exacerbation of the invasive species problem: transport and establishment of polygyne fire ants in Tallahassee, Florida, USA

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Received: 4 February 2008 / Accepted: 11 March 2008

Abstract Understanding how exotic invasive species are spread is fundamental for ecology and conservation biology. Human transport has become one of the primary modes of dispersal for exotic species. We examined how the multiple queen, or polygyne, social form of the fire ant *Solenopsis invicta* is spread along roadsides in Tallahassee, Florida, USA. We then determined the likely source of this expanding population, which was a central soil depot. A survey of road maintenance practices in counties of several southeastern states and Texas revealed that the use of a central soil depot is a common practice. Road maintenance therefore may be the primary source for the establishment of new polygyne fire ant populations in this region and elsewhere. Control efforts focused on the soil depots will help to limit further spread of polygyne fire ants and perhaps other invasive organisms, particularly invasive weeds.

Keywords Human transport · Invasive ants · Polygyny · Roadsides · Soil depots · *Solenopsis invicta*

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Introduction

Understanding how invasive exotic species are introduced into and become established in new habitats has broad implications for ecology and conservation biology. First, by understanding how these species are spread it is possible to understand the mechanisms that drive invasion dynamics and to predict potential ecological outcomes. Second, an understanding of spread and establishment will create the best opportunities for managing invasive species.

Human transport has almost certainly become the most important vehicle for spreading invasive exotic species (Deyrup et al. 2000; Ruiz et al. 2000), and the fire ant *Solenopsis invicta* is no exception. This South American ant was first detected in the USA around the harbor of Mobile, Alabama. It is highly likely that the initial colonies arrived on a ship, although the product in which they stowed away is unknown (Tschinkel 2006). Moreover, once established in the USA, most of the range expansion likely occurred by means of transport in nursery plants and other soil-containing products. A quarantine imposed in 1958 came too late to prevent the establishment of dozens of incipient populations throughout the southeastern USA. Most of the subsequent range increase represented the filling-in of areas between these human transported populations. The more recent appearance of *S. invicta* in Puerto Rico, Australia, China, and Taiwan was always in or near a port city, and thus also associated with shipping

(Tschinkel 2006). Range spread of *S. invicta* through its natural dispersal during mating flights has only been at local scales.

In the early 1970s, it became clear that *S. invicta* exists in two social forms, monogyne (single queen per colony) and polygyne (multiple queens per colony) (Glancey et al. 1973). The polygyne form is distributed in scattered enclaves throughout its range in the USA, with a higher frequency of polygyny evident in Louisiana and Texas than the remainder of the range (Porter et al. 1991; Porter 1992). Population densities, and therefore ecological and human impacts, are higher for polygyne than monogyne populations (Macom and Porter 1996). However, it is not clear whether the polygyne social form displaces the monogyne form, and mixed populations are common in the USA as well as in South America (Porter 1992; Fritz and Vander Meer 2003; Mescher et al. 2003).

In contrast to the monogyne form, which disperses primarily by means of flight of newly mated queens, polygyne populations expand naturally primarily (or possibly only) through colony budding. Colony budding is a process in which workers and queens walk a short distance from their parent colony to establish a new colony (Vargo and Porter 1989). A detailed description of a polygyne invasion in Texas showed a discrete, dense front as the population expanded essentially "on foot" (Porter et al. 1988). Whether such a dense expansion front is typical of all polygyne populations is unknown. There is evidence that, in the USA, polygyne populations are rarely, if ever, founded by newly mated queens dispersing on the wing (Ross and Shoemaker 1997). When new populations of polygyne *S. invicta* appear, we must therefore look to dispersal agents other than natural mating flights. The most likely agent of spread is human transport, one particular form of which is the subject of this paper. The high densities and greater ecological impacts of polygyne fire ants make such transport of considerable concern.

Materials and methods

Survey

Extensive sampling over the past 30 years in the Tallahassee, Florida area previously indicated the presence of only the monogyne social form (Tschinkel 2006). The initial discovery of polygyne *S. invicta* colonies in the Tallahassee, Florida area was made accidentally during routine collection of colonies for laboratory experiments in 2006. Samples from several colonies at the discovery site were confirmed to be polygyne using the methods described below. Upon initial discovery, we set out to map the extent of the polygyne population in a variety of habitats. We chose sample sites outward from the discovery site, using a Tallahassee road map along with the relevant aerial orthophoto of the area (Fig. 1). All sample sites were along roadsides and adjacent appropriate nesting habitats, such as fields and lawns. We visually inspected parts of the area that were heavily wooded, but these lacked fire ants. At each sample site, we collected 50 or more adult workers from each of 10 mounds for genetic determination of social form.

Determination of social form

Social organization of the sampled colonies was determined by screening adult workers for the presence of the *b* allele of the gene *Gp-9* using horizontal starch gel electrophoresis (DeHeer et al. 1999). Previous work has shown that polygyne colonies in the USA always contain a large proportion of workers bearing the *b* allele, whereas monogyne colonies contain only workers bearing the alternate *B* allele (Gotzek and Ross 2007). Five workers per colony were pooled for an initial round of *Gp-9* protein extraction and electrophoresis. Any colonies in which the *b* allele was detected were scored as polygyne. Those in which only the *B* allele was detected were subjected to another round of electrophoresis on an additional five workers. Colonies for which the *b* allele was not observed among all 10 sampled workers were scored as monogyne. Based on the observed frequencies of *b*-bearing adult workers in the polygyne colonies from Georgia, USA studied by Ross and Keller (2002), the binomial probability of not detecting a *b* allele in a sample of 10 workers from a single polygyne colony is estimated at 0.002 or lower.

The genetic determinations invariably confirmed the determinations of colony social form made in the field on the basis of a combination of worker-size distribution, the presence of multiple, attractive dealates and neighborhood mound density (Macom and Porter 1996). We therefore surveyed the social

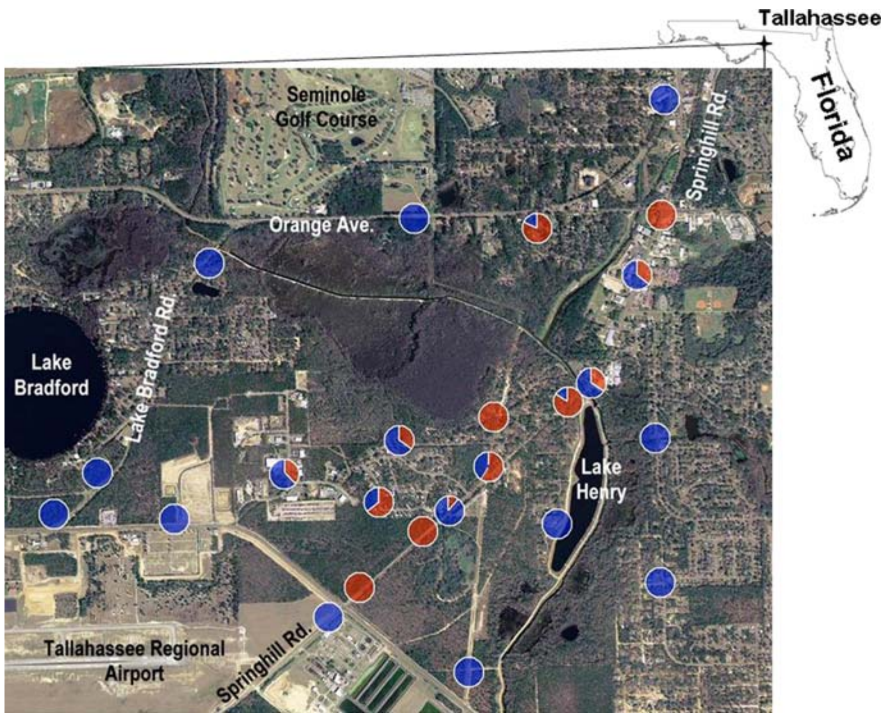

Fig. 1 Aerial orthophoto of southwest Tallahassee, Florida—the location of sampled fire ant colonies, and the proportion of each sample that was polygyne (red) or monogyne (blue). Polygyne colonies are limited to a distinct population centered on Springhill Road, and usually exist as mixed populations with monogyne colonies

form of colonies on several additional roadsides visually only. These visual surveys are identified in the Sect. 'Results'.

Results

Figure 1 shows the proportion of each sample of 10 colonies from a site that was polygyne and monogyne. In only a few cases were all sampled colonies polygyne, emphasizing that the two social forms often exist side by side in this area. The polygyne colonies are restricted to a distinct population bounded on all sides by strictly monogyne populations. The highest prevalence of polygyny is in proximity to the main arterial road through this area, Springhill Road, although some colonies of this form occur in an adjacent residential neighborhood and an industrial park. It seemed to us that the most likely initial source of the polygyne form was soil transported from elsewhere during maintenance work on the road shoulders. Maintenance work usually consists of adding soil to build up eroded road shoulders or removing soil accumulated in drainage ditches through erosion.

We discussed road maintenance practices with responsible officials of Leon County, Florida, where Tallahassee is located. We learned that soil removed from rights-of-way (for example, during the maintenance of drainage ditches) was stockpiled in an old claypit near Chaires in eastern Leon County (location: N30.43560 W84.13307), and that soil required for filling (for example, to restore road shoulders) was retrieved from these same stockpiles.

A visit to the claypit soil depot revealed about 20 large, loose soil piles, each measuring about $5 \times 15 \times 100$ m, and each occupied by multiple *S. invicta* mounds. Samples from 20 randomly chosen mounds showed that 90% of them contained polygyne *S. invicta*. Clearly, the soil stockpiles were a robust potential source of polygyne colonies, and road-maintenance practices were the probable mechanism of their transport and spread.

We therefore visually sampled four other roads that had been recently maintained by the Leon County road department, taking worker samples from 10 colonies every 2–3 km. Most of these samples yielded no indication of polygyny, but two small, extremely local enclaves of polygyne colonies were found, one at 10190 Moccasin Gap Rd. (N30.599382

W80.105796) in northern Leon County, and one at 5290 Crump Rd. (N30.530915 W84.129998). Visual sampling along several km of another major roadway (Thomasville Rd.) also revealed similarly low frequencies of polygyne fire ant colonies. Of a total of 258 inspected colonies, 16 were polygyne, and these were located in two tiny clusters, seven nests at N30.520418 W84.239529, and nine at N30.540981 W84.229080.

Discussion

Our observations suggest that the phrase, "mankind is the fire ant's best friend" (Tschinkel 2006), is even more true for the polygyne social form than the monogyne form. Without human transport of polygyne fire ants, it is likely that their annual spread would be measured only in tens of meters because of the physical limitations of dispersal by budding. We have identified roadway maintenance as a ready mode of human-mediated spread of the polygyne form, especially if road departments store soil in central depots, which apparently is a common practice across the southern USA. We interviewed personnel from 16 randomly selected county road maintenance departments throughout the southeastern USA and Texas, and learned that 13 of them had central soil depots from which they retrieved soil needed for roadside fill. A few departments also offered such soil to members of the public who wanted it. Clearly, the great majority of surveyed departments potentially spread polygyne fire ants along roads within their counties. It is less clear to what extent soil for roadwork is transported across county lines, but it seems likely that roadside improvement projects that cross county lines contribute to the spread of polygyne fire ants in the region. When maintenance or construction of roads is a state or federal responsibility, such inter-county projects are more likely.

While this particular case study represents a useful bit of detective work, it also raises the larger question of the consequences of human-mediated spread of polygyne fire ants. Fire ants are now recognized as a one of the 100 most important invasive exotic species in the world and have a rapidly expanding, global distribution (Lowe et al. 2004). It seems likely that residents of areas newly invaded by polygyne *S. invicta* will have a higher likelihood of contact with fire ants because of the high population densities characteristic of this form (Macom and Porter 1996). The increased potential for human contact is not trivial, as there will be an increased potential for incidences of envenomation, and wherever in the world the monogyne form has been transported, the polygyne form has been transported too (Tschinkel 2006).

Another important consideration is the added negative ecological effects of a polygyne invasion. To the extent that fire ants affect the disturbed ecosystems of which they are a part, the impact of "polygynization" will increase that impact in the short term (Porter and Savignano 1990). Polygyne *S. invicta* populations have been expanding along roadsides throughout the southern United States for decades (Porter et al. 1991; Porter 1992) and once established, these populations appear to be quite persistent (Porter 1993). Once established along roadsides, there will always be potential for them to spread into adjacent areas, such as lawns, old-fields, pastures, and open natural areas. In the north Florida region, we have not yet observed any spread beyond roadsides, but this is obviously very early in the establishment phase for this polygyne population.

It is not clear from our survey how readily polygyne colonies from the Chaires soil depot survive transport and deposition. Soil is spread, tamped and rolled largely by machine, making it likely that a large fraction of the transported ants are crushed in the process. However, all that is needed to establish a colony and a new incipient polygyne population is one surviving mated queen and a few workers, and this clearly happens at some non-zero frequency. The wide and non-uniform distribution of polygyne colonies along Springhill Road suggests that there were multiple points of establishment, and that survival of transported fire ants from the soil depot was common.

There is a bright side to the discovery that soil depots and roadside maintenance are the source of polygyne *S. invicta* spread, at least in the USA. Regular control efforts, such as application of poison baits on a semi-annual basis, should be directed at the populations that inhabit the soil depots because these are the likely source for the roadside populations. If poison is consistently applied to these populations, it seems likely that the increase in polygyne populations along roads will be slowed. This presumably would aid greatly in quarantine efforts in the southern United States. Such a strategy would be environmentally responsible because it avoids, for example, later, wider use of poisons that may affect non-target species and species of concern. At least in Tallahassee, the soil depot is not a valuable habitat, but a moonscape, completely devoid of any native plants or animals, and there need be no fear that the pesticides applied there will harm species of concern. Several poison baits are available that have low persistence and low potential for ecological impact by movement, for example, through the water table. This may also be a viable strategy for slowing the spread of some invasive weeds, including cogon grass and giant ragweed, which were also established at the claypit soil depot.

Acknowledgements We thank Leon County for information on roadside maintenance. We thank the "Winter Term Obies," Joshua Greenfield, Samuel Slowinski, Madeline Logowitz, and Laura Russo, for their help with the Thomasville Road survey. This research was carried out with partial support from NSF grant IBN-0212085 and USDA-NRI-CREES grant 2003-35302-13565.

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