Exotic Ants

Biology, Impact, and Control of Introduced Species

David F. Williams

Westview Press
BOULDER • SAN FRANCISCO • OXFORD

Westview Studies in Insect Biology

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Published in 1994 in the United States of America by Westview Press, Inc., 5500 Central Avenue, Boulder, Colorado 80301-2877, and in the United Kingdom by Westview Press, 36 Lonsdale Road, Summertown, Oxford OX2 7EW

Library of Congress Cataloging-in-Publication Data Exotic ants: biology, impact, and control of introduced species / edited by David F. Williams

p. cm. — (Westview studies in insect biology) Summaries also in Spanish.

Includes bibliographical references and indexes. ISBN 0-8133-8615-2

1. Ants. 2. Insect pests. 3. Ants—Ecology. 4. Ants—Control. 5. Pest introduction. I. Williams, David F., 1938—

II. Series. QL568.F7E97 1994 628.9'657—dc20

93-33266 CIP

Printed and bound in the United States of America

The paper used in this publication meets the requirements of the American National Standard for Permanence of Paper for Printed Library Materials Z39.48-1984.

10 9 8 7 6 5 4 3 2 1

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Ant Fauna of the French and Venezuelan Islands in the Caribbean

Klaus Jaffe and John Lattke

Introduction

Surveys of the ants of the islands in the Caribbean have been made by Wilson (1988) and Jaffe et al. (1991). These studies are somewhat contradictory, as Wilson reports that from the 89 genera and 176 species to be found in the Antilles, 46% can be classified as endemic, while Jaffe et al. found no endemic species after 6 months of intensive collecting in the French islands. Kempf (1972) and later Brandão (1991) report endemic subspecies and varieties from the Caribbean islands in their catalogs of neotropical ants, but given the splintering of the past, it is likely that most, if not all, of these epithets will be synonymized. These latter authors used data taken from various independent collectors who collected at different times in the past. Few comparative studies among islands exist. We report here data from recent collections which were identified by the same person and kept in the same collection (Museo de Ciencias Naturales, Universidad Simon Bolivar, Caracas). This allows a better comparison of the ant fauna on different islands as well as an opportunity to reassess the degree of endemism and the distribution patterns of ants in the Caribbean islands.

The accompanying Table presents the data of this recent effort. Ants were collected by hand using the sampling technique described by Romero and Jaffe (1989). Fifty ant species were found on only one island out of 88 species reported (57%). None of these 50 species can be classified unequivocally as endemic to a single island nor to the Antilles, since 18 species that could be identified to species level are known to

TABLE 15.1. Ant species found on the French islands (St. Martin: SM; Desirade: DE; Guadeloupe: GU; Marie Galante: MG; Les Saintes: LS; Martinique: MR); Venezuelan islands (La Blanquilla: BL; Margarita: MA; La Orchila: OR; Las Aves: AV) and Aruba (AR), in the Caribbean.

Species		SM	DE	no	MG	MG LS	MR	BI		MA OR	AV	AR
MYRMICINAE	IE								4.3	1		`
	Acromyrmex octospinosus			×					×			
	Cardiocondyla wroughtoni	×	×	×	×		×		×			
	Cyphomyrmex rimosus			×	×	×	×					
	Crematogaster sp1			×								
	Crematogaster sp2			×								
	Crematogaster sp3						×					
	Crematogaster sp4							×			×	
	Crematogaster sp5											×
	Crematogaster sp6								×			
	Monomorium minimum		×	×	×		×					
	Monomorium destructor		×	×		×	×					
	Monomorium carbonarium		×	×								
	Monomorium floricola		×	×		×	×	×	×			×
	Monomorium salomonis			×		×						
	Mycetophylax conformis							×	×			×
	Mycocepurus smithi			×	×		×					
	Pheidole fallax		×	×	×	×	×					
	Pheidole megacephala X	×	×	×		×			×			
	Pheidole sp1							×				×

Species	SM	DE	CM	MG	ST	MR	BL	MA	OR	AV
MYRMICINAE (continued)										H
Pheidole sp2			×		×					
Pheidole sp3			×							
Pheidole sp4			×		×					
Pheidole sp5			×							
Pheidole sp6			×							
Pheidole sp7			×							
Pheidole sp9			×							
Pheidole sp10			×							
Pheidole sp11			×							
Pheidole sp12								×		
Pheidole sp13								×		
Quadristruma emmae			×							
Solenopsis geminata		×	×	×	×	×		×		
Solenopsis sp1			×							
Solenopsis sp2		×	×							
Solenopsis sp3			×							
Solenopsis sp4							×	×		×
Solenopsis sp5							×			
Solenopsis sp6								×		
Solenopsis sp7								×		
Strumigenys smithi			×							
Smithistruma alberti			×							

× ××	Species	SM	DE	GU	MG	rs	MR	BL	MA	OR	AV	AR
Tetramorium bicairnatum Tetramorium simillimum Trachymyrmex jamaicensis Wasmannia auropunctata Rogeria foreli Zacryptocerus clypeatus Conomyrma sp1 Conomyrma sp2 Conomyrma sp3 Conomyrma sp4 Tapinoma nelanocephalum Tapinoma sp4 Tapinoma sp8 Tapinoma sp8 Tapinoma sp8 Tapinoma sp8 Anochetus emarginatus Anochetus mayri Ectatomma ruidum Cnamptogenys striatula Hypoponera gleadowi Hypoponera gleadowi Hypoponera sp8 Leptogenys arcuata Codontomachus insularis Leptogenys arcuata Codontomachus insularis					Ť							
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Wasmannia airropunctata X X X X Rogeria foreli X X X X X X X X X X X X X X X X X X X	Trachymyrmex jamaicensis			×	w.							
Rogeria foreli X Zacryptocerus clypeatus ODERINAE Azteca delpi antillana X X X Conomyrma sp1 Conomyrma sp3 Conomyrma sp4 Tapinoma melanocephalum X X X X Tapinoma itorale X Tapinoma itorale X Tapinoma sp X Anochetus emarginatus X Anochetus emarginatus X Anochetus enarginatus X Anochetus enarginatus X Hypoponera gleadowi X Hypoponera gleadowi X Hypoponera sp8 X Leptogenys arcuata X Leptogenys arcuata X Anothemachus insularis X Codontomachus insularis X X	Wasmannia auropunctata			×	×	×	×					
Zacryptocerus clypeatus ODERINAE Azteca delpi antillana X X X Conomyrma sp2 Conomyrma sp3 Conomyrma sp4 Tapinoma melanocephalum X X X Tapinoma melanocephalum X X X X Tapinoma itorale X Tapinoma itorale X Tapinoma sp X Tapinoma sp X X X X X X X X X X X X X X X X X X	Rogeria foreli			×								
ODERINAE Azteca delpi antillana X X X Conomyrma sp2 Conomyrma sp3 Conomyrma sp4 Tapinoma melanocephalum X X X X Tapinoma melanocephalum X X X X Tapinoma litorale X Tapinoma sp X Anochetus mayri X Anochetus mayri X X ERINAE Anochetus mayri X X Anochetus mayri X X Hypoponera gleadowi X X Hypoponera sp8 X X X X X X X X Leptogenys arcuata X X X X X X X X X X X X X X X X X X	Zacryptocerus clypeatus								×			
Azteca delpi antillana X X X X Conomyrma sp1 Conomyrma sp3 Conomyrma sp4 Tapinoma melanocephalum X X X X X Tapinoma litorale X Tapinoma litorale X Tapinoma litorale X Anochetus emarginatus X ERINAE Anochetus mayri X Ectatomma ruidum X Ectatomma ruidum X Hypoponera gleadowi X Hypoponera gleadowi X Hypoponera sp8 Leptogenys arcuata X Codontomachus insularis X Codontomachus insularis X Conomyrma sp1 X X X X X X X X X X X X X	DOLICHODERINAE											
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Conomyrma sp2 Conomyrma sp3 Conomyrma sp4 Tapinoma melanocephalum Tapinoma litorale Tapinoma sp Tapinoma sp Anochetus emarginatus Anochetus mayri Ectatomma ruidum Champtogenys striatula Hypoponera gleadowi Hypoponera sp8 Champtogenys arcuata Codontomachus insularis Conomyrma sp2 X X X X X X X X X X X X X X X X X X	Conomyrma sp1							×				
Conomyrma sp3 Conomyrma sp4 Conomyrma sp4 Tapinoma melanocephalum Tapinoma litorale X Tapinoma litorale X Anochetus emarginatus Anochetus mayri Ectatomma ruidum X Gnamptogenys striatula Hypoponera gleadowi Hypoponera sp8 X Leptogenys arcuata X Codontomachus insularis X X X X X X X X	Conomyrma sp2							×		×		
Conomyrma sp4 Tapinoma litorale Tapinoma litorale Tapinoma sp Tapinoma sp Tapinoma sp Anochetus emarginatus Anochetus mayri Ectatomma ruidum Champtogenys striatula Hypoponera gleadowi Hypoponera sp8 K Leptogenys arcuata Codontomachus insularis X X X X X X X X X X X X X	Conomyrma sp3											×
Tapinoma melanocephalum X X X Tapinoma litorale X X Tapinoma sp X X Anochetus emarginatus X Anochetus mayri X Ectatomma ruidum X Gnamptogenys striatula X Hypoponera gleadowi X X Hypoponera speadowi X X Leptogenys arcuata X X Leptogenys arcuata X X Leptogenys arcuata X X	Conomyrma sp4								×			
Tapinoma litorale X Tapinoma sp X Tapinoma sp X Anochetus mayri Ectatomma ruidum X Gnamptogenys striatula X Hypoponera gleadowi X Hypoponera sp8 X Leptogenys arcuata X Leptogenys arcuata X X X X X Aypoponera sp8 X X Codontomachus insularis X X X	Tapinoma melanocephalum	1	×	×	×		×					×
ERINAE Anochetus emarginatus Anochetus mayri Ectatomma ruidum Schamptogenys striatula Hypoponera gleadowi Hypoponera speadowi Hypoponera sp8 X Leptogenys arcuata X X X X X X X X X X X X X X X X X X	Tapinoma litorale	2,	×									
ERINAE Anochetus emarginatus Anochetus mayri Ectatomma ruidum Cnamptogenys striatula Hypoponera gleadowi Hypoponera speadowi Hypoponera sp8 Leptogenys arcuata Codontomachus insularis X	Tapinoma sp	,		×								
× ××××××	ERINAE											
× ××××××	Anochetus emarginatus								×			
× ××××××	Anochetus mayr						×					
× ×××××	Ectatomma ruidum	1		×			×		×			
× ××××	Gnamptogenys striatula	1		×								
× ××××	Hypoponera gleadow	į.		×								
× ×××	Hypoponera punctataissima	1		×			×					
× ××:	Hypoponera sp8	~		×								
×	Leptogenys arcuata	2		×								
	Odontomachus insularis			×	×		×					
×	Odontomachus bauri	1		×			×					

Species	SM	DE	Cn	MG	FS	MR	BL MA	_	OK	AN	
PONERINAE (continued)											
Pachycondyla stigma		×	×								
Platuthurea sinuata			×	×		×					
Prionopelta antillana			×			×					
PSEUDOMYRMECINAE											
Pseudomurmex curacaensis			×								
Pseudomyrmex flavidulaus			×	×							
Pseudomyrmex gracilis								×			
FORMICINAE											
Brachymyrmex sp1							×				
Brachymyrmex sp2			×	×		×					
Brachymyrmex sp3		×	×	×		×					
Brachymyrmex sp4			×			×					
Camponotus abdominalis							×				
Camponotus crassus									×	×	
Camponotus sexguttatus			×								
Camponotus lindigi											
Camponotus sp1								×			
Camponotus sp2			×			×					
Camponotus sp3			×								
Camponotus sp4			×								
Camponotus sp8			×			×					
Camponotus sp9											
Camponotus sp10											
Myrmelachista sp1			×								
Paratrechina longicornis		×	×	×	×	×	×	×	×	×	
Paratrechina sp1							×				
Paratrechina sp2								×			

exist elsewhere in the continent. The remaining 32 species are only classified as morpho-species belonging to genera which lack recent taxonomic revisions. Thus, the real number of endemic species in the Lesser Antilles is far lower than 36% and probably close or equal to zero. Wilson (1988) reported endemic species from islands close to South America, such as St. Thomas, St. Vincent, St. Lucia and Trinidad but none from the French islands. We confirm the absence of endemic species from the French islands, but suggest that endemism reported from other islands in the Lesser Antilles are probably due to incomplete taxonomic study of the collections rather than true endemism.

Few ant species have been found only on the Caribbean islands (Kempf 1972). The species which are clearly endemic are found only on the large islands of the Greater Antilles (Cuba, Jamaica, Puerto Rico and Hispaniola). Species collected only from the Lesser Antilles are generally distributed throughout the neotropics or have been collected from most parts of the Caribbean basin, including the mainland of the continent. We have found that ant species in our collections can be placed into 3 categories: those which are found (1) on most islands, (2) only on the islands of the southern Caribbean, close to the South American continent, and (3) only on the Lesser Antilles, north of St. Lucia. Among the two latter groups, species in the genus Conomyrma appear to be common on islands near the Venezuelan coast, but are absent in the French Antilles. On the other hand, species in the genus Tapinoma are common in the French Antilles but absent on Aruba and the Venezuelan Islands. Similar patterns can be found among species in the genera Crematogaster, Pheidole and Solenopsis. These results would suggest that the Lesser Antilles could be grouped into two distinct biogeographical zones coinciding with the southern and the northern arc of the Lesser Antilles. The limits between them would lay somewhere near St. Lucia. The fauna in the southern arc, including the islands close to Venezuela, would be partially or totally related to the South American fauna, whereas the fauna of the northern arc would be more closely related to that in the Greater Antilles.

As a whole, the Lesser Antilles seem to be biogeographically different from the Greater Antilles, if only because few of the known endemics from the Greater Antilles are found on the Lesser Antilles. Two notable exceptions which exemplify dispersal from the Greater Antilles to the Lesser Antilles are (1) Trachymyrmex jamaicensis which is found on Guadeloupe and is also common on islands of the Greater Antilles and (2) Azteca delpini antillana which occurs on Guadeloupe, Hispaniola and St. Lucia, but is absent from Venezuela which suggests

it dispersed from Hispaniola to the Lesser Antilles.

When data from this study is added to that summarized by Wilson

(1988) and then considered in the context of the biogeographic models discussed by Liebherr (1988), the biogeographic conclusion is that the southern arc of the Lesser Antilles seems to have been colonized by ants dispersing from Venezuela. This coincides with one of the four tracks of colonization proposed by Rosen (1975), the South American Caribbean track. The northern arc seems to have been colonized by ants that dispersed from South America and from the Greater Antilles. No indication as to vicariance (Croizat 1976) in the Lesser Antilles is evident from our data. This confirms suggestions by Liebherr, and others cited in Liebherr (1988), that the insect population of the Lesser Antilles is rather recent and has colonized the islands by dispersing from the mainland or from the Greater Antilles.

One interesting feature is that widely distributed ant species or tramp species; i.e. Tapinoma melanocephalum, Paratrechina longicornis, Cardiocondyla wroughtoni, Monomorium floricola, Pheidole megacephala, Solenopsis geminata, and Wasmannia auropunctata are never simultaneously found on all the islands sampled. Their absence from some islands is probably not due to sampling errors, as these species, when present, become the dominant ants in their habitat. However, the alternative hypothesis needs to be investigated since tramp species could become sub-dominant, i.e. cease to dominate other species. The lack of tramp species on some islands suggests that in some situations, they can be kept out of islands even in the presence of intense human commerce and activities.

The only ant species present which has been reported as a local pest is *Acromyrmex octospinosus* in Guadeloupe. Other species, although regarded as pests elsewhere do not seem to reach this status in all situations. For example, *W. auropunctata* is known as a stinging ant in Martinique and Guadeloupe but does not seem to be much of a problem to farmers. Old reports of ants becoming pests in the Caribbean do exist. For example, in 1500, an ant species, probably *S. geminata*, was reported as a pest on Hispaniola and Jamaica. Also, in 1760 reports of similar pest problems occurred on Barbados, Grenada and Martinique (Reaumurs report in an unpublished work of Wheeler cited by Holldobler and Wilson 1990). Today, no pest problems caused by *S. geminata* in the Lesser Antilles are known to us. Thus, interestingly, the only known pest ant today is *A. octospinosus*, which was introduced to Guadeloupe around 1954 (Blanche 1961).

The loss of an ant's pest status at some period of time after its initial introduction seems to be a general feature of pests. Two possible explanations are available. Either the ants become less ecologically aggressive, i.e. they disperse less, individual colonies may require larger foraging territories, or the species may specialize in certain ecosystems

and thus compete with fewer ant species. Also, humans may habituate to the ants and thus not consider them to be pests any more. For the first hypothesis to be confirmed, comparative behavioral studies of recently introduced ants vs. well established populations are needed. Evidence for the second hypothesis exists because many of the pest species in the Caribbean can be managed and can thus be used as biological control agents (Pollard and Persad 1991, Jaffe et al. 1991). The truth is probably a mixture of the two proposed hypothesis which could explain the "natural taming" of pest ants.

As previously mentioned, tramp species, although widely distributed among the islands have not colonized all of them. For example, W. auropunctata, a known tramp and pest species, was not found on the southern islands studied and P. longicornis was not found on Saint Martin, although it was present on all the other islands studied. P. megacephala seems to be absent or is very infrequent on Margarita and S. geminata could not be collected on Saint Martin. This pattern is congruent with a colonization model described by island biogeographic theories (MacArthur and Wilson 1967), where impediments to colonization and occasional extinction of some species determine the species distribution on islands.

Some of the islands, such as St. Martin, are poor in ant fauna, whereas the two islands with the largest diversity of ecosystems, Guadeloupe (which was well sampled) and Margarita (which was poorly sampled compared to its size and ecosystem diversity), have islands with the largest number of species. On the other hand, xeric islands such as Blanquilla, Las Aves, and La Orchila, have few species, confirming that the diversity of ecosystems is an important feature in determining the number of species on an island.

Our ant collection completes and corrects the data on the biogeography of the ant fauna in the Antilles (Wilson 1988), including species from Margarita, La Blanquilla, Las Aves and Aruba, and shows an increase in the number of species reported for Guadeloupe and Martinique. Our data also suggests that Wilson underestimated the ant population in this area, possibly due to the fact that intensive collecting had

not been done on these islands.

Conclusion

In conclusion, the ant fauna in the Caribbean islands, at least in the Lesser Antilles, appears to be of recent origin, as no clear endemism is apparent. Potential pest species seem to be very good colonizers, causing trouble to humans shortly after introduction to an island.

However, their importance as pests appears to decrease with time, suggesting that aggressive colonizing ant species develop a more passive ecological behavior as they adapt to their new environment.

Resumen

Se colenctaron hormigas por muestreo directo en la islas Francesas y Venezolanas de las Antillas y en Aruba. Los resultados revelan que la fauna de hormigas en el Caribe, al menos en las Antillas Menores, es de origen reciente, ya que no presentan endemismo aparente. Biogeograficamente, las Antillas Menores muestran dos zonas, una al sur de Saint Lucia, con especies provenientes de Venezuela, y otra al norte con especies tanto del continente Suramericano como de las Antillas Mayores. Especies plaga potenciales aparecen como buenas colonizadoras, creando problemas solo durante el periodos inmediatamente despues de su introducción, disminuyendo su importancia como plagas lo que sugiere que especies de hormigas agresivamente colonizadoras desarrollan comportamientos ecologicamente mas pasivos al adaptarse a su nuevo ambiente.

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