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WORLDWIDE SPREAD OF THE YELLOW-FOOTED ANT, *NYLANDERIA FLAVIPES* (HYMENOPTERA: FORMICIDAE)

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ABSTRACT

Nylanderia flavipes (formerly *Paratrechina flavipes*), an Asian species, was first found outside its native range in a Philadelphia park in 1939. To evaluate the geographic spread of *N. flavipes*, I compiled specimen records from >250 sites, documenting its earliest known records for 27 geographic areas (countries and U.S. states), including 7 U.S. states for which I found no previously published reports: California, Connecticut, Delaware, Maryland, New Jersey, Rhode Island, and Virginia. Almost all records of *N. flavipes* from its native range in East Asia come from sites 30.0°N-44.0°N, with a few records from lower latitudes. In the eastern U.S., *N. flavipes* records come from a somewhat narrower latitudinal range, 32.5°N-42.4°N (South Carolina to Massachusetts). In areas of the U.S. where it invades, *N. flavipes* seems to blend into the community like a native species. The only noted impact appears to be the disappearance of *Nylanderia faisonensis*, an ecologically similar species, with similar nesting sites, colony size, and appearance. In the eastern U.S. north of Washington DC, *N. flavipes* appears to have largely replaced *N. faisonensis*. Further south, *N. faisonensis* continues to dominate.

Key Words: biogeography, biological invasion, exotic species, invasive species

RESUMEN

Nylanderia flavipes (llamada *Paratrechina flavipes* anteriormente), una especie asiática, se encontró por primera vez fuera de su área de distribución natural en un parque de Filadelfia en 1939. Para evaluar la distribución geográfica de *N. flavipes*, fue compilado registros de especímenes de >250 sitios, la documentación de sus primeros registros conocidos para 27 áreas geográficas (países y estados de los EE.UU.), incluyendo 7 de los estados de EE.UU. para los cuales tenían informes publicados anteriormente: California, Connecticut, Delaware, Maryland, Nueva Jersey, Rhode Island y Virginia. Casi todos los registros de *N. flavipes* de su área de distribución en el este de Asia proceden de sitios de 30.0°N-44.0°N con unos pocos registros de las latitudes más bajas. En la región este de los EE.UU., registros de *N. flavipes* provienen de una gama algo más estrecho latitudinal de 32.5°N-42.4°N (de Carolina del Sur a Massachusetts). En las zonas de los EE.UU., donde esta especie invade, *N. flavipes* parece integrarse en la comunidad como una especie nativa. El único efecto observado parece ser la desaparición de *Nylanderia faisonensis*, una especie ecológicamente similar, con similares sitios de desarrollo, tamaño de la colonia, y apariencia. En la región este de EE.UU, norte de Washington DC, *N. flavipes* parece haber sustituido en gran medida a *N. faisonensis*. Más al sur, *N. faisonensis* continúa de dominar.

Nylanderia flavipes (formerly *Paratrechina flavipes*), an Asian species, was first found outside its native range in a Philadelphia park in 1939, but it was not recognized until several decades later. Trager (1984) was the first to note the arrival of *N. flavipes* in the U.S. Trager (1984) examined specimens of *N. flavipes* from Philadelphia, Pittsburgh, and Long Island, and at first thought they represented a northern race of the native *Nylanderia faisonensis*. Stefan Cover (personal communication) observed that in the U.S., *N. flavipes* was common under trees in urban parks and gardens. Pecarevic et al. (2010) found *N. flavipes* on 23 of 44 street medians surveyed in New York City, noting that *N. flavipes* "was most abundant at the medians that were more forest-like, increasing when a larger proportion of the median was tree covered."

Trager (1984) noted that the native *N. faisonensis* "is abundant in every state east of the Mississippi River and south of the Mason-Dixon line . . . and extends north of the Mason-Dixon line near the Atlantic seaboard to southern New Jersey." Trager (1984) speculated: "It may be that *faisonensis* has prevented the spread of *flavipes* further south, where the latter could very likely thrive, as it occurs in warm temperate forests in Japan and China." In fact, populations of *N. flavipes* in the U.S. have continued to spread. Ivanov & Milligan (2008) noted records of *N. flavipes* as far west as Cleveland, Ohio and south to Washington DC. Davis (2009) reported *N. flavipes* from South Carolina. In addition, there have been reports of *N. flavipes* from other parts of the world, most notably from the Middle East. Here, I examine the worldwide distribution of *N. flavipes*.

Taxonomy and Identification

Smith (1874) described *Tapinoma flavipes* (= *N. flavipes*) from Japan. Trager (1984) placed *N. flavipes* in the "Parvula complex" along with 5 other species: *Nylanderia parvula*, *Nylanderia faisonenensis*, *Nylanderia concinna*, *Nylanderia wojciki*, and *Nylanderia austroccidua*. Trager (1984) noted the resemblance in color of *N. flavipes* to *Nylanderia vividula*, a tramp species spread worldwide by human commerce, which Creighton (1950) had considered a senior synonym of *N. faisonenensis*. Trager (1984) wrote that *N. vividula* "is characteristic of open, usually rather disturbed habitats including beaches, parks and other landscaped areas, crop fields, fallow fields, vacant lots, parking lots, etc."

The Latin name "flavipes" means "yellow-footed." *Nylanderia flavipes* can be distinguished from *N. faisonenensis* by its shorter legs and antennal scapes, the yellow color of the legs and mesosoma, and by the broader, rounder-sided head with small, but visible ocelli (Trager 1984). *Nylanderia faisonenensis* is generally a uniform dark brown with lighter meso- and metacoxae, and with at most only a slightly lighter mesosoma. *Nylanderia flavipes* can be distinguished from *N. vividula* by a more generally yellowish hue of the mesosoma, sometimes the anterior gaster, and especially of the legs. *Nylanderia flavipes* also has more dense cephalic pubescence, visible ocelli, and relatively smaller compound eyes. *Nylanderia vividula* tends to be uniform dark brown or with the mesosoma only a little lighter than head and gaster, has sparse cephalic pubescence, especially between the clypeal margin and vertex, lacks visible ocelli, and typically has a subquadrate, nearly straight-sided head (J. Trager, personal communication).

MATERIALS AND METHODS

Using published and unpublished records, I documented the worldwide range of *Nylanderia flavipes*, and obtained unpublished site records from museum specimens in the collections of the Museum of Comparative Zoology (MCZ; identified by S. Cover) and the Smithsonian Institution (SI; identified by J. Trager). In addition, I used on-line databases with collection information on specimens by the Japanese Ant Image Database (ant.edb.miyakyo-u.ac.jp), Antweb (www.antweb.org), and the Global Biodiversity Information Facility (www.gbif.org). James Trager identified photographs of *N. flavipes* posted on bugguide.net.

I obtained geographic coordinates for collection sites from published references, specimen labels, maps, or geography web sites (e.g., earth.google.com, www.tageo.com, and www.fallingrain.com). If a site record listed a

geographic region rather than a "point locale," and I had no other record for this region, I used the coordinates of the largest town within the region or, in the case of small islands and natural areas, the center of the region. I did not map records of *N. flavipes* found in newly imported goods or intercepted in transit by quarantine inspectors, e.g., Forel's (1900) record of *N. flavipes* on plants imported into Germany from Japan. Published records usually included collection dates. In a number of cases, publications did not include the collection dates for specimens, but I was able to determine the approximate date based on information on the collector's travel dates or limit the date by the collector's date of death.

In an effort to fill in gaps in the distribution of *N. flavipes* in the northeastern U.S., on 15-22 Jun 2010, I collected ants at 21 landscaped sites (# in parentheses) in Rhode Island (4), Connecticut (10), Delaware (1), Maryland (1), Washington DC (2), Virginia (2), and North Carolina (1).

RESULTS

I compiled *Nylanderia flavipes* specimen records from >250 sites worldwide (Fig. 1). This included specimens I collected at 5 of 21 sites in the northeastern U.S. (geo-coordinates in parentheses): Rhode Island, Providence, grass under trees by capitol building (41.830, -71.413), 15 Jun 2010; Connecticut, Stamford, hotel flower garden (41.054, -73.533), 16 Jun 2010; Connecticut, Bridgeport, cemetery (41.196, -73.175), 17 Jun 2010; Connecticut, Greenwich, apartment flower garden (41.033, -73.620), 18 Jun 2010; Delaware, Wilmington, hotel flower garden (39.742, -75.542), 18 Jun 2010. At all 5 sites, *N. flavipes* workers were fairly inconspicuous, though in the Greenwich garden, they appeared to be the most common ant species present.

Around 1990, James Trager (personal communication) found a lone queen of *N. flavipes* in leaf litter from the Japanese garden section of the Huntington Botanical Garden in San Marino, California, "perhaps recently arrived there with plant material."

I documented the earliest known *N. flavipes* records for 27 geographic areas (countries and U.S. states), including 7 U.S. states for which I found no previously published records: California, Connecticut, Delaware, Maryland, New Jersey, Rhode Island, and Virginia (Table 1).

Most lowland records of *N. flavipes* from East Asia come from latitudes between 30°N and 44°N, spanning from the Ryukyu Islands of southern Japan to the Kuril Islands of the Russian Far East. In addition, there are a number of records from mountains further south in the Ryukyu Islands and Mainland China, e.g., Mt. Nishime-dake (26.8°N; Yamauchi & Ogata 1995) and Mt.

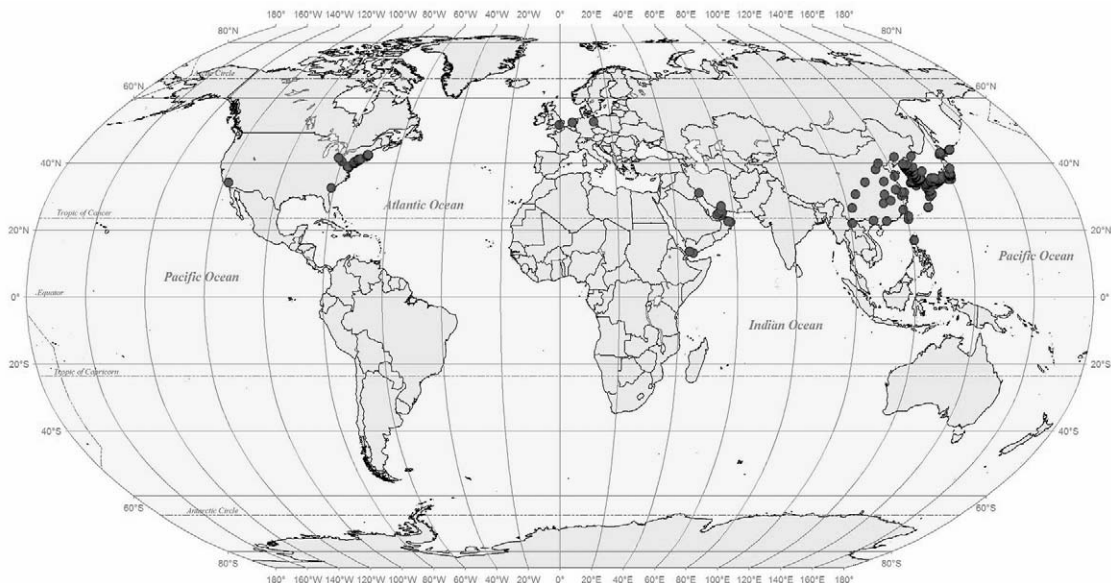


Fig. 1. Worldwide distribution records of *Nylanderia flavipes*.

Yonaha-dake (26.7°N; Yamauchi & Ogata 1995) and the mountains of southwestern Sichuan, China (~26.6°N; Zhang & Zheng 2002).

I found a few records of *N. flavipes* from four areas in East Asia at latitudes below 26°N. Trager (1984) examined *N. flavipes* specimens from Taiwan (~25°N), but gave no other locality information. Tropical records from China, from Heshan, Guangdong (22.7°N; Wei et al. 2004) and Xishuangbanna, Yunnan (22.0°N; Xu 1999) may or may not be misidentification.

The earliest records of *N. flavipes* in the U.S. come from Philadelphia, Pennsylvania (1939; Table 1), followed by Pittsburgh, Pennsylvania (1953; G. E. Wallace; MCZ & SI), Scarsdale, New York (1975; Table 1), and Forest Park, New York (1977; S. P. Cover; MCZ). More recent records of *N. flavipes* indicate an essentially continuous range along the East Coast of the U.S. from Washington DC and Northern Virginia (38.9°N) in the south to Malden, Massachusetts (42.4°N) in the north, with an isolated record from Jasper County, South Carolina (32.5°N). To the west, Ivanov & Milligan (2008) reported that *N. flavipes* "has well established populations in the greater Cleveland area of northeastern Ohio."

Finally, there have been several indoor records of *N. flavipes* from Northern Europe (Table 1; Fig. 1; Donisthorpe 1908; Eichler 1952; Boer & Vierbergen 2008).

Misidentified and Questionable Records

Some published records of *N. flavipes* have been confirmed to be misidentifications, including

a record of *N. flavipes* from Spain (Espadaler & Collingwood 2000) later identified as *Nylanderia vividula* (Gomez & Espadaler 2006) and a record from Niue (Collingwood & van Harten 2001a) later determined to be *Nylanderia vaga* (Wetterer 2006). Conversely, Radchenko (2005) concluded that Collingwood's (1976, 1981) records of *Nylanderia sakurae* from North Korea were actually *N. flavipes*.

Tropical records of *N. flavipes* from upland and lowland rice fields in the Philippines (Banaue at 16.9°N and other unreported localities; Way et al. 1998) seem very likely to be misidentifications, due to the low latitude and the open habitats.

There are several records of *N. flavipes* from parts of the Middle East: Iran, Oman, the United Arab Emirates, and Yemen (Collingwood & Agosti 1996; Collingwood et al. 1997; Alipanah & Dezhakam 2000 in Paknia et al. 2008; Collingwood & van Harten 2001b; Dezhakam & Soleyman-Nejadian 2002). These specimens, however, should be re-examined, especially since they come from arid areas with climates much different than those of other parts of the native and exotic range of *N. flavipes*. I agree with Trager (in Ivanov & Milligan 2008), who speculated that Middle East records of *N. flavipes* might actually be misidentified *N. vividula*.

DISCUSSION

In East Asia, *Nylanderia flavipes* ranges throughout Japan, Korea, and the Kuril Islands, as well as Taiwan and parts of China. Almost all records of *N. flavipes* from its native range in tem-

TABLE 1. EARLIEST KNOWN RECORDS FOR *NYLANDERIA FLAVIPES*.

	Earliest record
Asia	
Japan	≤1873 (Smith 1874)
China	≤1921 (Wheeler 1921)
South Korea	≤1928 (Wheeler 1928)
Kuril Islands, Russia	1962 (Kupianskaya et al. 2000)
North Korea	1970-71 (Collingwood 1976)
Taiwan	≤1984 (Trager 1984)
Philippines*	≤1996 (Way et al. 1998)
USA	
Pennsylvania	1939 (W. L. Brown, MCZ): Philadelphia
New York	1975 (C. Harrison, MCZ): Scarsdale
+Maryland	1987 (S. P. Cover, MCZ): Little Falls Branch Park
+California	~1990 (J. Trager, personal communication): San Marino
Washington DC	1990 (Ivanov & Milligan 2008)
+Virginia	1992 (S. P. Cover, MCZ): Rosslyn
Massachusetts	1992 (S. P. Cover, MCZ): Cambridge
+New Jersey	1994 (S. Beshers, MCZ): Tenafly
South Carolina	≤2000 (Davis 2009)
Ohio	2005 (Ivanov & Milligan 2008)
+Rhode Island	2010 (J. K. Wetterer, MCZ): Providence
+Connecticut	2010 (J. K. Wetterer, MCZ): Stamford
+Delaware	2010 (J. K. Wetterer, MCZ): Wilmington
Europe	
England	1907 (Donisthorpe 1908)
Germany	≤1952 (Eichler 1952)
Netherlands	1980 (Boer & Vierbergen 2008)
Middle East	
Oman*	1986 (Collingwood & Agosti 1996)
United Arab Emirates*	1991 (Collingwood & Agosti 1996)
Yemen*	1998 (Collingwood & van Harten 2001b)
Iran*	≤2000 (Alipanah & Dezhakam 2000 in Paknia et al. 2008)

Unpublished records include collector, museum source, and site.

MCZ = Museum of Comparative Zoology.

* = questionable record.

+ = no previously published records.

perate East Asia come from sites 30.0-44.0°N, with a few records from lower latitudes (Fig. 1). In the northeastern U.S., *N. flavipes* records come from a somewhat narrower latitudinal range of 32.5-42.4°N, i.e., South Carolina to Massachusetts.

Within its native range, *N. flavipes* can be quite common. For example, Kwon et al. (2005) found that *N. flavipes* was by far the most common ant collected in Korean forests. In areas of the U.S. where it invades, *N. flavipes* seems to blend inconspicuously into the community like a native species (S. Cover, personal communication). Its only notable impact appears to be the disappearance of *Nylanderia faisonensis*, an ecologically very similar species, with similar nesting sites, similar colony size, and even similar in

appearance, except for color. On the East Coast of the U.S. north of Washington DC, *N. flavipes* appears to have largely replaced *N. faisonensis* (S. Cover, personal communication), though observations of this replacement remain anecdotal. For example, King & Green (1993) noted that in Philadelphia, *N. flavipes* occurred "in shady habitats," whereas *N. faisonensis* occurred "in shady but disturbed habitats," amending this with "displaced by *flavipes*?" If this pattern is true, it is the opposite of the general rule that exotic ants displace natives in disturbed areas, but natives hold sway in intact native habitats (e.g., see Wetterer & Vargo 2003). It would be valuable to document conclusively whether *N. faisonensis* populations disappear in areas of *N. flavipes* population expansion.

It is a testament to its inconspicuousness that *N. flavipes*, which is apparently widespread in the eastern U.S., is only now being reported for the first time from 6 of these states. It is likely that *N. flavipes* has already spread unnoticed through an even broader area, particularly to the south and west, e.g., North Carolina, West Virginia, and Indiana. If *N. flavipes* populations in the U.S. spread south along the East Coast until 30°N (the southern limit of their main populations in the Ryukyu Islands), this would take them all the way to northern Florida. On the other hand, Trager (1984) wrote that *N. flavipes* collected in Taiwan (~25°N) more closely resemble the U.S. specimens and concluded that this "may indicate that the American population originated in Taiwan or adjacent mainland." Genetic analyses should help determine the geographic origin of *N. flavipes* populations in the U.S., and offer insight concerning future spread.

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