Global and Temporal Spread of a Taxonomically Challenging Invasive ant, Brachyponera chinensis (Hymenoptera: Formicidae)

Authors: Guénard, Benoit, Wetterer, James K., and MacGown, Joe A.

Source: Florida Entomologist, 101(4) : 649-656

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/024.101.0402

Global and temporal spread of a taxonomically challenging invasive ant, *Brachyponera chinensis* (Hymenoptera: Formicidae)

Benoit Guénard[1,*], *James K. Wetterer*[2], *and Joe A. MacGown*[3]

Abstract

The Asian needle ant, *Brachyponera chinensis* (Emery) (Hymenoptera: Formicidae), is an East Asian species currently spreading through the eastern US. Although not aggressive, *B. chinensis* has a painful sting that can induce a severe allergic reaction in humans and disrupt native ecological communities. To document the global distribution of *B. chinensis* and evaluate its potential for further spread, we compiled specimen records from over 780 sites in its native and introduced ranges. Unfortunately, in its native range, *B. chinensis* often has been confused with morphologically similar species, resulting in some unreliable published distribution records. Therefore, we designated confirmed identification records as "*B. chinensis* s.s." (sensu stricto). Our report chronicles the earliest known records of *B. chinensis* for 50 geographic areas in the Old World (36 countries and island groups) and New World (17 states in the US) and the recent expansion of *B. chinensis* into the eastern coast of the Black Sea along with new state distribution records from the US. We also provide new information on the phenology of *B. chinensis*. This ant species represents a potentially serious public health threat that warrants more epidemiological study.

Key Words: invasive species; invasion history; *Euponera solitaria*; *Pachycondyla chinensis*; Ponerinae

Resumen

La hormiga aguja asiática, *Brachyponera chinensis* (Emery) (Hymenoptera: Formicidae), es una especie de Asia oriental que se está extendiendo actualmente por el este de los Estados Unidos. Aunque no es agresiva, *B. chinensis* tiene una picadura dolorosa que puede inducir una reacción alérgica grave en los seres humanos e interrumpir las comunidades ecológicas nativas. Para documentar la distribución mundial de *B. chinensis* y evaluar su potencial para una mayor dispersión, compilamos registros de especímenes publicados y no publicados de > 780 sitios en sus rangos nativos e introducidos. Desafortunadamente, en su rango nativo, *B. chinensis* a menudo se ha confundido con especies morfológicamente similares que dan como resultado algunos registros de distribución publicados poco confiables. Por lo tanto, designamos los registros de identificación confirmados como "*B. chinensis* s.e." (sensu stricto). Nuestro informe se documenta los primeros registros conocidos de *B. chinensis* en 50 áreas geográficas del Viejo Antiguo (36 países y grupos de islas) y del Nuevo Mundo (17 estados de EE. UU.). También se proporciona documentación sobre la reciente expansión de esta especie de hormiga en la costa oriental del Mar Negro junto con los nuevos registros de distribución estatal de varios de los estados americanos. También proporcionamos nueva información sobre la fenología de *B. chinensis* y su impacto en las poblaciones humanas. Esta especie de hormiga representa una seria amenaza que debe considerarse como un potencial problema de salud pública que merece estudio epidemiológico.

Palabras Clave: especies invasoras; historia de invasión; *Euponera solitaria*; *Pachycondyla chinensis*; Ponerinae

Many invasive ant species cause major economic losses globally (Bradshaw et al. 2016) and negatively impact ecosystem functions and the associated native flora and fauna (Holway et al. 2002). The biology and distribution of some species, such as the red imported fire ant (*Solenopsis invicta* Buren), Argentine ant (*Linepithema humile* [Mayr]), and little fire ant (*Wasmannia auropunctata* [Roger]) (all Hymenoptera: Formicidae) have been extensively studied for several decades (Holway et al. 2002). However, other ant invaders have been recognized only recently, and key aspects of the ecology and spread of these species remain unresolved.

The Asian needle ant, *Brachyponera chinensis* (Emery) (Formicidae: Brachyponera) (formerly *Pachycondyla chinensis* Emery) (Hymenoptera: Formicidae), is an East Asian ponerine (Ponerinae) currently spreading through the eastern US. Although not aggressive, this species has a painful sting that can cause severe allergic reactions in humans (Smith 1979; Green 1992; Xu 1994; Cho et al. 2002; Fukuzawa et al. 2002; Leath et al. 2006; Nelder et al. 2006; Zungoli et al. 2006). *Brachyponera chinensis* is widespread in East Asia and can be quite common in some regions. For instance, Brown (1958) wrote that in China, *B. chinensis* "is seen everywhere on the rice paddy dikes and in the farm compounds, foraging in the open on tree trunks and on the ground in broad daylight." Smith (1934) first reported *B. chinensis* (as *Euponera solitaria* Smith) in the US, from sites in Georgia, North Carolina, and Virginia. More recently, several studies in North and South Carolina

[1]School of Biological Sciences, Kadoorie Biological Sciences Building, the University of Hong Kong, Pokfulam Road, Hong Kong, SAR, People's Republic of China; E-mail: zeroben@gmail.com (B. G.)
[2]Wilkes Honors College, Florida Atlantic University, 5353 Parkside Drive, Jupiter, Florida 33458, USA; E-mail: wetterer@fau.edu (J. K. W.)
[3]Mississippi Entomological Museum, 100 Old Hwy 12, Mississippi State University, Box 9775, Mississippi State, Mississippi 39762-9775, USA; E-mail: jmacgown@entomology.msstate.edu (J. A. M.)
*Corresponding author; E-mail: zeroben@gmail.com
Supplementary material in Florida Entomologist 101(4) (Dec 2018) is online at http://purl.fcla.edu/fcla/entomologist/browse

documented the largely overlooked threat that this ant poses (Nelder et al. 2006; Zungoli et al. 2006; Guénard & Dunn 2010). In the eastern US, *B. chinensis* has had a detrimental impact on native ants and other insects as well as on ant-seed dispersal mechanisms (Guénard & Dunn 2010; Rodriguez-Cabal et al. 2012; Warren et al. 2015; Suehiro et al. 2017; B. G. unpublished data). In contrast to most other invasive ants in the southeastern US, which are mostly located in disturbed habitats, *B. chinensis* commonly occurs in undisturbed forested habitats (Guénard & Dunn 2010; Warren et al. 2015; Suehiro et al. 2017). However, *B. chinensis* also has been collected in urban habitats with little vegetative cover (Menke et al. 2011; Guénard et al. 2014).

Unfortunately, identification of *B. chinensis* in its native range has been difficult due to the presence of other morphologically similar species, such as *B. luteipes* (Mayr), *B. nigrita* (Emery), and *B. obscurans* (Walker). Indeed, Brown (1958) recognized the taxonomic uncertainty of the *B. chinensis* complex, which he considered "taxonomically confused." *Brachyponera chinensis* from Shanghai, China, was described by Emery (1895) as *Ponera nigrita chinensis*, but Smith (1874) had previously described the species collected from Japan as *Ponera solitaria*. The name *solitaria* was unavailable because it was already occupied by a senior homonym, *Ponera solitaria* Smith, 1860 (= *Pachycondyla solitaria*), described from Bacan, Indonesia. Brown (1958) thought that *B. chinensis* might be a junior synonym of *Brachyponera luteipes*, and Taylor (1961) and Wilson and Taylor (1967) listed Brown's (1958) record from New Zealand as *B. luteipes*. However, Yashiro et al. (2010) confirmed that *B. chinensis*, *B. luteipes*, and *B. nigrita* (Emery) were 3 distinct species, based on consistent morphological and DNA sequence differences. For example, *B. chinensis* is larger than *B. luteipes*, but smaller than *B. nigrita* (Yamane 2007). Through numerous revisions, different authors have placed *B. chinensis* in 4 different genera: *Ponera*, *Euponera*, *Brachyponera*, and *Pachycondyla*. Most recently, Schmidt and Shattuck (2014) removed *B. chinensis* from *Pachycondyla*, placing it in the newly revived genus *Brachyponera*. In addition, a new Japanese species that was syntopic with *B. chinensis*, *Brachyponera nakasujii*, was recently described and was distinguished from *B. chinensis* by genetic and morphological analyses (Yashiro et al. 2010). Thus, the identity of ants from earlier records of *B. chinensis* from Asia should be viewed with caution. For example, Yashiro et al. (2010) concluded that the "*B. chinensis*" ants reported by Gotoh and Ito (2008) were most likely *B. nakasujii*. For the purposes of this study, we referred to confirmed *B. chinensis* records as "*B. chinensis* s.s." (sensu stricto), which include our own verified records of *B. chinensis*, those of Yashiro et al. (2010), the type specimen from Shanghai, China (Emery 1895), and recent records where the authors explicitly distinguished *B. chinensis* from *B. nakasujii* (e.g., Harada et al. 2012, 2014; Fukumoto & Yamane 2015). All North American records were *B. chinensis* s.s. (Yashiro et al. 2010).

Here, we analyze and synthesize the current known distribution of *B. chinensis* in its native and introduced ranges, considering the taxonomic uncertainty and the timing of invasion in North America. Based on these results, we discuss the invasion potential of this ant. We also present some elements of its reproductive biology and related data addressing the potential threat that this species represents for humans and biodiversity.

Materials and Methods

DATA COLLECTION

Using published and unpublished records, we documented the worldwide range of *B. chinensis*. We obtained unpublished site records from specimens in the collections of the Smithsonian Institution National Museum of Natural History, the Museum of Comparative Zoology, the Mississippi Entomological Museum, the North Carolina State University Insect Collection, personal collections (in native and introduced ranges) and communications (particularly from people who suffered stings and contacted the lead author, B.G.). In addition, collection information on *B. chinensis* distribution was gathered through the use of the online database (Antweb version 7.10.4; www.antweb.org) and through literature review.

Geographic coordinates for collection sites came from published references, specimen labels, maps, or geography websites (e.g., www.google.com/earth). However, many site names of older references and specimens, particularly in Asia, were obsolete or now spelled differently. If a site record listed a geographic region rather than a "point locale," and no other record existed for this region, we 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. Records of *B. chinensis* found in newly imported goods or intercepted in transit by quarantine inspectors were excluded. For example, Forel (1900) reported *B. chinensis* (as *P. solitaria*) arriving in Hamburg, Germany, with plants shipped from Japan, and Wilson and Taylor (1967) noted that *B. chinensis* (as *B. solitaria*) was intercepted in quarantine in Honolulu, Hawaii.

REPRODUCTIVE PRODUCTION PERIOD

Nests were collected opportunistically from dead wood from 2007 to 2011 in North Carolina to estimate the sociometry of *B. chinensis* colonies. The presence of alate females and males, as well as brood (eggs, larvae, pupae), during nest collection was recorded to provide bionomic information on the reproductive phenology of *B. chinensis* colonies, with further data compiled from records found in literature and websites (www.Antweb.org, BugGuide.net) for confirmation of the periods retrieved.

INFORMATIONAL WEBPAGE ON *PACHYCONDYLA CHINENSIS*

In 2009, the lead author created a webpage (http://www4.ncsu.edu/~bsguenar/Pachycondyla%20chinensis%20page.html [inactive]) to provide information on Asian needle ant biology and how to distinguish them from other common ants. People who viewed this webpage sent the lead author emails detailing their experiences with this ant. Those email exchanges, obtained from Jul 2010 to Mar 2017, were archived and the results were presented anonymously. Everyone who contacted the lead author voluntarily initiated the communication after reading about the research conducted on *B. chinensis*. All records of *B. chinensis* were confirmed by seeing photographed specimens or actual samples sent by mail.

Results

GEOGRAPHIC DISTRIBUTION

We compiled published and unpublished specimen records from 782 localities: 428 from the Old World and 354 from the New World. We report the earliest known *B. chinensis* records for 50 geographic areas in the Old World (36 countries, first-level administrative divisions, and island groups) and the New World (16 states in the US and Washington, D.C.).

In Asia, *B. chinensis* was reported from a large range, extending in latitude from North Korea (40.0000°N) to Java (6.6000°S), and in longitude from Nepal (87.1000°E) to the Ogasawara Islands (142.2000°E) (Fig. 1; Table 1), which most likely represents the extent of the *B. chinensis* species complex. The distribution of *B. chinensis* s.s. (based on

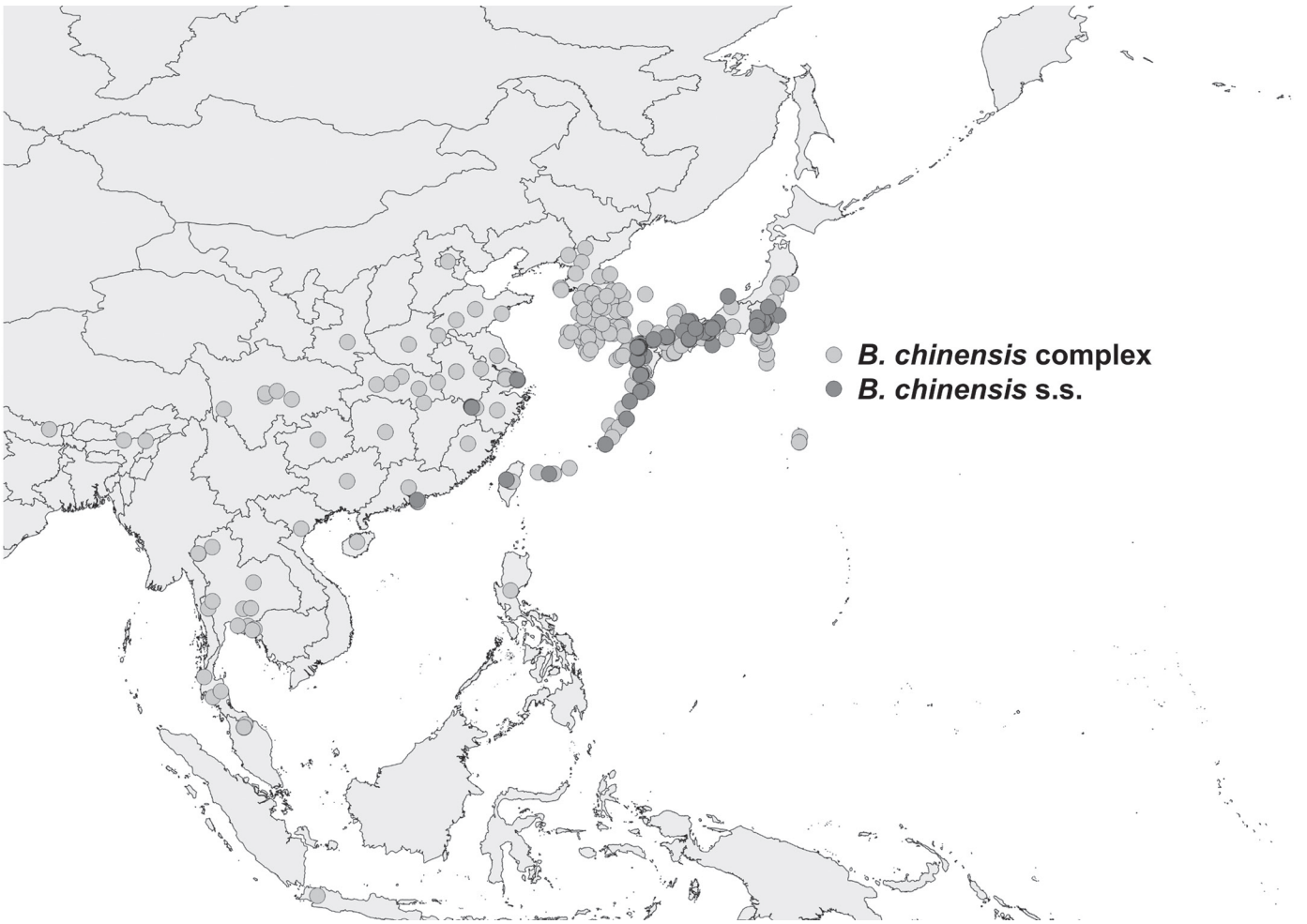

Fig. 1. Distribution of *Brachyponera chinensis* in Asia presenting records identified as part of the *B. chinensis* species complex (light gray) and confirmed records of *B. chinensis* s.s. (dark gray).

the type specimen from Shanghai, most recent and accurate species records, as well as new material examined) was confirmed for Japan, Taiwan, and some of the eastern provinces of China, extending at least from Shanghai to Hong Kong (Fig. 1). However, its presence in Hong Kong was rare and confined to an area around the Kadoorie Farm and Botanic Garden (New Territories). While no specimens were directly examined from the Korean Peninsula, the presence of *B. chinensis* s.s. seems likely.

Other records, particularly those from Southeast Asia, need more careful examination, but it seems unlikely for this species to be found in the Philippines, Thailand, or in Java. Records from southern China and Vietnam will need to be verified because *B. chinensis* can be easily confused with *B. obscurans* which is slightly smaller in size. Nelder et al. (2006) wrote, "the Museum of Comparative Zoology (Harvard University, Cambridge, Massachusetts, USA) contains *P. chinensis* specimens collected from Guam, India, Indonesia, Myanmar, Nepal, Papua New Guinea, Philippines, Solomon Islands, Sri Lanka, and Thailand" (S. C., personal communication, Museum of Comparative Zoology). However, Stefan Cover told us that this was a miscommunication and that Nelder was referring to the range of all species in the *B. chinensis* species group. However, we were unable to find any specimens or records of *B. chinensis* from Burma (Myanmar), Guam, Solomon Islands, or Sri Lanka.

In its introduced range, *B. chinensis* was recorded along a continuous range on the East Coast of the US from Florida to Connecticut, west to Arkansas, and with 2 isolated records from Wisconsin and Washington State (Fig. 2; Table 2). Over the past 10 yr, numerous new records of this species have been added, and this species is now recorded in 16 US states plus Washington, D.C., spanning an area of > 965,000 km^2. In the absence of standardized sampling efforts or detection programs, the conclusions that can be addressed are limited. However, the distribution pattern over time of *B. chinensis* shows a strong local establishment in Washington, D.C., Virginia, North Carolina, South Carolina, and Georgia, with populations recently confirmed in Alabama (J. A. M., personal observation) and Florida, and new populations detected in the past few years in Arkansas, Kentucky, Maryland, Mississippi, Ohio, Tennessee, and Wisconsin (Fig. 2; Table 2). In addition, some of the specimens from Kentucky and Mississippi were collected near the borders of Indiana and Louisiana (< 3 km). Collection records of this ant from western Arkansas were from only 1 county east of Oklahoma. Unfortunately, some of the northern records in coastal regions of Connecticut and New York were not available for examination and would thus require further confirmation. In the published literature, a collection record from New Jersey was mentioned (e.g., MacGown et al. 2013), but we could not find any records except for a quarantine specimen (Antweb CASENT0246023).

In the Old World, records of *B. chinensis* have been reported from shipments of plants in Hamburg, Germany, (Table 1) introduced from Japan; however, the identity of the specimens could not be confirmed.

Table 1. Earliest known records for *Brachyponera chinensis* Emery from the Old World. MCZ = Museum of Comparative Zoology. TARI = Taiwan Agricultural Research Institute. cu= collector unknown. *Indicates regions where species identification would require confirmation. +Indicates records which represent an introduced population.

Region	Earliest record
Japan	≤ 1874 (Smith 1874 as *Ponera solitaria*)
*India	< 1893 (Rothney 1903)
China	≤ 1894 (Emery 1895)
- Shanghai	≤ 1894 (Emery 1895)
- Jiangsu	≤ 1921 (Wheeler 1921)
- Zhejiang	≤ 1921 (Wheeler 1921)
- Hong Kong	≤ 1928 (Wheeler 1928)
- Beijing	≤ 1929 (Wheeler 1929)
- Shandong	≤ 1929 (Wheeler 1929)
- Guizhou	≤ 1994 (Xu 1994)
- Anhui	≤ 1995 (Tang et al. 1995)
- Fujian	≤ 1995 (Tang et al. 1995)
- Guangxi	≤ 2001 (Zhou 2001)
- Sichuan	≤ 2002 (Zhang & Zheng 2002)
- *Hainan	≤ 2006 (Li 2006)
- Henan	≤ 2006 (Li 2006)
- Hubei	≤ 2006 (Wang et al. 2006)
- Hunan	≤ 2006 (Li 2006)
- Shaanxi	≤ 2008 (Wang et al. 2008)
- Guangdong	≤ 2009 (Zhao et al. 2009)
- Liaoning	≤ 2010 (Wu 2010)
Taiwan	1895 (cu, TARI): Taipei
+Germany	1900 (Forel 1900): Hamburg, intercepted in plants from Japan
*Vietnam	1925 (Wheeler 1927)
*Philippines	≤ 1929 (Wheeler 1929)
*Papua New Guinea	1955 (E.O Wilson, MCZ): Karema
+*New Zealand	≤ 1958 (Brown 1958)
*Indonesia	< 1976 (Collingwood 1976)
North Korea	< 1976 (Collingwood 1976)
*Malaysia	1981 (W.L. Brown, MCZ): Genting Highlands
*Thailand	1981 (W.L. Brown & I. Burikam, MCZ): Khao Yai NP
South Korea	1984 (Kim & Choi 1987)
*Nepal	2005 (G. Alpert et al., MCZ): Makula Barun Nature Reserve
+Georgia (Abkhazia)	2006 (Dubovikoff & Yusupov 2018)
+Ogasawara Islands	2008 (Sugiura 2010)
+Russia (Krasnodar Krai)	2017 (Dubovikoff & Yusupov 2018)
+Georgia (Adjara)	2017 (Dubovikoff & Yusupov 2018)

Records of *B. chinensis* recently have been reported from 4 localities bordering the Russian and Georgian coasts of the Black Sea (Table 1).

Overall, most *B. chinensis* records were from sea level to 1,100 m asl, with a few records from higher elevations: 1,600 m asl; 1,620 m asl; 1,915 m asl; and a maximum elevation of 2,400 m asl in Nepal (M. C. Z., record collection) (Fig. 3).

REPRODUCTIVE SEASONALITY

From 49 nests collected, with collection records for every mo, the presence of alate females and males within *B. chinensis* nests was found to span continuously from early Apr to early Sept, while the production of brood was found continuously from early Apr to early Oct (Fig. 4). Because no collections were performed from mid-Feb to mid-Mar, we cannot exclude the possibility that reproductives and brood were produced during that time.

HEALTH RELATED PROBLEMS

From Jul 2010 to Jun 2017, 21 cases of health problems were reported to the authors after a sting by *B. chinensis* from Georgia, Kentucky, Mississippi, North Carolina, South Carolina, Tennessee, and Washington, D.C. Among those, at least 12 individuals reported having severe allergic reactions, including anaphylactic shock. The remaining individuals reported having symptoms such as moderate swelling, sweating, light-headedness, severe pain, stinging, and a burning sensation for a 2 h period. In at least 7 cases, multiple stings were reported, 4 of them associated with anaphylaxis. Several cases of stings happened during activities such as gardening or moving logs (which were used as nesting sites by *B. chinensis*). Other stinging events were by flying alate individuals falling into swimming pools or trapped underneath people's clothes. While we could not test this directly with the data available here, stinging events may be particularly frequent during summer swarming; 19 of 21 stinging cases were reported from Apr to Sep, with a peak in May to Jul (14 cases).

Discussion

At the time of the first discovery of *B. chinensis* populations in the US in 1932, the species was already broadly distributed in the coastal regions of 3 states (Smith 1934). This distribution pattern suggests that

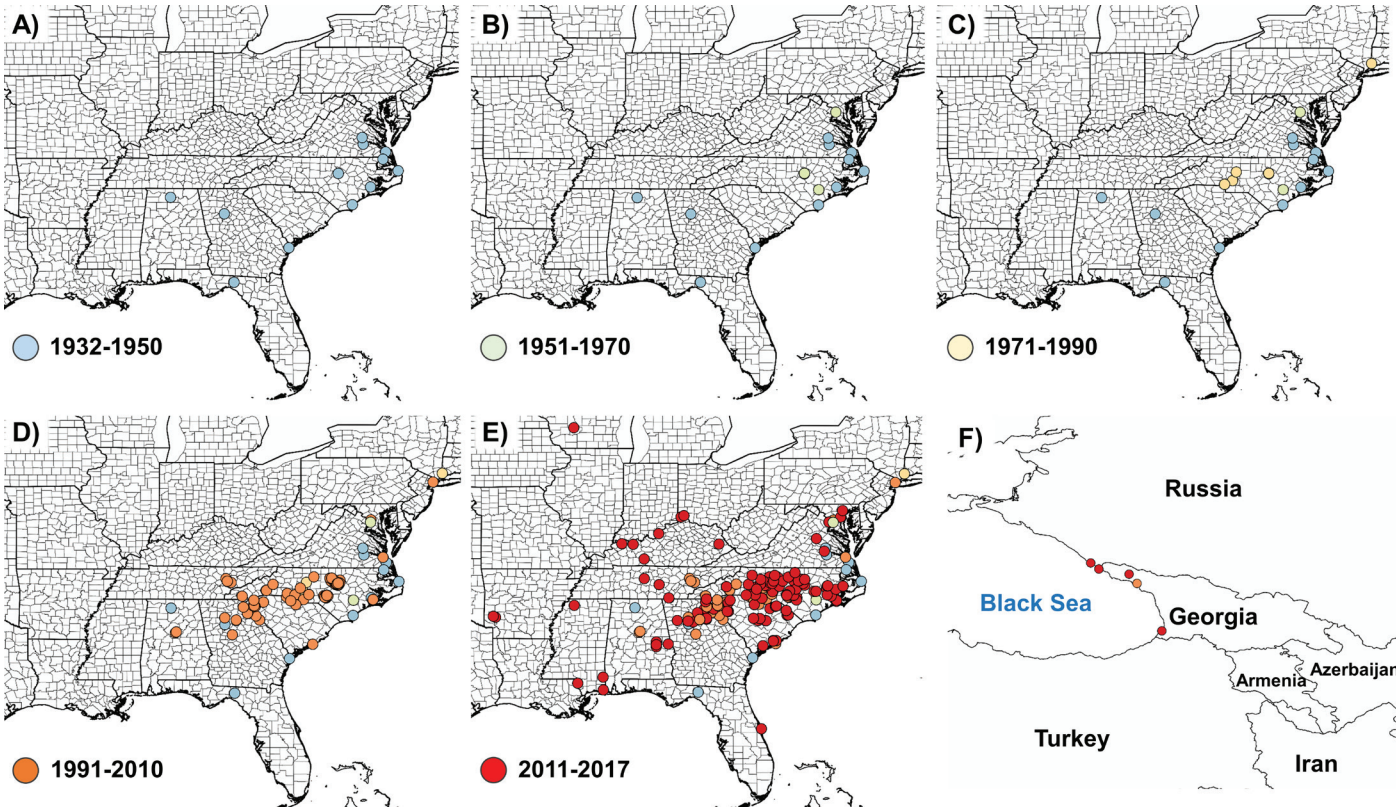

Fig. 2. Introduced range distributions. (A-E) Spread over time of *Brachyponera chinensis* from the earliest record in 1932 to 2018 in the US presented by 20-yr periods, with 1 record from Washington State not displayed; (F) and along the east coast of the Black Sea in south Russia and Georgia (with color code for temporal periods similar to Figs. D, E).

the initial introduction of this ant species in the US might have occurred years earlier, perhaps in the early 1900s, or resulted from multiple independent introductions facilitated by human-mediated dispersal events from Asia to new regions of the New World. Indeed, there are several records of *B. chinensis* intercepted on imported plants (e.g., *Prunus* spp., *Gentiana makoni*) in the late 19th century (Forel 1900, Germany) and 20th century (Brown in 1965, New Jersey, Antweb record CASENT0246023). By 1950, *B. chinensis* was recorded from 6 US states, showing that the large scale spread of this species over large areas was not a recent phenomenon. However, the abundance of this species might have been very low and restricted to a few locations. For instance, Carter (1962), in 1 of the first lists of the ants of North Carolina, reported *B. chinensis* (as *Euponera solitaria* Smith) only from the eastern region of North Carolina known as the Coastal Plain (not including the sandhills region) based on 1938 records. Also in this report, Carter mentioned that he never collected this species himself, despite major sampling efforts in different habitats and parts of the state.

Recent records of *B. chinensis* from southern Russia (Krasnodar Krai) and Georgia (Abkhazia and Adjara regions) represent newly established populations within a new introduced region. Notably, all 4 records originate from coastal cities (Adler, Sochi, Sokhumi, and Batumi) along a 280-km front (Dubovikoff & Yusupov 2018; D. Dubovikoff, personal communication). These records were collected from botanical gardens (Adler and Bathumi), urban parks, as well as from protected natural habitats, and included both workers and queens (Yusupov collection; D. Dubovikoff, personal communication), supporting the presence of an established population in this region. These populations, along the coastal area of the Black Sea, resemble the initial 1932 records of *B. chinensis* in the US reported along the coastline of Virginia and North Carolina (Smith 1934). Important measures should thus be quickly developed to control the spread of *B. chinensis* and limit the risk of a population outbreak in this region. Bertelsmeier et al. (2013) developed models that identified the East Coast of the Black Sea (in Russia and the Republic of Georgia) and more western states of the southeastern US (e.g., Arkansas) as highly suitable areas on the basis of environmental conditions for *B. chinensis* population establishment. Similarly, the record from Bellingham (Whatcom County) in Washington State on the West coast of the USA would require further work to determine if it represents an independent introduction event directly from the native range of *B. chinensis*. This indicates that this species not only is increasing its invasive range within North America but also into new regions of the world. Important biosecurity measures for early detection should be considered in regions where similar suitable conditions are present, including countries along the Adriatic Sea, southern Brazil, Uruguay, northern Argentina, and New Zealand. In New Zealand, Brown (1958) reported the record of a single worker of *B. chinensis* from Waikino (Auckland Province) collected at an unknown date. In April 1959, Taylor (1961) collected 2 workers that he identified as *B. luteipes* from a timber yard in Penrose (Auckland Province). However, the author acknowledged the taxonomic confusion around southeastern Asian *Brachyponera* and hypothesized that the previous record from Brown was likely the same species. It is unclear whether the records collected in the late 1950s belonged to *B. chinensis* or to a similar introduced species. Because both localities were separated by about 100 km, this could suggest a potential widespread distribution at this period. Neither *B. chinensis* nor *B. luteipes* have been recorded from New Zealand for the past 60 yr. However, faunal ant surveys to reexamine those sites should be conducted for discovery of potential

Table 2. Earliest known records for *Brachyponera chinensis* Emery from the United States.

States	Earliest record
Georgia	1932 (Smith 1934)
North Carolina	1932 (Smith 1934)
Virginia	1932 (Smith 1934)
Alabama	1939 (cu, University of Kansas collection): Decatur
Florida	1947 (cu, University of Kansas collection): Lamont
South Carolina	<1950 (Creighton 1950)
Connecticut	1980 (cu, American Museum of Natural History): Lewisboro
Tennessee	<2006 (Zungoli et al. 2006)
New York	2006 (Pecarevic et al. 2010)
Washington, D.C.	2007-2010 (S. A., personal communication): National Zoo
Washington State	2011 (Lucky et al. 2014): Bellingham
Wisconsin	2011 (Lucky et al. 2014): Reedsburg
Mississippi	2013 (MacGown et al. 2013)
Kentucky	2013 (S. Y., personal communication): Louisville
Maryland	2016 (D. Hudgins, online picture at https://bugguide.net/node/view/1257993/bgimage): Baltimore County
Arkansas	2017 (MacGown et al., 2017): Howard County
Ohio	2017 (J. Boggs, The Ohio State University Extension): Cincinnati

remnant populations, as similar circumstances existed for several decades after the initial detection of *B. chinensis* in the US mainland.

Unfortunately, few faunal ant studies were conducted in the US before the 1990s where *B. chinensis* may have been initially collected. This information would have allowed a clear understanding at which point abundance of this pest reached the high population levels observed today. Nonetheless, these results suggest a relatively prolonged lag time between introduction and ecological invasion. These 2 sets of occurrences have been characterized for many biological invaders (Crooks & Soulé 1999), including the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae). In this instance, the first established populations of *S. invicta* occurred in habitats corresponding to their native range but later spread to novel habitats within their introduced range (Fitzpatrick et al. 2007). However, the mechanisms that caused *B. chinensis* to suddenly reach high abundance are unclear, though diet diversification has been proposed recently as a potential result of ecological change compared with native ant populations (Suehiro et al. 2017). At a distributional range of over 965,000 km^2, *B. chinensis* is now one the most widespread invasive ant species within the US; compared with *S. invicta*, the former has spread across an area of over 1.3 million km^2 in the US (Williams et al. 2001). Currently, the temporal spread of several local *B. chinensis* populations is well documented illustrating the detrimental effects of this species on native ants in forested (Guénard & Dunn 2010; Warren et al. 2015; Suehiro et al. 2017) and urban habitats (Spicer-Rice & Silverman 2013). Basic understanding of this species' biology in its native and introduced ranges represent an important avenue that may lead to a management strategy to limit its spread locally (see example with *Anoplolepis gracilipes*, Hoffman 2015).

In addition, the well-publicized spread of the highly destructive *S. invicta* through the southeastern US has probably helped over-shadow the significance of *B. chinensis*, particularly regarding the public health issue. Every year, *B. chinensis* is responsible for several cases of strong allergic reactions, including anaphylaxis in the US (Leath et al. 2006). Within its native range in South Korea, an estimate of 2.1% of the human population present allergic reactions following *B. chinensis* stings (Cho et al. 2002). Allergic cases have been reported in Japan (Fukuzawa et al. 2002), and stinging has been reported from many parts of southern China (Srisong et al. 2016). Based on the results we obtained from voluntary communication from people stung by this ant coupled with

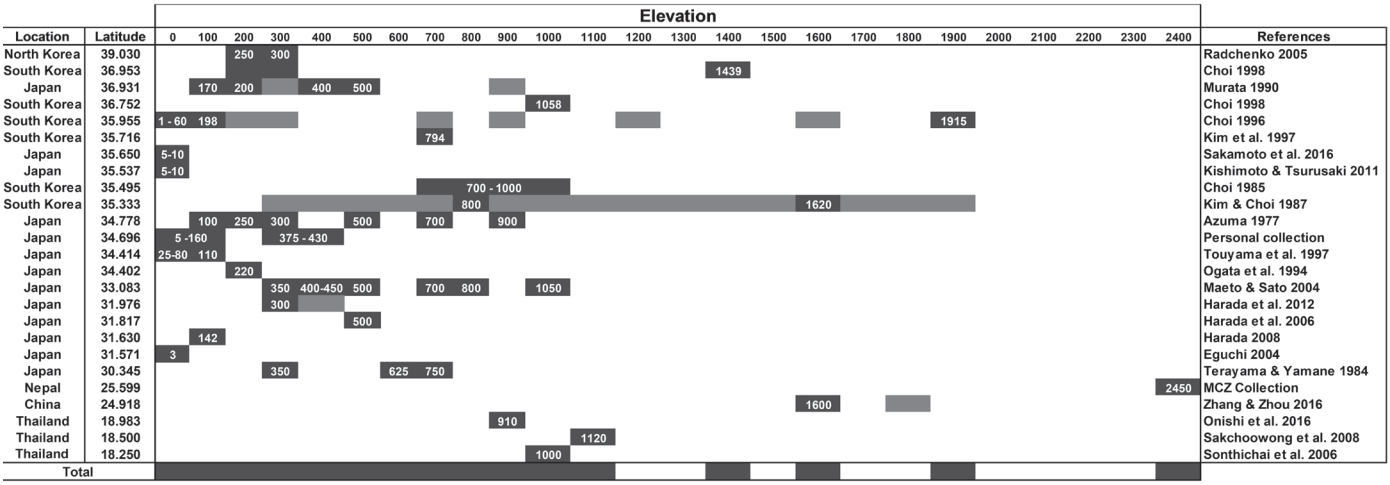

Fig. 3. Elevation distribution of *Brachyponera chinensis* in its native range. Shaded areas correspond to the elevation at which *B. chinensis* has been collected for each specific reference. Light gray areas were sites at a given altitude that were sampled, but no *B. chinensis* were found. References used are presented in

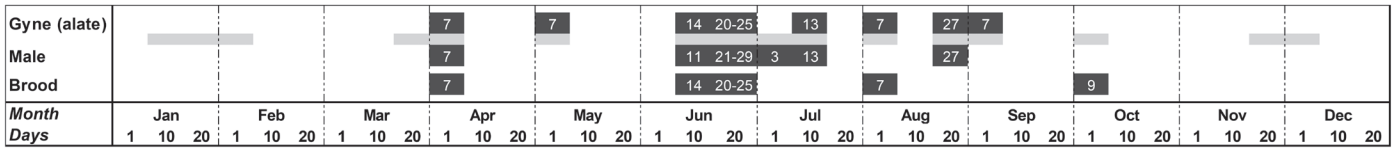

Fig. 4. Temporal distribution of reproductive individuals (female and male alates) and brood presence within *Brachyponera chinensis* nests (dark gray) with overall sampling period shown in light gray. Numbers indicated when sampling occurred during the yr.

those reported by Leath et al. (2006), it is suggested that the public health importance of *B. chinensis* might be greatly underestimated in the US. Moreover, the public health reputation of *S. invicta* and lack of public awareness regarding reactions to *B. chinensis* venom may have resulted in misdiagnosis of *B. chinensis* stings as fire ant stings. Interestingly, desensitizing treatments available for allergic reactions to fire ant stings appear ineffective in treating *B. chinensis* stings (Srisong et al. 2016). The combined association of the spread of *B. chinensis* with the sensitivity of human populations to venom from its sting represents a serious health concern that needs to be addressed by governmental institutions, particularly within the zone of invasion.

Acknowledgments

The authors would like to warmly thank the following persons for providing records information, specimens to examine, or assistance during field work: J. Boggs, J. Costa, R. Dunn, D. Dubovikoff, A. Lucky, K. Matsuura, S. Cover, K. Shimizu, M. Staab, K. Tsuji, E. Vargo, T. Yashiro, S. Yanoviak, and K. Yearly. The authors would also like to thank the sting victims of *B. chinensis*, who reported their experiences, pictures, and locality information used within this study. This research was supported in part by the National Institute of Food and Agriculture, Mississippi Agricultural and Forestry Experiment Station State Project MIS-012040, the USDA-ARS Areawide Management of Invasive Ants Project (Richard L. Brown, P.I.), and USDA-APHIS-PPQ Beetle Trapping Survey.

References Cited

Antweb.org. www.antweb.org (last accessed 8 Feb 2017).

Bertelsmeier C, Guénard B, Courchamp F. 2013. Climate change may boost the invasion of the Asian needle ant. PLoS ONE 8: e75438. doi:10.1371/journal.pone.0075438.

Bradshaw CJA, Leroy B, Bellard C, Roiz D, Albert C, Fournier A, Barbet-Massin M, Salles JM, Simard F, Courchamp F. 2016. Massive yet grossly underestimated global costs of invasive insects. Nature Communications 7: 12986. doi.org/10.1038/ncomms12986.

Brown Jr WL. 1958. A review of the ants of New Zealand. Acta Hymenopterologica 1: 1–50.

BugGuide.net. www.bugguide.net (last accessed 8 Feb 2017).

Carter WG. 1962. Ant distribution in North Carolina. Journal of the Elisha Mitchell Science Society 78: 150–204.

Cho YS, Lee YM, Lee CK, Yoo B, Park HS, Moon HB. 2002. Prevalence of *Pachycondyla chinensis* venom allergy in an ant-infested area in Korea. Journal of Allergy and Clinical Immunology 110: 54–57.

Collingwood CA. 1976. Ants (Hymenoptera: Formicidae) from North Korea. Annales Historico-Naturales Musei Nationalis Hungarici 68: 295–309.

Creighton WS. 1950. The ants of North America. Bulletin of the Museum of Comparative Zoology 104: 1–585.

Crooks JA, Soulé ME. 1999. Lag times in population explosions of invasive species: causes and implications, pp. 103–125 *In* Sandlund OT, Schei PJ, Viken A [eds.], Invasive Species and Biodiversity Management. Kluwer Academic Publishers, Dordrecht, Netherlands.

Dubovikoff, DA, Yusupov ZM. 2018. Family Formicidae – Ants, pp. 197–210 *In* Belokobylskij SA, Lelej AS [eds.], Annotated Catalogue of the Hymenoptera of Russia. Proceedings of the Zoological Institute of the Russian Academy of Sciences 6.

Emery C. 1895. Viaggio di Leonardo Fea in Birmania e regioni vicine. LXIII. Formiche di Birmania del Tenasserim e dei Monti Carin raccolte da L. Fea. Parte II. Annali del Museo Civico Storia Naturale di Genova 34: 450–483.

Fitzpatrick MC, Weltzin JF, Sanders NJ, Dunn RR. 2007. The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? Global Ecology and Biogeography 16: 24–33.

Forel A. 1900. Fourmis du Japon. Nids en toile. *Strongylognathus* Huberi et voisins. Fourmilière triple. *Cyphomyrmex* Wheeleri. Fourmis importées. Bulletin de la Société Entomologique Suisse 10: 267–287.

Fukumoto S, Yamane S. 2015. Records of ants from Uke–jima, Amami Islands, Japan (Hymenoptera, Formicidae). Nature of Kagoshima 41: 195–197.

Fukuzawa M, Arakura F, Yamazaki Y, Uhara H, Saida T. 2002. Urticaria and anaphylaxis due to sting by an ant (*Brachyponera chinensis*). Acta Dermato-Venereologica 82: 59.

Gotoh A, Ito F. 2008. Seasonal cycle of colony structure in the Ponerine ant *Pachycondyla chinensis* in western Japan (Hymenoptera, Formicidae). Insectes Sociaux 55: 98–104.

Green OR. 1992. New Zealand ants (Hymenoptera: Formicidae). Distribution and effects, pp. 67–72 *In* Symposium: Social and Harmful Insects. Proceedings of the 41st Annual Conference of the Entomological Society of New Zealand, Heretavnga, Hutt Valley, New Zealand.

Guénard B, Dunn RR. 2010. A new (old), invasive ant in the hardwood forests of eastern North America and its potentially widespread impacts. PLoS ONE 5: e11614. doi:10.1371/journal.pone.0011614.

Guénard B, Cardinal-De Casas A, Dunn RR. 2014. High diversity in an urban habitat: are some animal assemblages resilient to long-term anthropogenic change? Urban Ecosystems 18: 449–463.

Harada Y, Enomoto M, Nishimata N, Nishimuta K. 2014. Ants of the Tokara Islands, northern Ryukyus, Japan. Nature of Kagoshima 40: 111–121.

Harada Y, Koto S, Kawaguchi N, Sato K, Setoguchi T, Muranaga R, Yamashita H, Yo A, Yamane S. 2012. Ants of Jusso, Isa City, Kagoshima Prefecture, southwestern Japan. Bulletin of the Biogeographical Society of Japan 67: 143–152.

Hoffman BD. 2015. Integrating biology into invasive species management is a key principle for eradication success: the case of yellow crazy ant *Anoplolepis gracilipes* in northern Australia. Bulletin of Entomological Research 105: 141–151.

Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ. 2002. The causes and consequences of ant invasions. Annual Review of Ecology and Systematics 33: 181–233.

Kim CH, Choi BM. 1987. On the kinds of ants (Hymenoptera: Formicidae) and vertical distribution in Jiri Mountain. Korean Journal of Plant Protection 26: 123–132.

Leath TM, Grier TJ, Jacobson RS, Fontana-Penn ME. 2006. Anaphylaxis to *Pachycondyla chinensis*. Journal of Allergy and Clinical Immunology 117: S129.

Li ZH. 2006. List of Chinese Insects. Vol. 4. Sun Yat-Sen University Press, Guangzhou, China.

Lucky A, Savage AM, Nichols LM, Castracani C, Shell L, Grasso DA, Mori A, Dunn RR. 2014. Ecologists, educators, and writers collaborate with the public to assess backyard diversity in The School of Ants Project. Ecosphere 5: 78. doi.org/10.1890/ES13-00364.1.

MacGown JA, Richer H, Brown RL. 2013. Notes and new distributional records of invasive ants (Hymenoptera: Formicidae) in the Southeastern United States. Midsouth Entomologist 6: 104–114.

MacGown JA, Wang S, Hill JG, Whitehouse RJ. 2017. A list of ants (Hymenoptera: Formicidae) collected during the 2017 William H. Cross Expedition to the Ouachita Mountains of Arkansas with new state records. Transactions of the American Entomological Society 143: 735–740.

Menke SB, Guénard B, Sexton JO, Weiser MD, Dunn RR, Silverman J. 2011. Urban areas may serve as habitat and corridors for dry-adapted, heat tolerant species; an example from ants. Urban Ecosystems 14: 135–163.

Nelder MP, Paysen ES, Zungoli PA, Benson EP. 2006. Emergence of the introduced ant *Pachycondyla chinensis* as a public-health threat in the southeastern United States. Journal of Medical Entomology 43: 1094–1098.

Pecarevic M, Danoff-Burg J, Dunn RR. 2010. Biodiversity on Broadway - enigmatic diversity of the societies of ants (Formicidae) on the streets of New York City. PLoS ONE 5: e13222. doi.org/10.1371/journal.pone.0013222.

Rodriguez-Cabal MA, Stuble KL, Guénard B, Dunn RR, Sanders NJ. 2012. Disruption of ant-seed dispersal mutualisms by the invasive Asian needle ant (*Pachycondyla chinensis*). Biological Invasions 14: 557–565.

Rothney GAJ. 1903. The aculeate Hymenoptera of Barrackpore, Bengal. Transactions of the Entomological Society of London 51: 93–116.

Schmidt CA, Shattuck SO. 2014. The higher classification of the ant subfamily Ponerinae (Hymenoptera: Formicidae), with a review of ponerine ecology and behavior. Zootaxa 3817: 1–242.

Smith F. 1874. Descriptions of new species of Tenthredinidae, Ichneumonidae, Chrysididae, Formicidae, etc. of Japan. Transactions of the Entomological Society of London 7: 373–409.

Smith MR. 1934. Ponerine ants of the genus *Euponera* in the United States. Annals of the Entomological Society of America 27: 557–564.

Smith MR. 1979. Superfamily Formicoidea, pp 1323–1467 *In* Krombein KV, Hurd Jr PD, Smith DR, Burks BD [eds.], Catalog of Hymenoptera in America North of Mexico. Volume 2. Apocrita (Aculeata). Smithsonian Institution Press, Washington, D.C., USA.

Spicer-Rice E, Silverman J. 2013. Propagule pressure and climate contribute to the displacement of *Linepithema humile* by *Pachycondyla chinensis*. PLoS ONE 8: e56281. doi:10.1371/journal.pone.0056281.

Srisong H, Daduang S, Lopata AL. 2016. Current advances in ant venom proteins causing hypersensitivity reactions in the Asia-Pacific region. Molecular Immunology 69: 24–32.

Suehiro W, Hyodo F, Tanaka HO, Himuro C, Yokoi T, Dobata S, Guénard B, Dunn RR, Vargo EL, Tsuji K, Matsuura K. 2017. Radiocarbon analysis reveals expanded diet breadth associates with the invasion of a predatory ant. Scientific Reports **7**: 15016. doi.org/10.1038/s41598-017-15105-1.

Sugiura S. 2010. Species interactions-area relationships: biological invasions and network structure in relation to island area. Proceedings of the Royal Society of London. Series B, Biological Sciences 277: 1807–1815.

Tang J, Li S, Huang E, Zhang B, Chen Y [eds.]. 1995. Hymenoptera: Formicidae (1). Economic Insect Fauna of China, 47. Academy of Science Publishing House, Beijing, China.

Taylor RW. 1961. Notes and new records of exotic ants introduced into New Zealand. New Zealand Entomologist 2: 28–37.

Wang W, Huang J, Zhou J. 2006. Survey of ant species in three nature reserves in Eastern Hubei province. Journal of Anhui Agricultural Sciences 34: 3131–3132.

Wang ZC, Li G, Ma LB, Xu SQ. 2008. Ant fauna in Longchi Nature Reserve of Shaanxi province. Journal of Yulin University 18: 16–20.

Warren RJ, McMillan A, King JR, Chick L, Bradford MA. 2015. Forest invader replaces predation but not dispersal services by a keystone species. Biological Invasions 17: 3153–3162.

Wheeler WM. 1921. Chinese ants. Bulletin of the Museum of Comparative Zoology 64: 529–547.

Wheeler WM. 1927. Ants collected by Professor F. Silvestri in Indochina. Bollettino del Laboratorio di Zoologia Generale e Agraria della Reale Scuola Superiore d'Agricoltura. Portici 20: 83–106.

Wheeler WM. 1928. Ants collected by Professor F. Silvestri in China. Bollettino del Laboratorio di Zoologia Generale e Agraria della Reale Scuola Superiore d'Agricoltura. Portici 22: 3–38.

Wheeler WM. 1929. Ants collected by Professor F. Silvestri in Formosa, the Malay Peninsula and the Philippines. Bollettino del Laboratorio di Zoologia Generale e Agraria della R. Scuola Superiore d'Agricultura. Portici 24: 27–64.

Williams DF, Homer L, Oi DH. 2001. An historical perspective of treatment programs and the development of chemical baits for control. American Entomologist 47: 146–159.

Wilson EO, Taylor RW. 1967. Ants of Polynesia. Pacific Insects Monographs 14: 1–109.

Wu W. 2010. The taxonomic and fauna study on the Formicidae of Liaoning Province (Insecta: Hymenoptera). Dissertation, Northeast Normal University, Changchun, Jilin Province, China.

Xu Z. 1994. A taxonomic study of the ant genus *Brachyponera* Emery in southwestern China (Hymenoptera: Formicidae: Ponerinae). Journal of Southwest Forestry College 14: 181–185.

Yamane S. 2007. *Pachycondyla nigrita* and related species in Southeast Asia. Memoirs of the American Entomological Institute 80: 650–663.

Yashiro T, Matsuura K, Guénard B, Terayama M, Dunn RR. 2010. On the evolution of the species complex *Pachycondyla chinensis* (Hymenoptera: Formicidae: Ponerinae), including the origin of its invasive form and description of a new species. Zootaxa 2685: 39–50.

Zhang W, Zheng Z. 2002. Studies of ant (Hymenoptera: Formicidae) fauna in Sichuan Province. Entomotaxonomia 24: 216–222.

Zhao S, Jia FL, Liang GQ, Ke YL, Tian WJ. 2009. Ants and their distributions in Guangdong Province, China. Journal of Environmental Entomology 31: 156–161.

Zhou SY. 2001. Ants of Guangxi. Guangxi Normal University Press, Guilin, China.

Zungoli PA, Paysen ES, Benson EP. 2006. *Pachycondyla chinensis* (Emery) an emerging ant pest of medical importance. Clemson University Extension Insect Information Series MV-18. Clemson University, Clemson, South Carolina, USA.