# Distribution, behavioral dominance and potential impacts on endemic fauna of tropical fire ant *Solenopsis geminata* (Fabricius, 1804) (Hymenoptera: Formicidae: Myrmicinae) in the Galápagos archipelago

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# Distribution, behavioral dominance and potential impacts on endemic fauna of tropical fire ant *Solenopsis geminata* (Fabricius, 1804) (Hymenoptera: Formicidae: Myrmicinae) in the Galápagos archipelago

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*Abstract.* Tropical fire ant (TFA), *Solenopsis geminata* (Fabricius, 1804), is considered as one of the most serious threats to the terrestrial fauna of Galápagos, yet little is known about its distribution and impact in the archipelago. We reviewed literature, studied museum specimens and sampled over 62 sites on ten islands and islets in order to update the distribution of TFA. Since the 1980's, species occurrences for TFA have increased from three to 115 localities, and the species is now recorded on seven islands and 11 islets. Sixty-six new records were registered since the last review in 2008, including the islets Bayas, Champion, Cuevas, and Eden. TFA seems to be present in a wide range of habitats with a clear predominance in human-disturbed zones. Our data, compiled with previous studies, suggest that TFA can behaviorally dominate other ants. TFA was collected on 28 nesting sites of endangered and/or endemic vertebrate species, where it constitutes a potential or proven threat. This study identifies potential invasion sites as well as endemic species that may further be impacted by this highly invasive ant. It also recommends regular monitoring to prevent further invasion.

*Key Words.* Biological invasion, Endangered species

## Introduction

Invasive species represent a major threat to worldwide biodiversity (Clavero & García-Berthou 2005, Sanu & Newport 2010, Simberloff et al. 2013) and have dramatic effects on the economy and public health (Everett 2000, Pimentel et al. 2000). Because of their geographic isolation and reduced area, insular biotas are considered unique environments, but extremely sensitive to the introduction of alien species (MacArthur & Wilson 1967). Among invasive species in the Galápagos, goats, pigs, rats, feral cats and dogs, and several species of invertebrates such as *Polistes* wasps and the bird ectoparasite *Philornis downsi* (Dodge & Aitken 1968) are the most common (Causton et al. 2006, Walsh & Mena 2013). Ants are also highly successful invaders in Galápagos and other oceanic archipelagos. They can be ecologically and economically devastating and often outcompete native ant species (Clark et al. 1982, Holway et al. 2002, LeBrun et al. 2013, Porter & Savignano 1990, Suarez & Tsutsui 2008). Tropical fire ant (TFA), *Solenopsis geminata* (Fabricius, 1804), is a well-known tramp species. TFA is considered one of the most damaging and widespread introduced species (Holway et al. 2002) and is regarded as an environmental and economic pest having a major impact on the ecological balances of ecosystems (Risch & Carroll 1982, Plentovich 2009). A native of Central and South America, TFA has been extraordinarily successful in spreading into six continents and has colonized many tropical islands on all the oceans (Wetterer 2010). In disturbed tropical ecosystems, TFA is often the species at the top of dominance hierarchies (Morrison 1996, Perfecto 1994). TFA preys on vertebrates such as loggerhead sea turtles (Wetterer & Lombard 2010, Wetterer et al. 2007), sea birds hatchlings and chicks (Plentovich et al. 2009, Wetterer 2010), rats and mongooses (Pimentel 1955). TFA also has an impact on invertebrates: it preys on butterfly eggs (Nafus & Schreiner 1988, Way et al. 1998) and alters populations of other invertebrates (Geetha et al. 2000). TFA is considered an agricultural pest as ants harvest seeds and destroy irrigation tubes (Chang & Ota 1990, Perfecto 1994). TFA also affects humans and domestic animals because of its painful sting, sometimes causing severe allergic reactions (Knight & Bangs 2007).

The first record of TFA in the Galápagos archipelago dates back to 1891 on San Cristóbal Island (Emery 1893), followed by two records in 1905 on Floreana and San Cristóbal (Wheeler 1919), the two islands with the earliest (1800's) settlements (Jackson 1993). The first record for TFA on the other islands with established human settlements is 1981 for Isabela Island and 1982 for Santa Cruz Island (Herrera & Causton 2008b). After the establishment of the Charles Darwin Research Station (CDRS) in 1964 in Puerto Ayora on Santa Cruz Island, more extensive studies were carried out on the ant fauna, many of which mention TFA as a dominant species (Clark et al. 1982, Lubin 1984, Pezzatti et al. 1998, Von Aesch & Cherix 2005). In 1999, the Terrestrial Invertebrates Reference Collection was established at the Charles Darwin Research station and regular ant censuses were conducted on various islands. In a review conducted in 2008, TFA was recorded on seven islands and six islets (Herrera & Causton 2008b).

Here, we update the distribution of TFA in the Galápagos by compiling existing data and by sampling new sites, in order to determine potential new invasion sites and potentially threatened species. To assess the potential impact of TFA on native ant communities, we also investigate TFA's activity cycle and dominance with respect to other ant species. Finally, we discuss the need for monitoring and conservation of vulnerable areas and endemic species.

## Methods and Materials

*Study site.* The Galápagos archipelago is located 972 km off the Ecuadorian coast and is constituted of 121 islands, islets and rocks, in which 18 are bigger than 100 ha (Snell et al. 1995, Tye et al. 2002). The archipelago was discovered in 1535 and was used as a base by a succession of buccaneers, sealers and whalers during the next three centuries. The first human settlements followed in the 19$^{th}$ century and were primarily concentrated on Floreana (Post Office Bay) and Santiago (Puerto Egas) (Jackson 1993). Ninety-seven percent of the archipelago officially became a national park in 1959. This late human colonization combined with its early protection as a national park makes the Galápagos one of the most pristine archipelagos on Earth. Nevertheless, tourism has been growing exponentially since it began in the late 1960s, and now attracts over 180,000 visitors a year with around 25,000 people residing in Galápagos (Benitez-Capistros et al. 2014, Epler 2007). Seventy sites are now open to visitors accompanied by Galápagos National Park (GNP) guides. This increase in the presence of humans has led to ecological degradation through land transformation and the introduction of invasive species (Watson et al. 2009). As of today, a large part of the fauna and flora of the archipelago is still intact and its endemism level is very high (Myers et al. 2000). Out of 500 native plant species, 43% are endemic. Roughly 50% of the 1900 native invertebrate species are endemic and 59% of the 117 vertebrate species are endemic (with 100%, 88% and 52% of endemism for reptiles, mammals and birds, respectively). However, the survival of these taxa depends strongly on conservation and monitoring efforts (Walsh & Mena 2013).

*Sampling and data analysis.* During three sampling expeditions in the Galápagos archipelago in February–March 2010, March–April 2011 and March–April 2012 (rainy season), we visited over 62 sites on seven islands and four islets (i.e., islands smaller than 100 ha; Snell et al. 1995) (Baltra, Floreana, Fernandina, Isabela, Mao 1 and 2, San Cristóbal, Santa Cruz, Santa Fé, Santiago, Plazas Sur) (Fig. 1). We sampled the following vegetation zones of the archipelago: coastal zone, arid zone, transition zone, *Scalesia* and *Miconia* endemic forests and pampa (Hamann 1979, Jackson 1993). Human-disturbed areas such as urban areas, agricultural zones (e.g., coffee and banana plantations, pastures) were also sampled. The sampled sites were also classified on the base of the land use status according to the classification system used by the GNP Service (galapagospark.com): 1) inhabited areas, 2) recreational, 3) nearby intensive (touristic sites close to populated areas, with outstanding natural features), 4) managed intensive (natural attractions with tourist infrastructures), 5) natural intensive (touristic sites in excellent state of conservation) and 6) restricted sites (well-preserved ecosystems, with severe restrictions imposed on tourist visitations).

Ants were sampled using complementary techniques such as hand sampling, baiting, pitfall traps and Winkler extractions following the ALL protocol (Agosti et al. 2000). Samples were stored in absolute ethanol and a GPS point with elevation was marked for every collection site. Collections and identifications of museum specimens made by Henri W. Herrera from 2001 to 2014 were included in the study, as well as specimens collected during an expedition conducted in 2009 by Wouter Dekoninck and

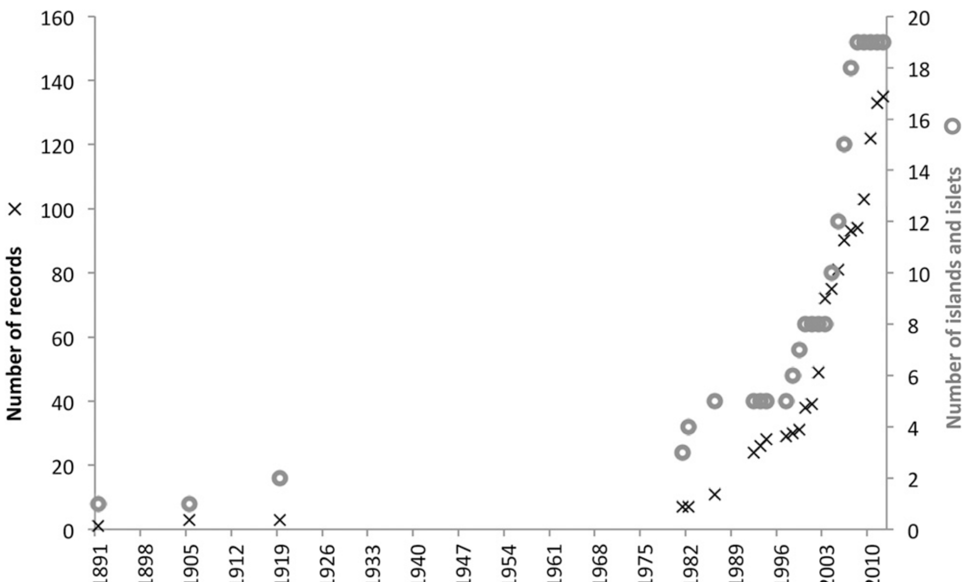


Figure 1. Cumulative number of records (black crosses) and islands or islets (open grey dots) where TFA was observed.

Frederik Hendrickx. The material studied is deposited in the terrestrial Invertebrates Collection of the Charles Darwin Research Station (ICCDRS) and the Royal Belgian Institute of Natural Sciences (RBINS).

*Baiting experiments.* On the island of Santa Cruz, we conducted baiting experiments to attract foraging ants. The abundance of ant foragers at baits can help to measure ecological and behavioral dominance (Bestelmeyer et al. 2000). The experiments were setup at three sites: one human-disturbed area (soccer field of Bellavista town, altitude 205 m, 24 March 2011) and two agricultural zones: one abandoned pasture (trail to El Chato, altitude 367 m, 30 March 2011) and one mixed coffee-banana plantation (road to Media Luna, altitude 291 m, 6 April 2011). Twenty-five baiting stations were placed on each site 5 m apart in a 5×5-m$^2$ array. At each baiting station, three types of baits were set out to avoid food preference bias (tuna in water, peanut butter and liquid honey; i.e., proteins, lipids and carbohydrates), yielding a total of 225 observations. Each station consisted of approximately 2 g tuna, peanut butter and honey placed about 2 cm apart on a 10×10-cm aluminum foil. Ants were identified and counted, and baits were monitored after 20, 45 and 120 minutes to evaluate the rate of species replacement. All experiments took place between 15:00–17:00 hours. Most species were identified in the field; others were collected for later identification at CDRS. Abundance scores were assigned for each bait type as follows: 1= 1–5 individuals; 2 = 6–15; 3 = 16–50; 4 = >50 (Ward & Beggs 2007). We assessed the dominance of species using criteria from Andersen (1992) and Ward & Beggs (2007): 1) proportion of occurrences (i.e. the absence or presence of a species in a given sample) at baits; 2) dominated baits (defined as the proportion of abundance score ≥3); 3) mean abundance score for the three monitoring times (only at baits where the species occurs); 4) ability to monopolize baits (being the only species at baits at the end of the 120 min baiting period) and 5) ability to rapidly discover baits (proportion of occurrence at baits after 20 min). Criteria were calculated for each bait separately (total of 225 occurrences), and for each bait station (considering the 3 baits as single bait; 75 occurrences).

*Daily activity cycle.* To study the daily activity of TFA, we observed a foraging trail on a tree, traced a line at 150-cm height and counted all ants crossing it in both directions during a 5- min period. Ants were counted every two hours within a timeframe of 24 hours (adapted from Klotz (1984)). The experiment was conducted on 22 February 2010 (11.8 mm precipitations, mean air temperature = 27.6°C, relative humidity = 91%) (CDF 2014). As heavy rains started during the experiment, it was repeated on 8 March 2010 when the weather conditions were more suitable to avoid impact of water ravines on foraging (0 mm, 27.5°C, 97%).

## Results

*Current distribution.* We compiled a total of 194 records of TFA in Galápagos from 129 localities on 21 islands and islets, 66 of which are new since the last review (Herrera & Causton 2008b) (Table 1). TFA is now documented from 20 islands and islets (Albany, Bainbridge 1, Baltra, Bayas, Champión, Cuevas, Edén, Fernandina, Floreana, Gardner, Isabela, Mao, Marielas 1 and 2, Plazas Sur, San Cristóbal, Santa Cruz, Santa Fé, Santiago and Seymour Norte. New records of islets include Bayas, Champión, Cuevas and Edén (Fig. 1, 2).

Eighty-six records for TFA in Galápagos mention the altitude of the location sampled and indicate that TFA is found up to at least 989 m above sea level. TFA was

Table 1. Distribution of TFA in the Galápagos archipelago. For islets, the name of the closest major island was added between brackets. * indicate new records of TFA since the review of Herrera & Causton (2008). Dates between brackets are unconfirmed records.

| Island | Localities | First record | Reference |
|---|---|---|---|
| Albany (Santiago) | Islet | 2004 | Herrera & Causton 2008 |
| Bainbridge (Santiago) | Islet | (2000) | Herrera & Causton 2008 |
| Baltra | Airport*, Canal Itabaca*, captaincy housing*, iguana repatriation zones*, Landfill*, North landfill*, Tame airline hold* | 2005 | Herrera & Causton 2010 |
| Bayas (Floreana) | Islet* | 2007 | Herrera & Roque-Albelo 2007 |
| Champion (Floreana) | Islet* | 2006 | ICCDRS |
| Cuevas (Santa Cruz) | Islet* | 2007 | Herrera & Roque-Albelo 2007 |
| Eden (Santa Cruz) | Islet* | 2007 | Herrera & Roque-Albelo 2007 |
| Fernandina | Punta Mangle | 2005 | Herrera & Causton 2008 |
| Floreana | Cerro Pajas, Las Palmas, Punta Cormorant, Varias Fincas, Asilo de la Paz, Puerto Velasco Ibarra* | 1905 | Wheeler 1919 |
| Gardner (Floreana) | Islet* | 1999 | CDRS database |
| Isabela | Agriculture zones*, Alcedo volcano, Alfaijia*, Cerro Azul, Cerro Grande*, Cinco Cerros, Concha de Perla*, El Cura*, Electric plant*, Iguana Cove, Infiernillo*, La Esperanza*, Las Merceditas*, Loja*, Los Ceibos*, Los Mellizons*, Los Tintos, Puerto Villamil, Playa Tortuga Negra, Punta García, San Juaquín*, San Pedro, Santo Tomás*, Sierra Negra volcano, tortoise nesting sites* | 1981 | Lubin 1984 |
| Mao (Santiago) | Islet | 2004 | Herrera & Causton 2008 |
| Marielas 1,2 (Isabela) | Islets* | 1998 | Herrera & Causton 2008 |
| Plazas Sur (Santa Cruz) | Islet | 2006 | ICCDRS |
| San Cristobal | Cerro Gato*, Cerro Mundo*, Cerro Verde*, Electric plant*, El Junco lagoon*, El Mango*, El Progreso*, Farm El Progreso*, La Lobería, Naval zone*, Puerta Negra*, Puerto Baquerizo Moreno, Puerto Chino, Santa Monica*, Sector cerro Azul*, El Socavón*, Soledad | 1891 | Emery 1893 |

Table 1. Continued.

| Island | Localities | First record | Reference |
|---|---|---|---|
| Santa Cruz | Barranco*,Bellavista, Caleta Tortuga Negra*, Camino Media Luna*, Canal Itabaca*, Charles Darwin research station*, Cerro Crocker, Cerro Dragón, Cerro Mesa*, Coffee plantation*, El Camote, El Carmen*, El Cascajo*, El Chato*, El Garrapatero*, El Mirador*, El Occidente*, La Caseta*, Landfill*, La Torta*, Las Grietas*, Los Gemelos*, Media Luna houses*, Media Luna, Playa Estación*, Puerto Ayora, Punta Nuñez, red gravel mine*, Salasaca*, Santa Rosa*, Supply center Fabricio Valverde*, Tortuga Bay | 1982 | Williams & Whelan 1991 |
| Santa Fe | La Caleta | 1986 | ICCDRS |
| Santiago | Punta Baquerizo | 2004 | ICCDRS |
| Seymour Norte (Baltra) | Islet | 2008 | ICCDRS |

found in all investigated habitats: agricultural areas (39 localities), coastal zone (23), human-disturbed areas (20), arid zone (16) and humid zone (*Scalesia* forest, *Miconia* forest, humid zones, pampa; 14 records). Records were located in intensive unprotected

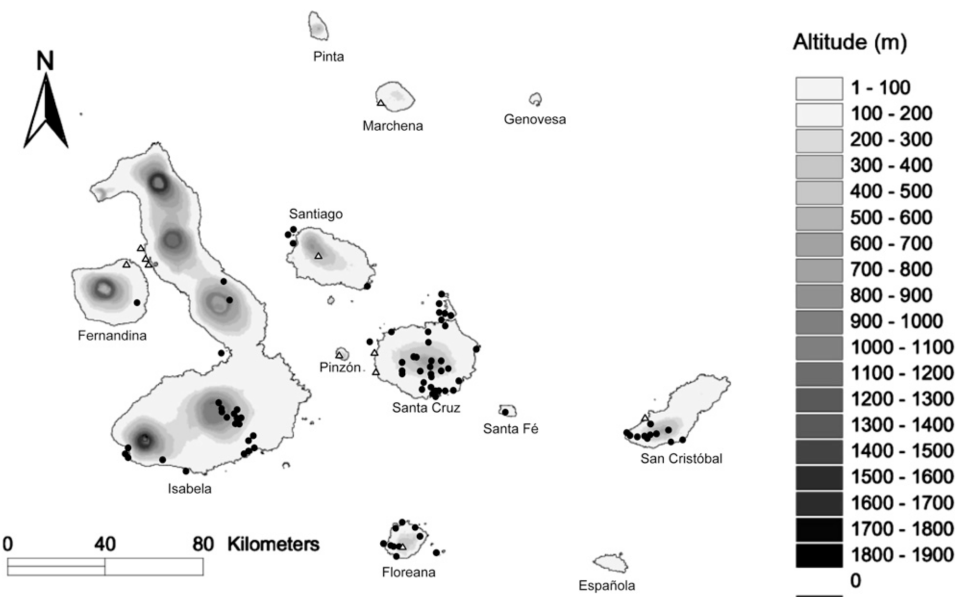


Figure 2. Distribution of the tropical fire ant (TFA) in the Galápagos archipelago. Dots indicate the presence of TFA and triangles indicate the sites where it was not found during our expeditions in 2010–2012.

areas (51 localities), restricted areas (30), nearby intensive (13), recreational (9), managed intensive (5), intensive (1) and natural intensive (1). Four remaining sites are undetermined. TFA was or is currently present in the immediate proximity of at least 28 localities constituting the nesting sites of 25 endemic or threatened taxa, including endemic land tortoises and iguanas, and many seabirds (Table 2, detailed information available online in the Charles Darwin Foundation datazone, www.darwinfoundation.org/datazone/).

Records of absence (i.e., negative records) were only available for the sites we sampled ourselves and for ants surveys on Española, Santa Fé and Marchena islands (Causton et al. 2012, Herrera & Causton 2008a, Roque-Albelo et al. 2000). A total of 24 records were negative for TFA, four of which are from Española and Marchena, uninvaded islands. The remaining records are from invaded islands: Fernandina, Floreana, Isabela, Plazas Sur, San Cristóbal, Santa Cruz and Santa Fé. TFA was not found during our study at six sites where it had been previously recorded: Punta Mangle (Fernandina), Asilo de la Paz (Floreana), Plazas Sur Islet, Playa de los Alemanes and Tortuga Bay (Santa Cruz) and Santa Fé Islet. All of the sites were located in arid zones or coastal areas, except for one site on Santa Cruz Island (Black gravel mine). The majority of negative records (19/24) were located in restricted areas (detailed information on www.darwinfoundation.org/datazone/).

*Baiting experiments.* TFA was the only species collected at baits at El Chato and Bellavista (except for two occurrences of *Brachymyrmex heeri* (Forel, 1874) in El Chato and two occurrences of *Wasmannia auropunctata* (Roger, 1863) in Bellavista; both of which are introduced species (Herrera 2014)). At both sites, TFA was found in 100% of the baits stations, and its mean abundance score ± SD was 2.51 ± 0.86 in Bellavista and 2.63 ± 0.41 in El Chato. In the banana plantation, four species were recorded at the baits: TFA, *W. auropunctata, Odontomachus bauri* (Emery, 1892) and *Nylanderia* sp. (Table 3). *Nylanderia* sp. was the most common species at baits, with a high discovery rate (0.76) and the highest monopoly rate (0.16). It dominated the majority of baits during all baiting sessions but only rated third in abundance after TFA and *W. auropunctata.* Both species had low discovery abilities; however, TFA had medium monopoly abilities (0.12) and the highest abundance score (2.22 ± 0.81). TFA was the dominant species after 120 minutes on all bait types, replacing *Nylanderia* sp. Finally, *O. bauri,* a possible native species, is a more discrete species and never dominates or monopolizes baits.

TFA was found at all bait types, but more commonly on the peanut butter (mean ± SD of abundance score for all three sites on peanut butter, tuna and honey = 2.84 ± 0.11, 2.17 ± 0.81 and 1.93 ± 0.61, respectively). *Wasmannia auropunctata* and *Nylanderia* sp. were also found on all bait types with a respective preference for peanut butter and honey, whereas *O. bauri* was found on peanut and honey but not tuna.

*Daily activity cycle.* TFA was active during the entire day in both experiments, with a mean of almost 300 individuals passing on the foraging trail in five minutes on a dry day, 30 March (mean ± SD = 296.67 ± 58.36; min–max = 166–366), and 88 individuals on a rainy day, 24 March (88.17 ± 61.86; 24–221) (Fig. 3).

## Discussion

*Distribution of TFA.* The first records of TFA in the archipelago date back to 1891 in San Cristóbal Island and 1905 on Floreana Island; however, TFA probably arrived

Table 2. List of endemic or threatened species documented on localities with TFA. Island names are between brackets. BAL= Baltra, FER= Fernandina, FLO= Floreana, ISA= Isabela, SCZ= Santa Cruz, SCB= San Cristóbal.

| Species | Common name | Origin | IUCN Status | Locality |
|---|---|---|---|---|
| *Aegialomys bauri* (Waterhouse, 1839) | Santa Fé rice rat | Endemic to Santa Fé Island | Vulnerable | Santa Fé Island |
| *Zalophus wollebaeki* (Sivertsen, 1953) | Galápagos sea lion | Near endemic | Endangered | Concha de Perla (ISA,) Plazas Sur Islet, La Lobería (SCB) |
| *Amblyrhynchus cristatus* (Bell, 1825) | Marine iguana | Endemic | Vulnerable | Iguana Cove (ISA), La Lobería (SCB, El Garrapatero, Punta Nuñez (SCZ) |
| *Conolophus pallidus* (Heller, 1903) | Santa Fé land iguana | Endemic to Santa Fé Island | Vulnerable | Santa Fé Island |
| *Conolophus subcristatus* (Gray, 1831) | Land iguana | Endemic | Vulnerable | Iguana repatriation sites (BAL), Punta Mangle (FE), Plazas Sur Islet, Syemour Norte Islet |
| *Chelonoidis spp.* (Fitzgerald, 1835) | Land tortoise (several spp.) | Endemic | Not evaluated for the genus | Asilo de la Paz (FLO), Alcedo volcano, Cinco Cerros (ISA), El Chato, El Chato camino, La Caseta, La Torta (SCZ) |
| *Chelonia agassizii* (Baillie & Groombridge, 1996) | Galápagos green turtles | Subspecies only in Galapagos | Near threatened | Punta Cormorant (FLO), Tortuga Bay (SCZ) |
| *Anas bahamensis galapagensis* (Linnaeus, 1758) | White-cheeked pintail duck | Endemic | Not Evaluated | El Garrapatero, Las Grietas (SCZ) |
| *Arenaria interpres* (Linnaeus, 1758) | Ruddy turnsone | Native | Least Concern | Las Grietas (SCZ) |
| *Buteo galapagoensis* (Gould, 1837) | Galápagos hawk | Endemic | Vulnerable | Punta Mangle (FER) |
| *Creagrus furcatus* (Neboux, 1846) | Swallow-tailed gull | Near endemic | Least Concern | Seymour Norte Islet |
| *Fregata magnificens* (Matthews, 1914) | Frigate bird | Endemic | Not Evaluated | La Lobería (SCB), Seymour Norte |
| *Geospiza spp.* (Gould, 1837) | Galápagos finch (several spp.) | Endemic | Not evaluated for the genus | La Lobería, El Mango (SCB), El Chato, El Chato Camino, El Garrapatero, La Caseta (SCZ) |
| *Himantopus mexicanus* (Müller, 1776) | Black-necked stilt | Native | Least Concern | Las Grietas (SCZ) |
| *Laterallus spilonota* (Gould, 1814) | Galápagos rail | Endemic | Vulnerable | Cerro Crocker, Media Luna (SCZ) |
| *Leucophaeus fuliginosus* (Gould, 1841) | Lava gull | Endemic | Vulnerable | Las Grietas (SCZ) |

Table 2. Continued.

| Species | Common name | Origin | IUCN Status | Locality |
|---|---|---|---|---|
| *Mimus parvulus (*Gould, 1837) | Galápagos mockingbird | Endemic | Least Concern | El Garrapatero (SCZ) |
| *Mimus trifasciatus (*Gould, 1837) | Floreana mockingbird | Endemic | Critically endangered | Champion and Gardner Islets |
| *Numenius phaeopus* (Linnaeus, 1758) | Whimbrel | Native | Least Concern | Las Grietas (SCZ) |
| *Phalacrocorax harrisi* (Rothschild, 1898) | Flightless cormorant | Endemic | Vulnerable | Punta Mangle (FER) |
| *Phoenicopterus sp* (Linnaeus, 1758) | Flamingos | Native | Vulnerable | Punta Cormorant (FLO), El Garrapatero (SCZ) |
| *Pterodroma phaeopygia* (Salvin, 1876) | Galápagos petrel | Endemic | Critically endangered | Cerro Pajas 1 and 2 (FLO), Cerro Crocker, Media Luna (SCZ) |
| *Pyrocephalus rubinus* (Boddaert, 1783) | Vermillion flycatcher | Endemic | Not Evaluated | El Chato, El Chato camino, La Caseta, Los Gemelos (SCZ) |
| *Spheniscus mendiculus* (Sundevall, 1871) | Galápagos penguin | Endemic | Endangered | Punta Mangle (FER) |
| *Sula nebouxii* (Milne-Edwards, 1882) | Blue-footed boobie | Endemic | Least concern | Seymour Norte Islet |

Table 3. Dominance measures of species for the baiting experiment of the banana plantation, all baits types confounded (see Andersen 1992, Ward 2007). Species are sorted in decreasing order of occurrences.

| Site | Species | Occurrences at baits | Dominated baits | Mean abundance score ± SD | Monopoly | Discovery |
|---|---|---|---|---|---|---|
| Banana | *Nylanderia sp.* | 1.00 | 0.52 | 1.80 ± 0.39 | 0.16 | 0.76 |
| | *W. auropunctata* | 0.64 | 0.24 | 1.85 ± 0.20 | 0.04 | 0.20 |
| | *S. geminata* | 0.32 | 0.28 | 2.22 ± 0.81 | 0.12 | 0.20 |
| | *O. bauri* | 0.20 | 0.00 | 1.20 ± 0.36 | 0.00 | 0.08 |
| Bellavista | *S. geminata* | 1.00 | 0.39 | 2.51 ± 0.86 | 0.68 | 0.13 |
| *El Chato* | *S. geminata* | 1.00 | 0.15 | 2.62 ± 0.41 | 1.00 | 0.84 |

in the archipelago at an earlier date on whaling or pirate ships (Constant 2006, Jackson 1993). It is notable that expeditions conducted in the archipelago before 1965 did not find TFA on any other islands (Stitz 1932; Wheeler 1919, 1924, 1933). TFA was either present on these islands but remained undetected, or it might only have colonized them later. After a time lag between initial invasion and subsequent population explosion (Williamson 1996), the introduced ants might have discretely dispersed between islands, either by nuptial flights (Taber 2000) or by boat transportation (Herrera 2011). Another hypothesis is the invasional meltdown (i.e., introduction of one invasive species promoting the establishment or spread of other invasive species) (O'Dowd et al. 2003, Simberloff & Von Holle 1999). A newly introduced invasive species might have facilitated the invasion of TFA. Finally, the increase of TFA populations can also be a consequence of a global environmental modification (e.g., climate change) facilitating its dispersal and opening new habitats (Trueman & D'Ozouville 2010), or a combination of both factors.

The number of records of TFA has dramatically increased in the Galápagos Islands since the 1980's, and it is now documented from seven islands and 11 islets and in 135 sites, among which 66 are recorded here for the first time. TFA has been documented from sea level to an altitude of 989 m and in all types of habitats. We have shown that TFA is very common in unprotected or touristic areas, whereas negative records are often made in restricted areas. TFA is also common in open habitats, as are the majority of the disturbed sites and the islets. This concurs with TFA usually

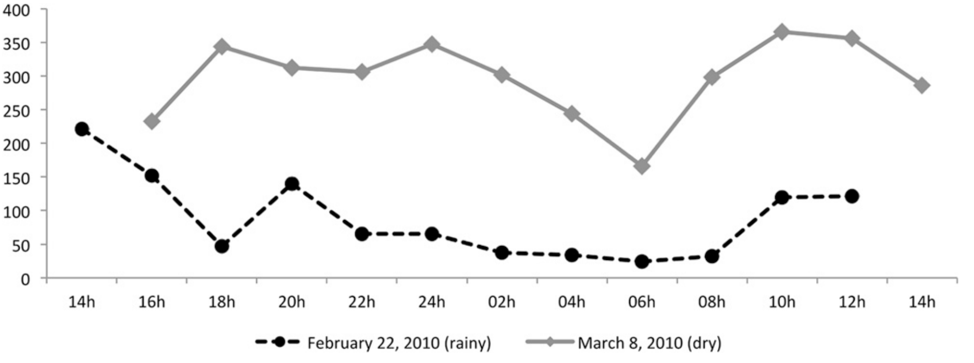


Figure 3. Daily activity cycle of TFA (in numbers of individuals passing on a foraging trail in 5 minutes) on a dry (8 March 2010) and on a rainy day (22 February 2010).

being more common in disturbed environments, as shown in Australia and Mexico (Hoffmann & O'Conner 2004, Risch & Carroll 1982) and in open habitats (Taber 2000). Most of the sites where TFA has not been recorded are pristine areas: the remote islands of Marchena, Pinta, Genovesa and Española; Pinzon Islet; Punta Espinosa on Fernandina Island; Ballena Bay, Las Palmas and Laguna Andrea on Santa Cruz Island; and Punta Basa and Puerto Grande on San Cristóbal.

TFA has been previously recorded from six localities (Punta Mangle on Fernandina Islands, Asilo de la Paz on Floreana, Plazas Sur Islet, Playa de los Alemanes and Tortuga Bay on Santa Cruz Island and Santa Fé Island), but it has not been found in more recent surveys, thus suggesting a local extinction due to eradication programs. On Santa Fé Island, an eradication program against *W. auropunctata* was conducted in 1987 (Abbedrabo 1994) and probably eradicated TFA as well. Another eradication program was conducted in Playa Negra on Isabela Island in 2004 (Causton et al. 2012). Official eradication programs did not take place in the remaining four sites, but sometimes the GNP rangers use toxic baits (Amdro® or Siege-Pro®) in infested areas when they think it is necessary (GNP rangers, personal communication). In certain cases, such toxic baits might be sufficient to eradicate TFA from a small area. This might have been the case for Punta Mangle on the pristine Island of Fernandina, Plazas Sur Islet, Asilo de la Paz on Floreana (endemic tortoise reserve) and Tortuga Bay on Santa Cruz (green turtle nesting site). Local eradication might also explain why TFA was never found in two sites on Isabela, Tagus Cove (a very touristic area) and Canal Bolivar (a base for GNP Rangers). Private owners also use baits and other toxic products, as probably happened on Santa Cruz on Playa de los Alemanes, which is located near a luxury hotel in Puerto Ayora or in the black gravel mine. It is to be noted that S. Peck conducted intensive surveys in the 1980s (Causton, personal communication). Part of this material is still to be studied, which may provide extra records of TFA, among others.

*Potential impact on wildlife.* TFA is competitive towards other ant species, can displace native ant communities (Von Aesch & Cherix 2005, Wauters et al. unpublished data), and is often considered as an "extirpator", i.e., a species that is very good at recruiting large numbers of ants to aggressively compete against other ant species (Perfecto 1991, Wilson 1971). Our study showed that TFA is active 24 hours a day in both dry and rainy weather and has a good monopoly rate and high abundance scores in the baiting experiments. TFA was also the dominant species on Floreana Island, both in disturbed and natural areas (Von Aesch & Cherix 2005). Moreover, the density of TFA mounds can attain four to 20 nests/ha and up to 6000 nests/ha in India (Wauters, personal observations, McInnes & Tschinkel 1995, Veeresh 1990), and workers are prompt to use their painful and venomous sting against vertebrate and invertebrate intruders (Wetterer 2010, Wheeler 1910). In our study, the only two species occurring with TFA are *Nylanderia* sp. and *W. auropunctata.* The first species quickly discovered and dominated baits, but it was progressively displaced by TFA, as was observed in Philippines by Way et al. (1998). The other species, *W. auropunctata*, causes major changes in Galápagos invertebrate populations (Clark et al. 1982, Lubin 1984). TFA is recognized as the only ant species capable of competing with *W. auropunctata* (Causton et al. 2006, Lubin 1984). We have observed that sites invaded by *W. auropunctata* in the 1980s are now infested by TFA, suggesting a progressive replacement of one invasive species by the other (Causton et al. 2006, Lubin 1984, Wauters unpublished data, Herrera personal observation).

TFA belongs to a small group of invertebrate species that are having a significant impact on Galápagos ecosystems (Causton et al. 2006). TFA is known to feed on endemic butterflies eggs (Roque-Albelo 2008) and to attack juvenile reptiles and birds, such as giant tortoises and Galápagos petrels (Causton et al. 2006, Williams & Whelan 1991, Williams & Wilson 1989, Galápagos National Park, personal communication). Our exhaustive survey of the presence of TFA in the Galápagos archipelago shows that TFA was or is currently present in the immediate proximity of 25 endemic or threatened taxa. All of these species are potentially threatened by TFA in the 28 sites where TFA has also been recorded. However, the land tortoises on Isabela (Cinco Cerros, Alcedo) and Santa Cruz (El Chato, La Caseta, La Torta) and the Galápagos petrels on Floreana (Cerro Pajas) and Santa Cruz (Cerro Crocker, Media Luna) are particularly at risk since there have been direct observations of attacks. TFA has also been reported attacking Galápagos penguins (H. Vargas personal communication), being present inside the nests of finches in El Garrapaterro, Santa Cruz Island (S. Knutie, personal communication), and would probably threaten the endangered Mangrove Finch *Camarhynchus heliobates* (Snodgrass & Heller 1901) if TFA were to (re)colonize Playa Negra on Isabela Island (H. Herrera, personal communication).

*Prevention and control.* The creation of the CDRS in 1964 allowed a more accurate picture of the species in the archipelago, and from the 1980s we effectively observed an increase in TFA surveys, and subsequently of TFA records, which also coincides with an increase in resident and tourist population (Watkins & Cruz 2007). The likelihood of biological invasions is often associated with tourism on islands (Mwebaze et al. 2010): (i) anthropogenic activities lead to habitat degradation that may favor the installation of the invasive species; and (ii) the inadvertent transportation of alien species by car, boat and plane traffic ensures its dispersal and/or new introduction (Causton 2008, Causton et al. 2006). Peck et al. (1998) also reported that insect introductions are increasing exponentially in the archipelago and are directly related to the growing human population. Furthermore, new introductions or reintroductions of species occur despite the quarantine control system set up in 2000 by the Biosecurity Agency for Galápagos (Causton & Sevilla 2008, Herrera 2011 & Herrera et al. 2014). After seven years of application, this system was evaluated as technically ineffective and inefficient (Zapata Erazo 2007) because of low numbers of inspectors, inadequate training and equipment, low knowledge transfer between inspectors, and lack of autonomy of the system (Bigue et al. 2012). In 2012, the Agency for the Regulation and Monitoring of the Galápagos Biosecurity and Quarantine (ABG) was created in order to execute more efficiently actions to control and eradicate invasive species in urban and rural areas. Considerable efforts have been made, including citizen outreach events and checkpoints for control of luggage and quarantine at Baltra airport (www.bioseguridadgalapagos.gob.ec).

Since 1987, GNP has led eradication programs of invasive ants using hydramethylnon (Amdro® or Siege-Pro®). Specific programs against TFA have been conducted on Marielas islets (beginning in 2000, actual state undetermined), Albany and Bainbridge (2004, undetermined), Mao (2004, unsuccessful, reintroduction of TFA from Santiago), Champion (2006, unsuccessful, reintroduction from Floreana), Baltra (2009, localized in iguanas nesting sites), Isabela (undetermined date, localized on land tortoise nesting sites) and Seymour Norte (2011, undetermined). Two other programs mentioned above were successful on Santa Fé and Isabela. TFA is particularly difficult to eradicate because it is the only long-established invasive ant on the archipelago that also disperses by nuptial flights (Taber 2000).

*Conclusion and recommendations.* Although the number of records increased since the last review in 2009, no new island was colonized by TFA (except for small islets that had not been surveyed previously). However, as TFA is a good disperser, we recommend a close monitoring of the uninvaded pristine islands, especially the ones that have not been surveyed yet: Pinta, Genovesa, Wolf and Darwin. These islands are especially vulnerable to introduced species and the consequences of TFA introduction could be disastrous. Furthermore, we suggest a monitoring of the distribution of TFA on the already invaded high priority areas such as Santiago, Fernandina, Alcedo and Wolf volcanoes, Playa Tortuga Negra on Isabela, and Champión Islet. These areas have been prioritized for invasive ant management following the values and singularities of ecosystem and species present (Causton et al. 2012). The material collected in the 1980s by S. Peck and now deposited at the University of California, Riverside, the Los Angeles County Museum (LACMA) and the Harvard Museum of Comparative Zoology (MCZ) should be studied, as it might also provide valuable information concerning the distribution of TFA. As the use of toxic baits can be efficient at very local scale, it might be a short-term solution to protect wildlife from fire ants. However, TFA reintroductions from other islands are common, therefore there is a need for long-term management tools. Hopefully the improvement of the ABG system will help preventing new introductions and limiting within- and inter-island dispersal of established invasive species. Working on the prevention and on early stages of colonization is essential to preserve the diversity of the Galápagos archipelago.

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