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BOOM AND BUST OF THE TAWNY CRAZY ANT, *NYLANDERIA FULVA* (HYMENOPTERA: FORMICIDAE), ON ST. CROIX, US VIRGIN ISLANDSJAMES K. WETTERER^{1*}, OLASEE DAVIS² AND JOE R. WILLIAMSON²¹Wilkes Honors College, Florida Atlantic University, 5353 Parkside Dr., Jupiter, FL 33458²Cooperative Extension Service, University of the Virgin Islands, Kingshill, St. Croix, VI 00850

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ABSTRACT

The tawny crazy ant, *Nylanderia fulva* Mayr (formerly *Paratrechina fulva*) (Hymenoptera: Formicidae), is a South American species first recorded in the US in 1938 from Brownsville, Texas. Recent population explosions of *N. fulva* in parts of the southeastern US have received much media attention, often including predictions of tremendous long-term ecological and economic impacts. Here, we examined the status of on-going population explosions of *N. fulva* on the island of St. Croix, US Virgin Islands. Beginning in 2002, St. Croix local inhabitants started reporting dense populations of *N. fulva*. All early reports of *N. fulva* came from the north-central part of the island. A 2006 study found 3 geographically discrete populations of *N. fulva*: a main population in north-central St. Croix, and 2 smaller area populations in northwestern and south-central St. Croix. Our new survey in December 2013 indicates that *N. fulva* populations have expanded tremendously in northwestern St. Croix, while *N. fulva* populations have completely crashed throughout its 2006 range in north-central and south-central St. Croix. This pattern of an extreme population boom followed by a bust may be a common characteristic of *N. fulva* and might distinguish this species from the closely related *Nylanderia pubens*. It seems likely that the current dense populations of *N. fulva* at sites in St. Croix and the southeastern US will crash within a few years, leaving little long-term impact, but that new population explosions of this species will arise elsewhere.

Key Words: biological invasion, crazy ants, exotic species, invasive species, population explosion

RESUMEN

La hormiga loca leonado, *Nylanderia fulva* Mayr 1862 (anteriormente *Paratrechina fulva*) (Hymenoptera: Formicidae), es una especie de América del Sur que fue registrada por primera vez en los EE.UU. en 1938 en Brownsville, Texas. Recientes explosiones de poblaciones de *N. fulva* en varias partes del sudeste de los EE.UU. han recibido una gran atención en los medios de comunicación, a menudo incluyendo predicciones a largo plazo de impactos ecológicos y económicos enormes. Aquí, examinamos el estado de explosiones continuas de poblaciones de *N. fulva* en la isla de St. Croix, Islas Vírgenes de Estados Unidos. A partir del 2002, la gente de St. Croix comenzó a reportar densas poblaciones de *N. fulva*. Todos los informes anteriores de *N. fulva* fueron de la parte norte-central de la isla. Un estudio del 2006 encontró tres poblaciones geográficamente separadas de *N. fulva*: una población principal en la parte centro-norte de St. Croix, y dos poblaciones más pequeñas en el noroeste y en el centro-sur de St. Croix. Nuestro nuevo sondeo en diciembre del 2013 indica que las poblaciones de *N. fulva* se han expandido enormemente en el noroeste de St. Croix, mientras que las poblaciones de *N. fulva* han caído por completo en todo su rango del 2006 en el centro-norte y centro-sur de St. Croix. Este patrón de un auge extremo en la población seguida de una caída drástica puede ser una característica común de *N. fulva* y podría distinguir esta especie de *Nylanderia pubens* una especie estrechamente relacionada. No parece probable que las poblaciones actuales densas de *N. fulva* en los sitios de St. Croix y de sudeste de los EE.UU. decaeran en pocos años, dejando poco impacto a largo plazo, sino que las nuevas explosiones de población de esta especie se incrementará en otro lugar.

Palabras Clave: invasiones biológicas, hormigas locas, especies exóticas, especies invasoras, explosión demográfica

The tawny crazy ant, *Nylanderia fulva* Mayr (Hymenoptera: Formicidae) (formerly *Paratrechina fulva*), is a South American species first recorded in the US in 1938 from Brownsville, Texas (Trager 1984). Recent population explosions of *N. fulva* have been reported from several sites in the southern US, most notably in eastern Texas where these ants have become a serious household, agricultural, and ecological pest, often displacing the red imported fire ant, *Solenopsis invicta* Buren (Meyers 2008; LeBrun et al. 2013). Accounts in the popular press about this ant in Texas have included predictions of tremendous long-term ecological and economic impacts (e.g., Friedman 2013; Mooallem 2013) and the end of *S. invicta*'s "60-year dynasty" in the southeastern US (Pennisi 2014). Little attention, however, has been paid to similar outbreaks of this ant, past and present, in other locations, and the lessons we may learn from them. In part, this is because of confusion about the identity of the ant species involved. In many earlier reports, *N. fulva* was misidentified as *Nylanderia pubens* Forel (formerly *Paratrechina pubens*), a closely related species whose workers cannot currently be differentiated reliably from *N. fulva* using only morphological characters (MacGown & Layton 2010; Gotzek et al. 2012).

Wetterer & Keularts (2008) reported an outbreak of *N. fulva* (misidentified as *N. pubens*) on the island of St. Croix, US Virgin Islands that began around 2002. All early reports of *N. fulva* problems came from the north-central part of the island. In 2006, there were 3 geographically discrete high-density populations of *N. fulva* occupying ~5% of the island: a main population in north-central St. Croix spread over ~9 km² centered on Calquohoun, and 2 smaller populations occupying <1 km² each in northwestern and south-central St. Croix (Fig. 1). Here, we update the status of *N. fulva* on St. Croix.

Taxonomic Problems

Mayr (1862) described *N. fulva* from Rio de Janeiro, Brazil, based on specimens collected by the Novara expedition in 1857. Unfortunately, almost all subsequent records of *N. fulva* are of unknown reliability because of problems with distinguishing *N. fulva* from other closely related species, notably *N. pubens* (Trager 1984; Gotzek et al. 2012). *Nylanderia fulva* and *N. pubens*, however, may be distinguished using genetic analyses and male morphology (Gotzek et al. 2012). Genetic analyses determined that the ants currently undergoing population explosions on St. Croix, first reported as *N. pubens* (Wetterer & Keularts 2008), are actually *N. fulva* (Gotzek et al. 2012). We confirmed this conclusion in the present study using the morphology of males we collected on St. Croix.

METHODS

In the time since the Wetterer & Keularts' (2008) study, complaints of *N. fulva* problems continued to be reported to the Cooperative Extension Office at the University of the Virgin Islands on St. Croix. In 14-24 Dec 2013, we investigated all areas where recent outbreaks had been reported to evaluate current conditions and collect voucher specimens. We also surveyed in and around all the areas where *N. fulva* had been found in 2002-2006 (marked with 'X' in Fig. 1). In addition, we interviewed people living in different parts of the island concerning their experiences with *N. fulva* and other ant species. We mapped all sites where we collected *N. fulva* in Dec 2013 (Fig. 1; circles).

We deposited voucher specimens of *N. fulva*, including males from 5 sites, at Harvard University's Museum of Comparative Zoology.



Fig. 1. *Nylanderia fulva* records on St Croix. X = 2002-2006 (from Wetterer & Keularts 2008). Circle = Dec 2013. A and B = last reported in 2009 and 2011, respectively, but no longer present in Dec 2013 (see Results).

RESULTS

Between 2011 and 2013, almost all complaints of *N. fulva* recorded by the Cooperative Extension Office came from northwestern St. Croix. The one exception was a report from the Cane Bay Campground in north-central St. Croix (see below).

In our Dec 2013 survey, we found *N. fulva* over a wide area in northwestern St. Croix covering ~10 km², with the outer edge from the north coast from Annaly (geo-coordinates: 17.762, -64.847) to Sweet Bottom (17.762, -64.831), south to Cane Valley (17.721, -64.848), and from Little La Grange (17.727, -64.867) in the west to Springfield (17.730, -64.829) in the east (Fig. 1). Most of this area is hilly and heavily forested and has greater rainfall than other parts of the island.

Hiking the Trumbull Trail from the Carambola Beach Resort (17.761, -64.831) to Annaly Bay (17.762, -64.847), we found almost the entire stretch was swarming with high densities of *N. fulva*, though numbers appear to be declining from a peak about 2 years earlier (O. Davis, pers. obs.). We found only a small number of *N. fulva* at the Carambola Beach Resort itself. The highest density of *N. fulva* we observed in December 2013 was around a house in Cane Valley. The owner said that the ants had arrived about 3 months earlier and now they covered the walls of her house, inside and out. We noted a mat of dead ants surrounding her house and found nests of *N. fulva* under every stone in her yard. At Mt Victory Camp (17.748, -64.869), which in 2005 had high densities of *N. fulva* (Wetterer & Keularts 2008), the owner, Matt Corradino (pers. comm.), had not recently seen any *N. fulva* at the camp itself. However, he still found *N. fulva* in the surrounding forest, and we found a single *N. fulva* queen near the camp headquarters. Corradino (pers. comm.) noted that with the decline in *N. fulva*, fire ants had moved in and we found large colonies of both *Solenopsis invicta* Buren and *Solenopsis geminata* (Fabricius) near the camp headquarters. At the neighboring Ridge to Reef Farm in Mt Victory (17.753, -64.867), the proprietors reported an earlier outbreak of *N. fulva* around their "tree house," but in 2013, a different invasive ant, *Technomyrmex difficilis* Forel, now dominated this area. Nonetheless, we found high densities of *N. fulva* in a bamboo grove on the property. In a forested area of Caledonia Valley in Hams Bay (17.762, -64.876; labeled "A" in Fig. 1), where OD found swarms of *N. fulva* on a visit in 2009, we found none in Dec 2013. Instead, *T. difficilis* dominated the area.

In contrast to conditions in much of northwestern St. Croix, locals throughout the north-central part of the island consistently reported that *N. fulva* had previously reached high densities, but then disappeared between 2 and 4 years ago. We made a thorough search of Cruzan Gardens

(17.739, -64.800), the nexus of the earlier outbreak in 2002-2006, but found no *N. fulva*. The owner of Cruzan Gardens, Ken Holmes (pers. comm.), said he had not seen any *N. fulva* on the property for several years. At Discovery Grove camp in Canaan (17.762, -64.800; labeled "B" in Fig. 1), at the northern edge of where Wetterer & Keularts (2008) found *N. fulva* in 2006, Try McRae (pers. comm.) reported that *N. fulva* arrived on the property around 2006. Populations grew to high densities, with "rivers" of ants in some places. But then the *N. fulva* populations crashed, completely disappearing in 2011. We searched the area and saw no *N. fulva*, but instead found a large population of *T. difficilis*.

The only extant population of *N. fulva* that we found in north-central St. Croix was at the Cane Bay Campground (17.772, -64.811), on the coast to the north of the earlier north-central population. Bryan Updike (pers. comm.), who runs the campground, reported that *N. fulva* arrived about 4 years earlier, first in south end of the property and later spreading throughout the campground in high densities. The populations, however, began crashing about a year ago. Although in some areas there were still substantial numbers of *N. fulva*, these were much lower than when the population was at its peak. Updike (pers. comm.) noted that when *N. fulva* arrived, *S. invicta* disappeared, but when *N. fulva* declined, high numbers of *S. invicta* returned.

We searched all 5 sites in south-central St. Croix (just east of the airport: 17.708, -64.787; 17.702, -64.785; 17.701, -64.781; 17.697, -64.780; 17.699, -64.788) where Wetterer & Keularts (2008) collected *N. fulva* in 2006. We found a wide variety of native and exotic ants, but no *N. fulva*. Interestingly, one of these sites was now overrun with high densities of the exotic penny ant, *Tetramorium bicarinatum* (Nylander).

DISCUSSION

Although the on-going *N. fulva* population explosions on St. Croix only date back to 2002, there are reports of *N. fulva* from St. Croix that are much older. Beatty (1944) recorded *N. fulva* from 2 sites in St. Croix further to the east than any of the recent outbreaks (at Blessing in 1933: 17.71, -64.76; and at Sight in 1936: 17.74, -64.67). Miskimen and Bond (1970) reported *N. fulva* from sugarcane fields in St. Croix. It is unclear whether the recent population explosions of *N. fulva* St. Croix originated from a new invasion of this species or from the expansion of existing populations on St. Croix. The population explosions of *N. fulva* may have been triggered by the introduction of a new mutualist aphid, scale insect, or other Hemiptera. The arrival of a new Hemiptera mutualist has been suggested as the possible trigger of population explosions of other invasive ants,

including *Solenopsis geminata* and *Linepithema humile* (Mayr) (Franquinho-Aguiar & Wetterer 2006; Wetterer 2011). Alternatively, the earlier records of *N. fulva* on St. Croix may have been based on misidentification of *N. pubens*.

A pattern of tremendous population expansion followed by a collapse may be a common characteristic of *N. fulva*. For example, Zenner-Polania (1990) described great outbreaks of *N. fulva* in different parts of Colombia, impacting crops and livestock, followed by population declines: "to reach a peak abundance, the population has to occupy an area for at least two years and after that, a slow but continuous decline culminates in restoration of the natural equilibrium about 10 years later." In 2005-2007, an enormous population of *N. fulva* took over the winter home of JKW's parents in Palm Beach Gardens, Florida (26.856, -80.104), as well as their yard, where the ants tended large numbers of Hemiptera in the citrus trees (identification confirmed using males collected indoors in Apr 2006; additional workers collected on citrus trees in Jan 2007). In Dec 2005, JKW went to the house to prepare it for his parents' arrival and found *N. fulva* nesting in the plumbing; when JKW turned on the bathtub faucet, thousands of *N. fulva* poured out. This population, however, crashed in 2007 and was replaced by a large population of *T. difficilis* (see Wetterer 2013), which still dominates the yard and tends Hemiptera in the citrus trees in 2014. In 2006-2007, JKW observed a similar population explosion (collected in Jan 2007; presumed to be *N. fulva*, but without males for confirmation) in a forested area of Jupiter, Florida (26.896, -80.105), but this population has also disappeared. David Oi (pers. comm.) has noted similar population booms and busts of *N. fulva*, writing, "[I am] seeing similar crashes (occurred within 1-2 years in some sites perhaps it started declining earlier) in several collecting sites in Florida; and I still occasionally get reports of new sites with high densities . . . some intensive insecticide use may be a factor, but I have seen untreated areas decline. Habitat modification also could be a key factor. . . Sites I have seen declines in Florida are often in residential and woodlands/retention ponds areas, or in riparian woodland urban parks . . . Declines in honeydew-producing hemipterans may be a factor, but [I] have not seen a clear association as there are confounding factors like removal of invasive plants or occasional underbrush clearing." If population explosions and crashes are a characteristic that distinguishes *N. fulva* from the closely related *N. pubens*, then previous reports of enormous *N. pubens* outbreaks were probably based on misidentifications of *N. fulva*, e.g., Deyrup et al.'s (2000) report that *N. pubens* "is abundant on the campus of the University of Miami . . . foraging on sidewalks and running up and down tree trunks." Some records from Florida,

however, appear to be true *N. pubens* (e.g., specimen CASENT0104860 photographed on antweb; M. Deyrup, pers. comm.).

In the 1800s, Bermuda experienced a great plague of ants followed by a crash (Wetterer 2006) that seems similar to the booms and busts of *N. fulva* on St. Croix. For example, in a passage dated 10 Oct 1848, Hurdis (1897) wrote: "During the last seven summers this part of Bermuda has been infested with Ants to a fearful degree; not only did they teem on the streets and highways, so as to render it impossible to walk without destroying numbers, but hill and dale, and even the dwellings of men were equally alive with this insect pest. Dense columns of them might be seen travelling up and down every tree, and great was the havoc they occasioned among young Pigeons and Poultry, nor did full-grown domestic rabbit escape their deadly attack, and pigs are sometimes destroyed by them. In the present summer we have happily escaped this enormous nuisance, the legions of Ants being reduced within reasonable bounds. The cause of this extraordinary decrease is entirely unknown to me." Whereas Wetterer (2007) proposed that this plague species in Bermuda was probably *N. pubens*, it now seems that *N. fulva* is a more likely candidate.

Many invasive ant species have been known to show population expansions followed by declines (e.g., see Wetterer et al. 2006). The great booms and busts of *N. fulva* populations are fairly extreme, both in terms of the high peak densities and the thoroughness of their rapid decline. During population explosions, *N. fulva* displace other ants (LeBrun et al. 2013), but this displacement appears to be only temporary, at least in St. Croix and Florida. When *N. fulva* populations crash, other ant populations replace them, often dominated by other invasive species such as *S. invicta* and *T. difficilis*. It will be valuable to follow population trends in areas where *N. fulva* is now having outbreaks. It seems likely that the current dense populations of *N. fulva* at sites in St. Croix and the southeastern US will crash in a few years, leaving little long-term impact, however new population explosions of this species will arise elsewhere. What factors drive these boom and bust events remain unknown and deserve further attention. Whereas great ant plagues make news headlines, the collapse of pest ant populations may go relatively unheralded in the press.

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