

Current distribution and population dynamics of the little fire ant supercolony in Cameroon

M. Tindo · P. S. Mbenoun Masse · M. Kenne · R. Mony ·
J. Orivel · A. Doumtsop Fotio · A. Fotso Kuate · C. Djiéto-Lordon ·
A. Fomena · A. Estoup · A. Dejean · J. Foucaud

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Abstract The little fire ant, *Wasmannia auropunctata*, is native to Central America, but has been introduced into many parts of the world. We examined the current distribution of *W. auropunctata* in Cameroon, tested for aggression between workers from different parts of the country, and examined the genotypes of workers, queens, and males to evaluate the mating system. We found *W. auropunctata* at 36 sites in three provinces (Centre, East, and South). We found *W. auropunctata* only in human-disturbed habitats. Its spread appears to be primarily human mediated. Aggressive behaviour was almost non-existent between workers from different sites, indicating that there is only one supercolony in Cameroon. Our genetic analysis found that only one male/female pair of clones was introduced into Cameroon, probably from Gabon. No new male clonal lineage was identified, whereas new sexually derived

female clonal lineages were noted. Apart from the genotype of the founding queen, which was well distributed but generally not dominant, a new clonal queen genotype emerged and was both omnipresent and dominant at most sites. These results may be useful in the development of management strategies.

Keywords Dispersion · Invasive ants · Reproduction strategy · Unicoloniality · *Wasmannia auropunctata*

Introduction

Social insects, and especially ants, are among the most devastating invaders known, and their threat to native bio-

M. Tindo (✉) · M. Kenne · R. Mony
Département de Biologie des Organismes Animaux, Faculté des Sciences, Université de Douala, BP 24157 Douala, Cameroun
e-mail: tindodouala@yahoo.com

P. S. Mbenoun Masse · C. Djiéto-Lordon
Laboratoire de Zoologie, Faculté des Sciences,
Université de Yaoundé I, BP 812 Yaoundé, Cameroun

J. Orivel · A. Dejean
Centre National de la Recherche Scientifique,
Ecologie des Forêts de Guyane (UMR-CNRS 8172),
Campus Agronomique, Kourou, France

A. Doumtsop Fotio · A. Fotso Kuate
International Institute of Tropical Agriculture,
Cameroon Station, B.P. 2008 Yaoundé, Cameroun

A. Fomena
Laboratoire de Biologie Générale, Faculté des Sciences,
Université de Yaoundé I, BP 812 Yaoundé, Cameroun

A. Estoup · J. Foucaud
Centre de Biologie et de Gestion des Populations,
Institut National de Recherche Agronomique,
Campus International de Baillarguet, CS 30 016,
34988 Montferrier/Lez Cedex, France

A. Dejean
Université de Toulouse; UPS-ECOLAB,
118 route de Narbonne, 31062 Toulouse, France

J. Foucaud
Laboratoire Evolution Genome Speciation,
Centre National de la Recherche Scientifique,
Avenue de la Terrasse, F 91198 Gif sur Yvette, France

diversity and impact on agricultural production have been well documented (Vander Meer et al., 1990; Williams, 1994; Vinson, 1997; Chapman and Bourke, 2001; Holway et al., 2002; O'Dowd et al., 2003). About 150 out of the approximately 12,600 ant species known have been transported and introduced into many parts of the world, but only some of them became invasive in their introduced range (Holway et al., 2002). The most widespread, abundant and harmful ant species include the crazy ant *Anoplolepis gracilipes*, the Argentine ant *Linepithema humile*, the big-headed ant *Pheidole megacephala*, the red fire ant *Solenopsis invicta*, and the little fire ant *Wasmannia auropunctata* (Lowe et al., 2000; Holway et al., 2002).

Native to Central and South America, *W. auropunctata* has been introduced into various island groups in the Caribbean and Pacific Oceans, Australia, Florida and Israel (Wetterer and Porter, 2003; Vonshak et al., 2009). It has also been found in tropical green houses in Great Britain and Canada (Ayre, 1977). In Africa, it was first reported in Gabon (Santschi, 1914; Wetterer et al., 1999; Wetterer and Porter, 2003; Walsh et al., 2004; Walker, 2006; Ndoutoume and Mikissa, 2007), where it has invaded both human-disturbed and natural forest environments, and later in Cameroon in cocoa plantations along the Kribi–Ebolowa road (de Miré, 1969). In its native range, *W. auropunctata* is regarded as a dominant species in disturbed areas, while it is common but non-dominant in undisturbed areas such as the primary forest (Majer and Delabie, 1999; Armbrecht and Ulloa-Chacon, 2003; Orivel et al., 2009). Further demographic and reproductive differences have recently been identified between the two types of native populations. Natural forest habitats are occupied by low-density populations that reproduce via classical haplodiploidy. Human-disturbed habitats are generally occupied by populations where males and queens are produced clonally and workers are produced sexually (Fournier et al., 2005; Foucaud et al., 2009; Orivel et al., 2009). To date, all of the introduced populations of *W. auropunctata* studied share the biological features of the dominant, clonally reproducing populations of the native range (Foucaud et al., 2010).

Invading ants may spread by moving nests locally (budding), giving rise to a diffusion-like process; through the middle-distance migration of flying queens; and through long-distance jumps, which are often human-mediated. However, the relative contribution of each process to the rate at which most invasive ant species spread is still unclear (Holway, 1998; Hoffman et al., 1999; Suarez et al., 2001; Tsutsui et al., 2003; Abbott et al., 2007). Nevertheless, jump dispersal has been documented as the primary mode by which the Argentine ant has spread in the continental United States of America (USA). *Wasmannia auropunctata* relies on human-mediated dispersal, but also on natural means such as floating vegetation/debris (particularly logs) during

floods (Hölldobler and Wilson, 1990; Passera, 1994; Suarez et al., 2001; Walsh et al., 2004).

Since de Miré first reported the presence of *W. auropunctata* in Cameroon in 1969, little more is known of its invasion status. We examined the current distribution of *W. auropunctata*, tested for aggression between workers from different parts of the country and examined the genotypes of workers, queens, and males to evaluate the mating system.

Materials and methods

Distribution

Between March 2004 and December 2010, we surveyed more than 300 sites around Cameroon and received reports from additional sites.

We developed an informational note containing pictures and some biological features of *W. auropunctata* and distributed it to scientists working at various research institutions in Cameroon. When we received an indication of an occurrence of this species, we paid a visit to that location to verify and confirm its presence. At each location visited, we examined the bare ground and waste mounts for 10–30 min. We also randomly placed baits (a mixture of 50% tuna, 30% honey and 20% soybean oil) on the ground and re-examined them after 30 min to 1 h to check for the presence of ants. We also visited the coastal region (Bidou II and surroundings) where *W. auropunctata* was reported for the first time (de Miré, 1969). GPS readings of the locations visited were recorded to map the ant's distribution.

We conducted field investigations at 20 infested sites to identify and to quantify the nature of the infested habitat. This was done by placing baits every 10 m along four transects starting from a randomly selected point and going in the four cardinal directions.

Rate of dispersion and dynamics of colony boundaries

We monitored the position of eight invasion fronts for 1 year on a monthly basis in Biyem Assi. We calculated the mean rates of occupation per month and compared them between invasion fronts and between seasons using Student's *t* test and an ANOVA followed by a Tukey's post hoc test (GraphPad Prism 5.0 software).

Colony structure

We collected nest fragments containing workers, queens and brood at 50 m intervals from 12 infested sites: Biyem Assi, Mbalmayo, Adon-Mekomo, Akonetye, Djazeng, Sangmélima, Mkoemvone, Bidou II, Elon, Nlómôtô, Biton

and Bertoua and kept them in the laboratory. The ants were then transferred to a standard artificial nest consisting of a glass test tube (7.5×1.1 cm) containing a watering place (about 15 ml). The mouth of the test tube was then placed in a plastic container ($19.5 \times 12 \times 8.5$ cm) where food was deposited. The sides of the container were coated with Fluon[®] to prevent the ants from escaping. Food consisting of a sugary solution (6 ml of honey, two 8.88 mg of sugar and 60 ml of water) and pieces of grasshopper (*Homorocorifus nitidulus*, *Homorocorifus* sp.) was provided every 2 days during 1 month.

We conducted standard aggressiveness trials adapted from Suarez et al. (1999) between individual workers collected from (1) the same nest at each site (control), (2) different nests from the same sites and (3) different nests from different sites. The test consisted of one-on-one confrontations between workers in an arena (Petri dishes with $\varnothing = 1.5$ cm) whose walls were coated with Fluon[®]. Observations were made through a stereomicroscope (WILD M3Z). After the first contact between two individuals, we recorded their behavioural interactions and the outcome during 5 min. Each individual was used once we conducted. Ten confrontations for each pair of nests. The scale of aggressiveness was comprised of four levels (see Suarez et al., 1999): 1 = antennation and physical contact where neither ant showed any interest, 2 = avoidance (one or both ants retreated in opposite directions after contact), prolonged antennation, 3 = the pulling of legs or antennae, and 4 = fighting, grappling (resulting in the death of at least one worker). The highest escalation was retained for each confrontation and the mean value of the 10 trials was used as an aggressiveness index for the pair of nests. Two nests were considered as belonging to the same colony when the aggressiveness index was lower than 2.5.

Microsatellite genotyping

In total, 465 specimens (i.e., 196 queens, 250 workers, 19 males) collected from 55 nests at 12 sites (all of the sites, except for Bertoua and with the addition of Yaoundé, were used for the colony structure test) were genotyped at 12 microsatellite loci as described by Fournier et al. (2005). The spermathecal content of 60 queens was also analyzed (79 male genotypes in total). To characterize the reproductive systems and the relationships between genotypes, we visually searched for individual microsatellite genotypes and used three personal programs developed in the Pascal object programming language (see Foucaud et al., 2006, 2010). This particular genotypic dataset was previously used together with a much larger worldwide dataset to investigate routes of introduction on a global scale (Foucaud et al., 2010). In the present study, we use it in greater depth to decipher the local history of the invasion in Cameroon by

studying the identity and location of the various Cameroonian clones.

Results

Distribution

We visited a total of 334 sites in eight regions (i.e., Adamaoua, Centre, East, Littoral, Northwest, Southwest, South and West). *Wasmannia auropunctata* was recorded at 36 sites situated in three regions (i.e., East, Centre and South) of the country (Fig. 1). The South region is the most invaded area with 91.7% of the sites infested. Mbalmayo and Yaoundé were the only infested sites in the Centre region, while in the East region *W. auropunctata* was recorded only in Bertoua. Based on these results, the North and West regions of Cameroon have not yet been invaded (Fig. 1). *Wasmannia auropunctata* was not recorded in Campo or Edea, whereas *Solenopsis geminata*, another introduced invasive species whose sting is painful, was found. From its introduction point (Bidou II) in the South region (de Miré, 1969), *W. auropunctata* has therefore spread about 120, 300 and 600 km south, north and east, respectively.

Wasmannia auropunctata's progression into Cameroon has not been continuous since the invaded areas are not contiguous. This is also true even within some locations like Bertoua, Mbalmayo, Sangmélima and Yaoundé where several populations were recorded. No infestation was recorded in natural habitats ("primary forests" in Matomb, Korup, and the forest reserve in Dja; Fig. 1). Indeed, *W. auropunctata* mainly occupied disturbed habitats around houses and along roads. Infested habitats were subdivided into the following types ranked by order of preference: home gardens (55.4%, $n = 323$) where *W. auropunctata* occupied garbage piles; houses (37.5%, $n = 323$) including in cracks in the walls; cocoa plantations (4.6%, $n = 323$) where workers were found between cracks in the tree bark

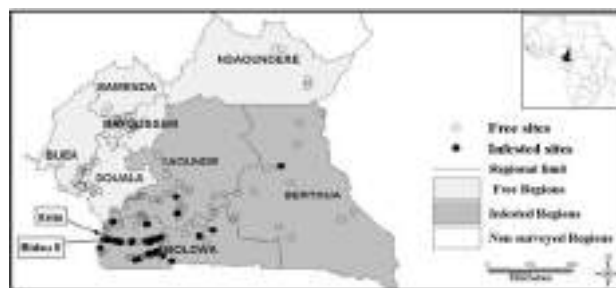


Fig. 1 Current distribution of the little fire ant *Wasmannia auropunctata* Roger in Cameroon. Results from surveys conducted between 2003 and 2010. Open circles *W. auropunctata* not found. Filled circles *W. auropunctata* found

Table 1 Monthly rate of occupation (Mean \pm SE) corresponding to eight invasion fronts of the ant *Wasmannia auropunctata* in Biyem Assi (Yaoundé, Cameroon) during 12 months and based on the rainy and dry seasons in 2006

Invasion fronts	N	Min	Max	Mean \pm SE	Group	Monthly rate of occupation (m)		Comparison: dry versus rainy seasons		
						Rainy season (8) Mean \pm SE	Dry season (4) Mean \pm SE	t test	df	P
1	12	-2.6	8.8	0.7 \pm 0.6 ^a	a	1.5 \pm 0.4	-0.6 \pm 0.5	3.28	34	0.002
2	12	-4.5	0.5	-1.9 \pm 0.5 ^c						
3	12	-4.7	0.7	-1.6 \pm 0.5 ^b						
4	12	-3.2	11.1	0.9 \pm 0.6 ^a	b	-1.4 \pm 1.0	-1.1 \pm 1.6	0.42	34	0.681
5	12	-3.7	1.3	-1.3 \pm 0.5 ^b						
6	12	-2.5	10.2	0.9 \pm 0.6 ^a	c	-2.6 \pm 1.3	-0.6 \pm 0.9	2.81	22	0.019
7	12	-5.4	0.2	-2.0 \pm 0.5 ^c						
8	12	-4.2	2.7	-1.1 \pm 0.7 ^b						
Overall means		-30.8	35.5	-0.7 \pm 0.2		-0.9 \pm 2.2	-0.8 \pm 1.0			

For statistical comparisons, we conducted a Fisher ANOVA followed by a Tukey's post hoc test. Mean values bearing the same letter are not statistically different from each other at the 5% significance level, and, therefore, formed the same group

N number of months, Min minimum, Max maximum

and in the leaf litter; cassava fields (1.5%, $n = 323$); and in the leaf litter of secondary forest fragments (0.6%, $n = 323$) which have developed around abandoned houses and cucumber fields (0.3%, $n = 323$).

Rate of dispersion and dynamics of colony boundaries

The shift in colony boundaries varied by -5.4 to 4.5 m/month, indicating that both contractions and expansions were recorded. The monthly shifts in the different invasion fronts varied significantly between the regions compared (Fisher ANOVA: $F_{7,88} = 5.27$; $P < 0.001$). The colony boundaries expanded for only three fronts (i.e., 1, 4 and 6) and receded for the other five fronts (Table 1). Contraction was more pronounced in fronts 2 and 7 compared to fronts 3, 5 and 8. The fronts expanded only during the rainy season while contractions occurred during both the rainy and the dry seasons (Table 1). The overall rate of occupation was negative (-0.7 ± 0.2 m), showing that the areas occupied by colonies contracted.

Colony structure

Dyadic confrontations using workers from 58 nests collected from 12 infested sites (3–6 nests per site) showed no aggressiveness between workers from the same nest, while inter-nest confrontations always showed a low level of aggressiveness between workers from the same site (98.7% of the cases with no aggressiveness; $n = 5972$ confrontations) and from different sites (98.4% of the cases with no aggressiveness; $n = 2354$ confrontations).

The average aggressiveness index ranged from 1 to 1.1 (Mean \pm SE = 1.08 ± 0.13 , $n = 13$ nests) within nests,

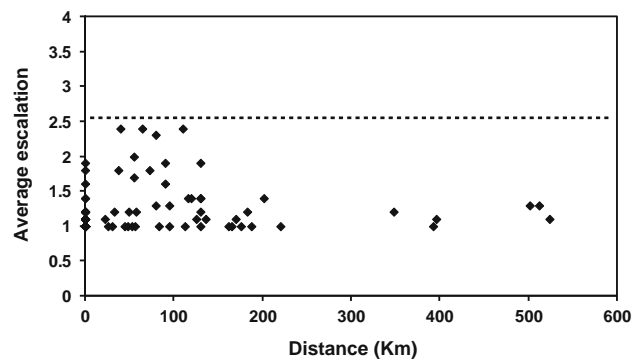


Fig. 2 Mean aggressiveness index according to distance recorded during one-on-one confrontations between *Wasmannia auropunctata* workers belonging to the same nest, different nests from the same location and different nests from different locations in Cameroon in 2006

1–1.9 (Mean \pm SE 1.1 ± 0.2 , $n = 71$ pairs of nests) between nests at the same site and 1–2.4 (Mean \pm SE 1.4 ± 0.5 , $n = 68$ pairs of nests) between nests from different sites (Fig. 2). The highest recorded aggressiveness index (i.e., 2.4) was observed between nests from Mbalmayo and Sangmélina, Mbalmayo and Biyem Assi, Elon and Nlomôto.

Microsatellite genotyping

As previously mentioned in Foucaud et al., (2010), the analysis of queen, male and worker genotypes indicated that there was only one successful introduction of *Wasmannia auropunctata* in Cameroon since all of the genotypes originated from a single couple composed of a cloned male and a queen. The successful introduction of a single clonal

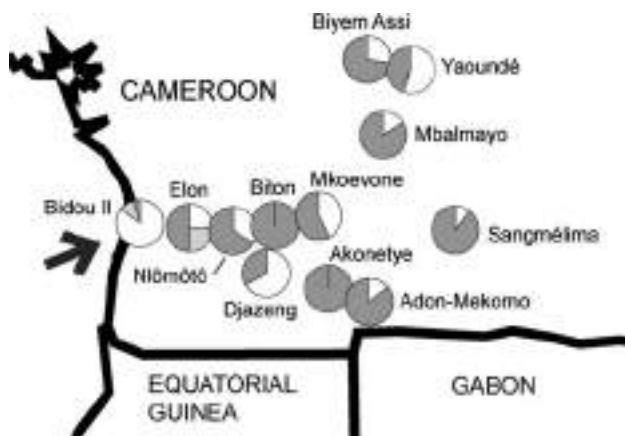


Fig. 3 Distribution of *Wasmannia auropunctata* clonal queen genotypes in Cameroon. White Q0 queen, dark grey dominant Q2 queen, light grey minor Q2 queens. The black arrow indicates the introduction point (Bidou II)

couple would explain the presence of a lone supercolony in Cameroon. The genotype of the clonal couple originally introduced into Cameroon is identical to the clonal couple introduced into Gabon.

While the clonal production of reproductives is the general rule, we detected some sexual reproduction events generating some new clonal lines, similarly to the situation investigated in New Caledonia (Foucaud et al., 2006). We did not detect any new clonal male lineage, as only the original clonal male genotype was found. However, some new clonal queen lineages were derived from sexual recombination by the introduced clonal queen and the male lineage. We could therefore distinguish three genotypes for the clonal queens (Fig. 3). First, the original clonal queen genotype (Q0) was still common (i.e., present at 10 of the 12 sites sampled), but generally not dominant on a local scale. Exceptions were Bidou II (the nearest site to the introduction point sampled), Djazeng and Yaoundé for which the Q0 clonal queen genotype accounted for more than 50%. Second, three sites displayed some minor derived clonal queen (Q2) genotypes, which were rare and always restricted to a single site (i.e., Bidou II, Elon and Yaoundé; Fig. 3). Third, we encountered a major derived queen (Q2) genotype, which was found at all of the sites surveyed, representing 62.0% ($n = 195$) of all of the queens analyzed.

Discussion

The present study documents changes in the distribution of *W. auropunctata* in Cameroon since 1969, the date it was first reported in the coastal region near Kribi (de Miré, 1969). It was then shown to have spread along the Kribi–Ebolowa road and in the interior in plantations on both sides of the road over a distance of 40 km around the village of

Bidou II and also along the old mine road that leaves from the south of this village. Our results show that this ant is no longer limited to this axis, but has spread out and is now present in 36 locations in three regions of Cameroon (Fig. 1). It is likely that *W. auropunctata* is more widely distributed in Cameroon than what is reported in this study, since we were unable to survey the entire country. Our results show that the town of Kribi has not yet been invaded by this ant, even if Bidou II, the assumed introduction point, is only 12 km west of Kribi. Similarly to many coastal sites, like Edea and Douala, Kribi has instead been invaded by *S. geminata* (Foguieng 2007; MT, pers. obs.). Further investigations are needed to clarify habitat partitioning between these two invasive ants in Cameroon.

Most of the sites invaded by *W. auropunctata* are situated within the greater southern region, and distributed around Bidou II. This distribution pattern around the introduction site confirms the report by de Miré (1969) stating that local residents intentionally transported *W. auropunctata* colonies to use in the biological control of mirids in their cocoa fields. However, the custom of using *W. auropunctata* as a biological control agent was lost somewhere between the Seventies and the Nineties likely due to the intensive use of insecticides. Consequently, none of the farmers interviewed during the present study knew of this potential biological control practice; instead, they complained of the problems this ant poses especially its painful bite which has led many of them to abandon their fields (A.D., MT pers. comm.). Indeed, using *W. auropunctata* as a control agent should not be encouraged considering the negative impacts this ant has on the population abundance, species richness, and community structure of native ants as well as other ground-dwelling arthropods and on the health of wild mammals in its introduced range (Le Breton et al., 2003; Walsh et al., 2004; Walker, 2006; Vonshak et al., 2009).

Based on our results, the greater southern region that shares a border with Gabon is the most invaded. This may indicate that *W. auropunctata* entered Cameroon from Gabon. In fact, this ant was observed in Gabon as early as 1913 (Santschi, 1914) and so, a long time before being reported in Cameroon in 1969 by de Miré. Note that there was a single successful introduction of one clonal couple of *W. auropunctata* in western Africa (Foucaud et al., 2010). Because the clonal couple originally introduced into Cameroon is identical to the one introduced earlier into Gabon, the Gabonese origin of the *W. auropunctata* invasion in Cameroon is highly probable.

Along the same lines, the results of our aggressive behavioural assay showed low levels of aggressiveness between workers from different sites (1.6% of the encounters). However, relatively high levels (but lower than the 2.5 mark generally accepted as a sign the two ants did not belong to the same colony) were observed in some cases. In ants,

workers recognize nestmates through a colonial identity based on chemical cues represented by cuticular hydrocarbons that constitute the “colony odour”. The cuticular hydrocarbon profile is influenced by genetic (Beye et al., 1998; Tsutsui et al., 2003; Dimarco et al., 2010) and environmental factors such as diet, the odour of the nesting material, and microorganisms associated with the colonies (Heinze et al., 1996; Liang and Silverman, 2000; Buczkowski and Silverman, 2006). Our genetic analysis uncovered a new sexually derived clonal lineage, but sexual events are too rare to think that there is a genetic basis for the aggressiveness in *W. auropunctata* in Cameroon. Therefore, differences in environmental factors are the most plausible explanation for some cases of relatively high aggressiveness, leading us to conclude that there is only one supercolony in Cameroon. This is probably true for all of Central Africa, given that genotypes are shared between Cameroon and Gabon. However, the hypothesis of a single African supercolony has to be confirmed empirically by conducting behavioural assays for aggressiveness.

The invaded sites recorded during this study are rather isolated, even within the same area, suggesting that *W. auropunctata* did not only diffuse naturally to invade new sites. Locally, the monitoring of the shifting of colony boundaries in Yaoundé showed that it was not constant, and that some boundaries even receded, resulting in an overall reduction in the surface area colonized. It would be interesting to investigate the causes of this reduction, which might be attributed to the biotic and/or abiotic resistance of the environment. Holway (1998), for example, found that Argentine ants spread to sites with a permanently flowing stream but did not to sites with an intermittently flowing stream, illustrating the abiotic resistance of the environment. It has already been speculated that, compared to islands, continental lands are less susceptible to bio-invasion due to their high species richness (Rejmánek, 1996). Some studies on the impact of *W. auropunctata* on native mainland diversities have supported this hypothesis (Klotz et al., 1995; Deyrup et al., 2000; but see Walker, 2006 for Gabon). Current studies on its impact on native ants in Cameroon and aggressive interactions between *W. auropunctata* and the most common local ant species such as *Pheidole megacephala* and *Myrmicaria opaciventris* will help in understanding the mechanisms of biotic resistance. Corroborating our results demonstrating the slow local movement of *W. auropunctata* colonies, it was reported from Gabon that infestation fronts advance slowly, only on the scale of tens of meters per year (Walsh et al., 2004; Walker, 2006). It is known that this species naturally expands mostly or entirely by nest budding rather than through nuptial flights (Hölldobler and Wilson, 1990), which have never been observed in Cameroon (MT, pers. obs.). In fact, the slow expansion or even contraction of

invasion fronts does not seem to be a rare phenomenon in invasive ants.

On a worldwide as well as on a countrywide scale (e.g., Cameroon), *W. auropunctata* has spread mainly through jump dispersal mediated by human activity such as the transportation of plants and construction material and the food trade (Wetterer and Porter, 2003; Foucaud et al. 2010, the present study). Our genetic analysis confirmed this stepping-stone migration pattern. Indeed, the two major clonal queen lineages (i.e., the originally introduced Q0 queen genotype and the dominant Q2 queen genotype) are found at virtually all of the invaded sites. This suggests a complex migration pattern with repeated jump dispersal events, far from the directional migration pattern uncovered in Gabon (JF, pers. comm.) and New Caledonia (Foucaud et al., 2006). This mode of dispersal, already noted in previous studies (Wetterer and Porter, 2003; Vonshak et al., 2009), is predominant for *W. auropunctata*, similarly to other invasive ant species such as *Linepithema humile* (Suarez et al., 2001).

The nature of the infested area in Cameroon, mainly human-disturbed environments, contrasts with data obtained in Gabon where *W. auropunctata* also occurs in forest reserves (Wetterer et al., 1999; Walker, 2006). However, even in forest reserves, it was found predominantly along riverbeds (which may help in its dispersal) and around petroleum platforms (Mikheyev et al., 2009) and less so in the undisturbed forest. According to these authors, it was only whenever a platform perimeter was fully colonized that a *W. auropunctata* population would inevitably spread for tens of meters into the surrounding forest. It is noteworthy that *W. auropunctata* is absent from “primary forests”, something previously observed in the Dja Forest Reserve (Deblauwe and Dekoninck, 2007). Interviews with scientists and technicians working in the Campo National Park and Korup Reserve indicated that this ant was not yet present in these areas. We should not forget that Gabonese and Cameroonian *W. auropunctata* populations very likely originated from human-disturbed habitats in Guadeloupe (Foucaud et al., 2010). Factors preventing *W. auropunctata* from entering natural environments in Cameroon should be elucidated and promoted to aid in its management. In addition, surveillance measures should be put into place to prevent its introduction into these wildlife reserves.

We found that a specific sexually derived clonal queen genotype (Q2) was clearly dominant over all of Cameroon, contrary to all other known introduced areas that are dominated by the originally introduced clonal queen genotype (Q0) (Foucaud et al., 2006, 2010; Vonshak et al., 2009). New Q2 clonal lineages are expected to be counter-selected because their genotype shares at least some part of the male genome, and, thus, their nests could suffer from inbreeding depression in the worker offspring or from diploid male load

(Foucaud et al., 2006). The success of this new clonal queen genotype across the entire country constitutes a unique illustration that the sexual production of new clonal lineages could be advantageous and does not preclude further invasion.

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