The Tramp Ant *Wasmannia auropunctata*: Autecology and Effects on Ant Diversity and Distribution on Santa Cruz Island, Galapagos[1]

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ABSTRACT

A large-scale ecological experiment is underway on Santa Cruz Island, Galápagos, where an introduced ant (*Wasmannia auropunctata*) is devastating all sympatric ants. Collecting, observation, and experiments were used to study the extent and mechanisms of *Wasmannia*'s success. Seventeen taxa of ants were collected, of which four were endemic, and most of the rest were well-known tropical tramp species. Current distribution of all species was determined. Greatest species diversity occurred in the arid zone, which was also the area of lowest *Wasmannia* density. Systematic collecting-transects showed that *Wasmannia* either exterminates or reduces to very low density all sympatric species on Santa Cruz. In many areas the ant fauna composition changes from 100 percent *Wasmannia* to 0 percent *Wasmannia* within 100 m. Experiments with artificial baits arranged in transects perpendicular to sharp boundaries showed that *Wasmannia* mobilized the greatest number of workers, was very successful in replacing other species, and remained the longest time at baits. *Wasmannia* ate primarily invertebrates, honeydew, and, in the hot season, plants parts. It was active 24 hr/day during three 24-hour periods. There were no central, intraspecifically defended nests. Nests were small and numerous. No intraspecific aggression was ever observed, either under natural conditions or at bait stations. *Wasmannia* density increased with altitude up to near the summit of the island. The species is not presently found in either the driest or wettest parts of Santa Cruz. Currently no ant species occurs on Santa Cruz which can coexist with *Wasmannia* in zones of high *Wasmannia* density. Because *Wasmannia* occurs in high density and consumes a variety of invertebrate prey, it is probably causing major ecosystem changes in invertebrate diversity and density.

RESUMEN

Un experimento ecológico de gran escala se desarrolla actualmente en Isla Santa Cruz, Galápagos, donde una especie introducida de hormiga (*Wasmannia auropunctata*) está diezmando a las otras especies. La extensión y los mecanismos del éxito de *Wasmannia* fueron estudiados por medio de colecciones, observaciones y experimentos. Diecisiete especies de hormigas fueron recogidas; 4 eran especies endémicas, mientras que la mayoría de las restantes eran especies bién conocidas en otras zonas de los trópicos. Se presenta la distribución actual de cada especie. La mayor diversidad de especies se observó en la zona seca; esta zona es a la vez la zona de menor densidad de *Wasmannia*. Por colecciones cuantitativas se demostró que en Santa Cruz *Wasmannia* extermina o diezma a las otras hormigas. En muchos sitios se pueden ver áreas de sólo *Wasmannia*, a la par de áreas sin una sola *Wasmannia*, en el curso de 100 m. Experimentos con cebos, que se llevaron a cabo en estas áreas de cambio abrupto, indicaron que *Wasmannia* estableció los grupos de trabajadoras más grandes, obtuvo más exito en reemplazar a otras especies en los cebos, y permaneció más tiempo que las otras hormigas en ellos. *Wasmannia* se alimentaba principalmente de in vertebrados, rocío de miel (excremento de Homóptera), y durante la estación seca y caliente de algunas partes de las plantas. Trabajadoras activas fueron observadas cada hora durante tres períodos de observación de 24 horas. *Wasmannia* no construyó grandes nidos centrales, los nidos fueron pequeños y nunca observamos agresión entre ellos. La densidad de las *Wasmannia* aumentó con la altitud, hasta llegar a un límite cerca de la cima de la isla. En el presente no se da ni en la parte más húmeda de la isla, ni en la más seca. Actualmente no existe ninguna especie que pueda coexistir con las *Wasmannia* en las áreas en que existe una mayor densidad de las mismas. Debido a sus hábitos alimenticios y su densidad alta es probable que *Wasmannia* haya causado grandes cambios en la diversidad y densidad de los invertebrados en los ecosistemas de Santa Cruz.

WITH THE RISE OF INDUSTRIALIZED MAN the natural processes of immigration and extinction have accelerated tremendously. Particularly on islands, human transport has led to countless cases of introduced species. Although these introductions have frequently led to extinction of indigenous island species, exact details of the introduction-competition/predation-extinction process have rarely been documented.

There are numerous examples of species of ants which have, with the help of man, spread over enormous areas. Today, few or no inhabited islands lack in-

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troduced ants. Species replacements and interactions between introduced and indigenous ants have been documented on many islands (Wilson and Taylor 1967, Wilson 1971, Greenslade 1972, Levins *et al.* 1973, Lieberburg *et al.* 1975). However, there are very few quantitative data on the mechanisms of these interactions.

We report here results of a study on an extremely successful introduced species, *Wasmannia auropunctata* (Roger), on Santa Cruz Island, Galápagos. *W. auropunctata* is a small (less than 2 mm long), golden or reddish brown ant distinguished by a painful sting and a broad geographic range. On the American continents the species occurs from Argentina to Florida (Spencer 1941, Kusnezov 1951), and it is also present on many Caribbean Islands, on the Galápagos, and in the Old World tropics (Creighton 1950). Spencer (1941), Fernald (1947), and Osburn (1949) have described the natural history of the species in agricultural and domestic environments in Florida, and Kusnezov (1951) has presented qualitative ecological observations on *Wasmannia* in Argentina.

The primary goal of the current study was to document the current status of *Wasmannia auropunctata* on Santa Cruz, and to study those aspects of the aut- and syn-ecology which appeared to be important to its success. As the work progressed, it became clear that *Wasmannia* was obliterating the other ants of Santa Cruz. A special effort was then made to study *Wasmannia* in areas where interactions with other ants were in progress, and to examine the nature of these interactions.

STUDY AREA AND HISTORY

Santa Cruz Island is a large (904 km^2, Wiggins and Porter 1971) oceanic island of volcanic origin, located approximately in the center of the Galápagos Archipelago. Because it is a relatively high island (maximum elevation 864 m, Wiggins and Porter 1971), it supports vegetation ranging from arid scrub to wet montane forest. Further descriptions of the vegetation and climate are provided by Wiggins and Porter (1971) and Hamann (1979).

The date of introduction of *Wasmannia* onto Santa Cruz Island is unknown. One early colonist recalls that *Wasmannia* first appeared between 1910 and 1920. Whatever the actual date of introduction, the species was not common in the first third of this century. It was not collected in 1905, 1924, or 1932 (Wheeler 1919, 1924, 1933). The first published record of *Wasmannia* in Galápagos was by Silberglied (1972), who described the history of the species in the islands and noted some ecological dangers posed by the introduction.

MATERIALS AND METHODS

Field work was carried out from July to September 1975 (the cool season) and from February to May 1976 (the hot season). Ants were collected by hand or with aspirators and preserved in 80 percent ethanol. Voucher specimens are stored in the Harvard Museum of Comparative Zoology. Foraging behavior of ants was studied with bait lines consisting of 22 (except one case of 11) bait stations in a straight line at 10 m intervals. Each station consisted of a petri dish filled with a concentrated water solution of table sugar. At each census of a station, the number and species of workers present was recorded. We could not distinguish between *Pheidole williamsi* Wheeler and *P.* species (*flavens* group) in these observations, so for the baiting experiments these taxa are combined. Baits were always observed sequentially, but the time between successive censuses at a station varied from five to 60 minutes.

Between February and May 1976, systematic collecting was carried out along 19 200 m transects perpendicular to the north-slope highway. Each transect (approximately 2 m wide) was searched for two person hours in an attempt to collect all species present. Transects were located at either 0.5 or 1.0 km intervals measured from the twin craters (Los Gemelos).

To determine the daily cycle of activity of *Wasmannia*, the behavior of ants in a 1 m^2 quadrat was monitored for 24 hours on three occasions. The quadrat was located above the cliff at the Charles Darwin Research Station (CDRS) in arid zone vegetation at the base of a *Bursera graveolens* tree. Dates of observation were 19 September 1975 (cool season, full moon), 29 February 1976 (hot season, new moon), and 16 March 1976 (hot season, full moon). Behavior was recorded during a five-minute period beginning every hour; a flashlight was used for nocturnal observations. Approximate density of *Wasmannia* at several sites was determined by counting all active workers up to a height of 2 m, in either 10 or 20 1 m^2 quadrats at 10 m intervals. Biomass of foods brought to nests was determined by observing 15 different nests for 25 minutes each in the south-slope arid, transition, and *Scalesia* zones. All solid foods brought to each nest were taken from workers and weighed. Number of workers bringing honeydew (as judged by swollen abdomens) was also recorded. The weight of an average load of honeydew was calculated by weighing 1000 *Wasmannia* with full abdomens

(0.27 g), subtracting the weight of 1000 *Wasmannia* maintained without food for 24 hours (0.08 g), and dividing by 1000.

SYNECOLOGY OF ANTS OF SANTA CRUZ ISLAND

We collected 17 species of ants on Santa Cruz (table 1). Four taxa were endemic; most of the rest were common tropical "tramp" species. The minimum rate of endemism on Santa Cruz is therefore 4/17 or 24 percent, a figure which is considerably lower than the presettlement rate of endemism, due to the numerous introduced species.

All four endemic species that were collected in the early part of this century (Wheeler 1919, 1924, 1933) were also collected by us. Thus, over a 50-year period no described endemic ant has become extinct on Santa Cruz.

It is difficult to document introductions in the last 50 years, since some species could have been overlooked by early collectors. However, both *Wasmannia* and *Monomorium floricola* (Jerdon) were missed by early collectors and yet are currently common to abundant. It therefore seems likely that at least two of the current 17 species represent recent introductions to Santa Cruz.

Table 1 shows the numbers and locations of collections for all species on Santa Cruz. The data do not reflect equal sampling effort in all areas, nor equal rates of collection of each species. Only qualitative data are given for *Wasmannia,* because we frequently ignored it when collecting other species. The data give a crude index of relative collectability within each zone. For example, *Cylindromyrmex williamsi* Wheeler was collected in only two of 429 samples (both samples from the same general area on the same day). While the true relative frequency of this species is unknown, it was clearly difficult to collect.

Of the 17 species collected, eight were concentrated in the arid and transition zones, seven had very broad altitudinal ranges, and two were confined principally to higher elevations (table 1). The arid zone had the highest ant diversity of the five major vegetation zones sampled; only two of 17 species were never collected in the arid zone. Note the greater species diversity and frequency of collection in the north *Scalesia* and transition zones relative to the

TABLE 1. *Number and location of collections of ants on Santa Cruz Island, Galápagos.*

Taxon (Abbreviation)	S. arid zone	S. transition zone	S. *Scalesia* zone	*Miconia* zone	Summit-fern/sedge zone	N. *Scalesia* zone	N. Transition zone	N. arid zone	Total
Tapinoma melanocephalum (Ta)	12	0	0	0	0	0	0	4	16
Conomyrma sp. (Co)	10	0	0	0	0	0	1	9	20
Tetramorium simillimum (Ts)	3	0	0	0	0	0	0	0	3
Cylindromyrmex williamsi[a] (Cw)	0	0	0	0	0	0	0	2	2
Camponotus macilentus[a] (Cm)	6	0	0	0	0	0	0	3	9
Paratrechina longicornis (Pl)	8	0	0	0	0	1	0	0	9
Monomorium floricola (Mf)	14	0	1	0	0	1	0	13	29
Solenopsis globularia (Sg)	17	0	0	0	0	3	11	21	52
Tetramorium guineense (Tg)	12	1	6	0	0	3	1	0	23
Pheidole williamsi[a] (Pw)	5	0	0	1	1	3	18	9	37
Camponotus planus[a] (Cp)	6	1	2	0	0	4	18	13	44
Pheidole sp. *flavens* group (P)	2	4	3	8	1	22	9	0	49
Paratrechina vaga (Pv)	23	2	7	5	2	27	10	17	93
Cardiocondyla sp. (Ca)	1	0	0	2	0	2	13	4	22
Hypoponera sp. (H)	0	0	2	4	1	13	4	0	24
Strumigenys sp. (S)	0	0	2	3	0	1	1	0	7
Total for zone	119	8	23	23	5	80	86	95	439
Wasmannia auropunctata[b] (Wa)	+	+	+	+	−	+	+	−	

[a]Endemic species. [b]+ = present, − = absent.

southern counterparts. The south-slope depression is due to *W. auropunctata* (see below).

EFFECTS OF *Wasmannia* ON ANT DISTRIBUTION.—Table 2 shows the results of a series of transects perpendicular to the north-slope highway. The depressing effect of *W. auropunctata* on ant diversity is obvious. At only one site did *Wasmannia* and other species co-occur. At this location we observed seven fights between *Wasmannia* and other species in a 45-minute period.

As the data in table 2 imply, boundaries of *Wasmannia* distribution were often extremely narrow and well demarcated. Composition of the ant fauna changed from 100 percent to 0 percent *Wasmannia* in the course of 100 or even 50 m. Table 3 shows the results of baiting experiments run perpendicular to sharp boundaries. Seven of the eight experiments were run in areas of what appeared to be uniform habitat, so we discount the possibility that these boundaries are due to vegetation, soil, climate, or a similar factor. Interspecific fighting on the baits was often observed.

In addition to sharp boundaries, we also observed areas where *Wasmannia* and other species co-occurred. We suspect that co-occurrence has at least two explanations. One is that in certain areas (e.g., the arid zone around Puerto Ayora) *Wasmannia* becomes dominant only during the hot, wet season. Other species may survive by being active during the rest of the year. A second explanation is historical. The northwest area of the island is undergoing rapid expansion of *Wasmannia* (according to residents), and co-occurrence may be a fairly ephemeral phenomenon. In all areas where the density of *Wasmannia* was high, other ants were either totally absent or extremely rare. Spencer (1941) encountered a similar situation in agricultural situations in Florida, where he reported that ". . . within the network of heavy (*Wasmannia*) infestation other ant species are conspicuous by their absence."

FORAGING PATTERNS.—Patterns of foraging in *Wasmannia* and other species were investigated at a series of sugar-water bait stations. We examined the following variables: size of foraging groups, ability to encounter baits, ability to persist at baits, ability to monopolize baits, and success at interspecific replacement.

Eleven of the 17 species that we collected on Santa Cruz appeared at the bait stations (table 3). Of the

TABLE 2. *Distribution of ants on the north slope of Santa Cruz. Data come from a two person-hour search of a 200 m transect at each location.* (Abbreviations correspond to genus and species of ants in table 1.)

Distance (km) from Los Gemelos	Altitude (m)	Vegetation	Ants										
			Wa	H	P	Pw	Pv	Pl	Tg	Cp	Ca	Sg	Co
0	619	S[a]		X	X		X						
0.5	600	S		X	X		X	X	X	X			
1.0	—	S		X	X		X		X	X			
1.5	510	T	X										
2.0	480	T	X										
3.0	418	T	X										
4.0	408	T	X	X		X				X	X	X	
5.0	344	T				X	X			X		X	
6.0	311	T				X	X			X	X	X	X
7.0	290	A			X					X		X	
9.0	134	A				X				X		X	
10	104	A					X			X		X	
11	91	A					X			X		X	
12	—	A				X	X					X	X
13	43	A				X	X			X			
14	37	A				X	X			X			
15	24	A					X			X		X	
16	18	A					X			X		X	
17	6	A								X		X	X

[a]S = *Scalesia* zone, T = Transition zone, A = Arid zone (after Wiggins and Porter 1971).

TABLE 3. *Results of sugar-water baiting experiments run at boundaries of* Wasmannia auropunctata *distribution.* X *indicates that a species was counted at a station during the course of the experiment.*

Location	Date	Species[a]	Distance from origin (m) 0	10	20	30	40	50	60	70	80	90	100	110	120	130	140	150	160	170	180	190	200	210
N. slope transition zone	8 V 76	Ca	X	X	X		X					X	X	X	X									
		Sg	X	X		X																		
		P	X	X	X	X	X	X	X	X	X		X											
		Pv		X				X	X	X	X													
		Cp										X												
		Wa											**X**	X	X	X	X	X	X	X	X	X	X	X
S. slope *Scalesia* Cerro Mesa	1 IV 76	P	X	X		X	X	X		X		X												
		Pv	X	X	X	X	X	X	X	X	X	X	X	X		X								
		Wa											X	X	X	X	X	X	X	X	X	X	X	X
N. slope *Scalesia* zone	1 V 76	Pv	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X					**X**		
		P											X											
		Wa												X	X	X	X	X	X	X	X	X	X	X
N. slope transition zone	22 V 76	P	X	X	X	X	X																	
		Ca		X		X		X																
		Wa				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Miconia zone	10 V 76	Pv	X	X					X			X												
		P	X		X																			
		Wa															X	X	X	X	X	X	X	X
N. slope *Scalesia*	25 V 76	P	X	X	X	X	X		X															
		Sg		X	X																			
		Tg			X		X	X		X	X	X	X	X										
		Cp				X																		
		Pv						X																
		Wa															X	X				X	X	X
S. slope arid zone	19 IV 76	Sg	X	X			X						X	X	X									X
		Pl	X	X				X	X		X	X		X										
		Mf	X										X	X										
		Tm	X		X					X	X		X		X							X	X	X
		Tg						X																
		Wa												X	X	X	X	X	X	X	X	X	X	X
S. slope arid zone	15 III 76[b]	Sg		X				X																
		Tm	X	X	X	X	X	X	X	X														
		Mf	X	X		X		X																
		Pl	X	X		X																		
		Wa	X						X		X	X	X											

[a]Species abbreviations correspond to Table 1.
[b]Only 11 stations were run for this experiment.

TABLE 4. *Species replacement by ants at sugar-water baits on Santa Cruz Island. Data are from eight experiments (table 3) combined. Species abbreviations correspond to table 1.*

Losers (species being replaced)	Winners (replacing species) Cp	P	Sg	Tg	Pv	Ca	Wa	Tm	Mf	Pl	Total losses	% Losses
Cp	X	3	—	—	—	1	—	—	—	—	4	67
P	1	X	1	1	9	1	2	—	—	—	15	42
Sg	—	3	X	1	—	2	3	1	2	4	16	67
Tg	—	—	—	X	—	—	—	—	—	1	1	17
Pv	—	9	1	—	X	1	10	—	—	—	21	66
Ca	1	4	—	1	1	X	7	—	—	—	14	74
Wa	—	2	1	—	1	—	X	1	—	3	8	25
Tm	—	—	5	—	—	—	2	X	5	6	18	82
Mf	—	—	—	—	—	—	1	1	X	1	3	21
Pl	—	—	—	2	—	—	—	1	4	X	7	32
Total wins	2	21	8	5	11	5	24	4	11	15		
% Wins	33	58	33	83	34	26	75	18	79	68		

species that did not appear, three were rare and one (*Camponotus macilentus* F. Smith) was nocturnal/crepuscular. Although *Conomyrmya* sp. and *Hypoponera* sp. were relatively common, for unknown reasons they never appeared at baits. Because the majority of common species appeared at the baits, the following results apply to a large percentage of ant interactions on Santa Cruz.

Because the dishes were checked in sequential series, we used species replacement in subsequent checks as an index of interspecific competitive ability. Table 4 presents the data on species replacement from all eight experiments combined. Species replacements did not occur randomly. There was extremely significant heterogeneity among the eight most common species in their rates of replacing and being replaced ($X^2_{7df} = 35.5$, $P < 0.005$).

Table 5 shows the number of consecutive observations that a species was present at bait stations. We hypothesized that species which were able to utilize dishes for a long time would also be the species which had good "win-loss" records. This assumption turned out to be true. There was a positive correlation between the percentage of wins and the percentage of observations at which a species was present three or more times in succession ($r_{s,8} = 0.685$, $P < 0.05$). There are at least two plausible explanations for this correlation. It might be due to random mixing of non-interacting species which have intrinsically different temporal resource utilization patterns, or alternatively, it could be due to interspecific competition: species which remained longer at baits did so because they were superior competitors.

TABLE 5. *Percentage occurrence of observation sequences of different lengths at sugar-water baits. Data from eight experiments (table 3) combined.*

Species	Percent of all observation sequences lasting: 1 check	2 checks	3 checks	N (sequences)
Wa	13	7	80	101
Tg	10	20	70	10
Mf	38	13	50	8
P	34	18	47	38
Pv	39	14	46	56
Pl	44	11	44	18
Tm	44	19	37	27
Cp	67	17	17	6
Ca	85	15	0	20
Sg	57	29	14	21

Another hypothesis was that species which had good win/loss records would also be successful at excluding all other species from their baits. However, the correlation between percent wins and percent exclusive occurrence on dishes (table 6) was not significant. Six of the eight species for which there were sufficient data to calculate a win/loss record did fall into the predicted relationship. Two species, however, differed greatly from expectation. *Tapinoma melanocephalum* (Fabricius) "won" only 18 percent of its replacement events, yet in 61.5 percent of its occurrences it was the only species at that station. Perhaps the high percentage of sole occupancy of a bait reflects rapid utilization of unoccupied baits rather than interspecific exclusion. *Monomorium floricola* had a high winning percentage (79%), but in only 30 percent of its occurrences was it the only species at the bait station. Evidently *M. floricola* can forage successfully with many species, even though it cannot exclude them.

Our definition of a "winning" species was based on species replacement at subsequent checks. Using this criterion there were at least two cases where species would incorrectly be recorded as "winners." Species encountering previously occupied but currently vacant baits would appear to have repulsed the previous species (as suggested for *T. melanocephalum*). Alternatively, species which were actively repulsed from a bait but occupied the bait after the dominant species left would be scored as "winners." The only way to determine if such cases are common relative to competitive exclusion would be to rerun the experiments using continuous observation (which would mean a greatly reduced sample size).

TABLE 6. *Percentages of solitary occurrence for species during baiting experiments on Santa Cruz.*

Species	Number occurrences	% of observations with no other species present
Wasmannia auropunctata	458	81.9
Tetramorium guineense	33	84.3
Paratrechina vaga	189	64.0
Tapinoma melanocephalum	65	61.5
Paratrechina longicornis	63	57.1
Pheidole spp.	127	52.8
Camponotus planus	10	50.0
Solenopsis globularia	56	46.4
Monomorium floricola	34	29.4
Cardiocondyla sp.	31	29.0

Table 7 shows the frequency distribution of the maximum number of individuals occurring at each dish at which a given species appeared. *Wasmannia auropunctata* showed the broadest range of maximum number recruited. It also recruited the largest groups. Thirty-five percent of *Wasmannia*'s maximum groups were composed of more than 128 workers, whereas only 4 percent of all other species' maxima were this large. A species' win/loss record was positively correlated with a crude index of size of group recruited (the octave in which the median group size occurred, table 7: $r_{s,8}=0.655$, $P < 0.05$). In general, species which recruited larger groups were "winners," species which recruited only small groups were "losers."

We were unable to detect any systematic temporal pattern in the order in which species found or took over baits. We compared the number of times each species was the first found on a bait with the number of times it was last on a bait, for the four species for which we had sufficient observations. There was no significant interaction between species identity and order of appearance. Sample sizes were not large, however, so the question deserves further study.

TABLE 7. *Frequency distribution (%) of maximum numbers observed foraging at individual sugar-water bait stations on Santa Cruz.*

	Maximum number observed										
Species	1-2	3-4	5-8	9-16	17-32	33-64	65-128	129-256	257-512	512	Number of bait stations
Wasmannia auropunctata	6	1	1	10	16	13	17	9	24	2	87
Paratrechina vaga	15	12	15	27	12	12	7	—	—	—	41
Pheidole spp.	10	13	10	16	6	26	13	3	3	—	31
Solenopsis globularia	35	—	24	—	24	12	6	—	—	—	17
Tapinoma melanocephalum	18	—	12	24	18	29	—	—	—	—	17
Cardiocondyla sp.	47	13	13	—	20	—	7	—	—	—	15
Paratrechina longicornis	36	9	9	—	9	18	18	—	—	—	11
Tetramorium guineense	—	—	11	—	11	22	56	—	—	—	9
Monomorium floricola	17	17	—	—	—	33	33	—	—	—	6
Camponotus planus	67	—	17	17	—	—	—	—	—	—	6
Total											240

AUTECOLOGY OF *Wasmannia auropunctata*

DIET AND FEEDING RATES.—*Wasmannia auropunctata* ate a wide variety of foods (table 8), primarily invertebrates, plant parts, and honeydew. Although the data in table 8 were not collected randomly, plant parts were more frequent in the hot season (46% of observations) than in the cool season (6%).

TABLE 8. *Food items collected from foraging* Wasmannia auropunctata *on Santa Cruz.*

ARTHROPODS	
Insects	
Coleoptera	26
Dictyoptera	28
Lepidoptera	42
Hemiptera	43
Orthoptera	5
Neuroptera	5
Pscoptera	1
Hymenoptera	39
Chilopoda	2
Arachnida	11
Crustacea (mainly isopods)	38
Unidentified arthropods	101
GASTROPODS	29
ANNELIDS	3
AVES (feather)	1
PLANT MATERIAL	
Seeds	69
Flowers, leaves, stems, unidentified	173
	616

Wasmannia has at least two common foraging patterns. In the case of large, solid objects workers cooperate; for example, during two hours of observation we observed 15 to 20 workers move an intact isopod about 50 cm. At honeydew and sugar-water baits, large groups are recruited. A common sight is two parallel lines of workers going in opposite directions, the full workers with swollen abdomens and the others with noticeably smaller abdomens.

In order to determine the relative importance of honeydew, during the 1976 hot season we observed foraging workers at a series of nests in the arid, transition, and humid zones on the southern slope. The data (table 9) show that in all zones honeydew was an order of magnitude more important (wet weight) than other items as a food source. For every worker transporting solid items, there were 60 to 110 transporting honeydew (table 9).

We do not know how these rates compare to night-time or cool-season rates; however, it is clear that *W. auropunctata* consumes substantial quantities of invertebrates. An assumed density of three nests of *Wasmannia* per m^2 and 24 hr year-round activity (see below) leads to a projected consumption of 0.55 kg of solid foods (mostly invertebrates) per m^2 per year in the transition zone. Some unknown portion of the invertebrates are scavenged, but many instances of active predation were observed; so *W. auropunctata* probably affects the native invertebrate fauna significantly, and may also affect higher trophic-level organisms such as birds and lizards that depend on invertebrates for food (cf. Brown and Davidson 1977).

TABLE 9. *Daytime feeding rates of* Wasmannia auropunctata. *Data are based on 25-minute observations of each of 15 nests in each vegetation zone.*

		Solid foods		Honeydew	
Vegetation zone	Date	# items/ min/nest	g x 10^{-4} wet wt./min/nest	# full workers/ min/nest	g x 10^{-4} honeydew (wet weight)/ min/nest
Arid	5,12 IV 76	0.58	2.9	34.3	65.2
Transition	6,13 IV 76	0.45	3.5	39.7	75.3
Humid	8,13 IV 76	0.36	1.1	40.1	76.1

SOCIAL STRUCTURE.—Three types of aggregations of *Wasmannia* were observed. One type consisted of only workers, and ranged from a few to more than 100; a second aggregation consisted of workers with immature stages (larvae, pupae, eggs); while the third type consisted of one to several queens with workers and immatures. Social relations between neighboring aggregations appeared to be non-exclusive. No intraspecific aggression between *Wasmannia* was ever observed. Using sugar-water baits colored with dyes, we observed workers from adjacent nests sharing baits without aggression, and we also noted a few cases of workers moving from nest to nest. *Wasmannia* workers placed in other *Wasmannia* nests, whether adjacent or far away, were not attacked. Workers of *Tetramorium guineense* (Fabricius), *C. planus* F. Smith, *C. macilentus, T. melanocephalum*, and *Paratrechina longicornis* (Latreille) (but not two *M. floricola*) were attacked when placed in *Wasmannia* nests.

Hölldobler and Wilson (1977) define the social structure exhibited by *Wasmannia* as unicolonial, that is, having no colony boundaries but rather with "intercommunicating aggregations of workers, brood, and fertile queens." They cite *W. auropunctata* as a unicolonial species that spreads largely or entirely by "budding off groups of workers accompanied on foot by inseminated queens." Although colony establishment was not observed, the existence of very sharp boundaries to *Wasmannia*'s distribution is consistent with the hypothesis of range expansion by budding.

Aggregations of *Wasmannia* were found in a variety of sites, such as under rocks and logs, around stems and trunks, and under loose bark or bryophyte mats. These sites offered a moist microhabitat in dry areas and relatively dry microhabitats in wet sites. Similar nest sites and social organization were found in both Florida (Spencer 1941) and Argentina (Kusnezov 1951).

Workers are apparently sterile and unable to lay viable eggs. During a 71-day period no signs of reproduction were seen in five flasks which originally each contained 50 workers. During the same period eggs, larvae, and pupae appeared in two of three flasks that originally contained 50 workers and one queen.

DIEL ACTIVITY.—During three 24-hr periods of observation, *W. auropunctata* were continuously active, but the level of activity varied, without obvious relation to day or night. During the cool-season observations, all active ants were counted each hour, and percent activity (relative to the mean activity of the 24 observations) ranged from 71 to 127 percent. Major activities observed were transporting food, attacking small invertebrates, and moving winged and wingless queens, as well as larvae and pupae, from one site to another. Other species of ants (*C. macilentus, C. planus, T. melanocephalum, P. longicornis*, and *Solenopsis globularia* (F. Smith), and two unidentified species) were observed foraging very close to *Wasmannia*. Only one instance of interspecific aggression was noted (two *Wasmannia* attacked a *T. melanocephalum*, which escaped).

To determine if nocturnal activity was an artifact of observation with a flashlight, two controls were run (18 and 26 March). A single observation at midnight on both occasions revealed apparently normal levels of activity. We therefore assume that 24-hr activity was normal in this nest and not induced by our observation technique.

These observations indicate that at least some *Wasmannia* colonies in the arid zone are active year-round, 24 hours a day. Activity patterns in the cooler humid zone were not studied; in these areas of lower temperature and higher rainfall *Wasmannia* behavior may be quite different.

RELATION OF DENSITY TO ALTITUDE AND CLIMATE.—Within broad limits, the density of *Wasmannia* increased with increasing altitude and rainfall. The species occurred up to the lower portion of the *Miconia* zone on the south slope, but was never found in the very moist fern-sedge zone of the summit. Guy Coppois (pers. comm.) has noted local expansion of *Wasmannia* into the lower *Miconia* zone during the hot season, and subsequent disappearance during the following cool season. On the north slope, which is drier than the south due to the prevailing southeasterly winds, *Wasmannia* occurred in a narrow band about 3 km broad (fig. 1), stretching from the lower *Scalesia* zone into the upper transition vegetation. Kusnezov (1951) reported a similar preference for mesic habitats in Argentina.

Figure 2 shows the results of quadrat sampling at different elevations on the south slope. Density in the *Scalesia* zone is very high, an estimated 1000-5000 workers/m^2. Since we only censused to a height of 2 m, actual densities are even higher.

These data support the common observation of inhabitants of Santa Cruz that *Wasmannia* is more numerous in the hot season. Density also responded to short-term weather conditions within each of the two major seasons. In a series of four censuses (two in each season) of a 25 m^2 plot in the transition zone, density of groups and queens in each season was substantially higher in the census with the greater amount of rainfall in the preceding 30 days.

DISCUSSION

The results of this study parallel those of several other studies on introduced ants. Greenslade (1972) examined native and introduced ants in coconut plantations on Guadalcanal. He identified four characteristics associated with a species' success: small workers, unicolonial social structure, honeydew an important food source, and terrestrial as opposed to strictly arboreal nests. *Wasmannia* corresponds closely to this suite of characteristics. It is one of the smallest species on Santa Cruz, and was the most successful species at mobilizing large groups of workers and maintaining them at bait stations. *Wasmannia*'s social structure was unicolonial; intraspecific aggression was never observed, and nests with multiple queens were common. Honeydew was an important food source (table 8). *Wasmannia* nested on the ground but also nested readily in trees, and was thus more versatile in this regard than the species Greenslade studied.

Similar conclusions were reached by Erickson (1971) in a study of the displacement of native ants by introduced *Iridomyrmex humilis* Mayr in Califor-

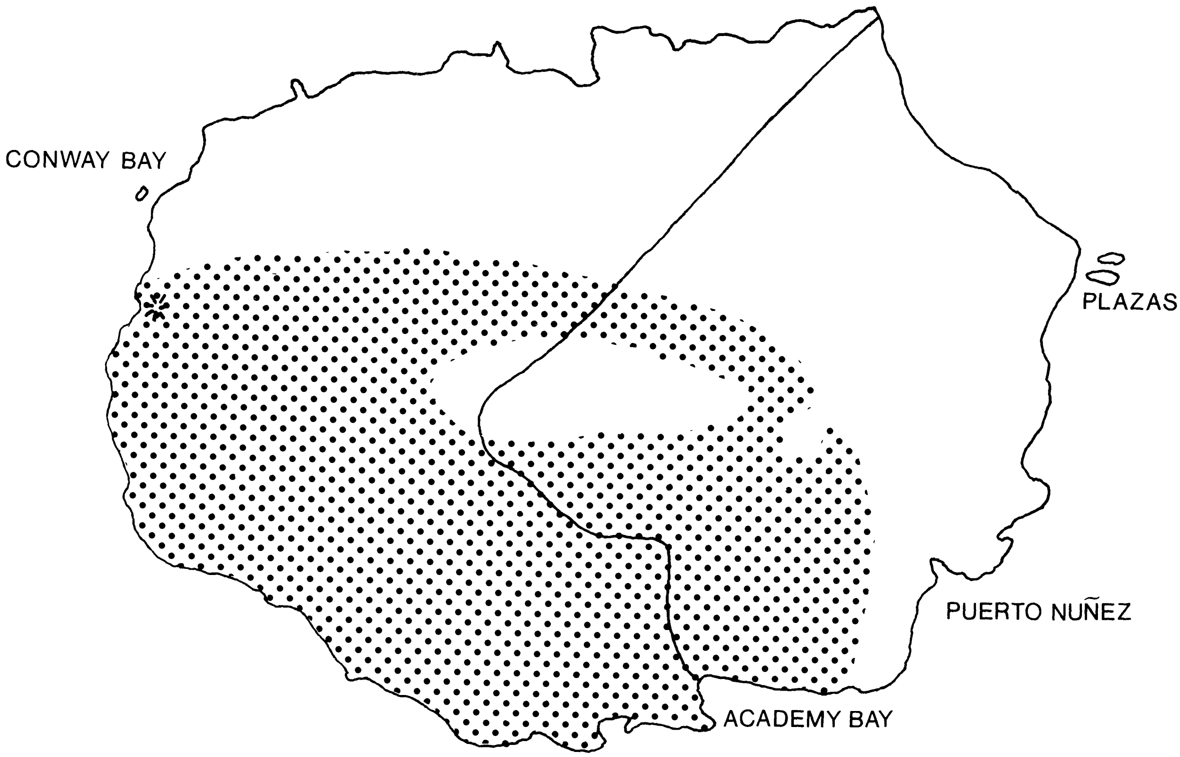

FIGURE 1. Approximate distribution (stippled area) of *Wasmannia auropunctata* on Santa Cruz Island in 1976.

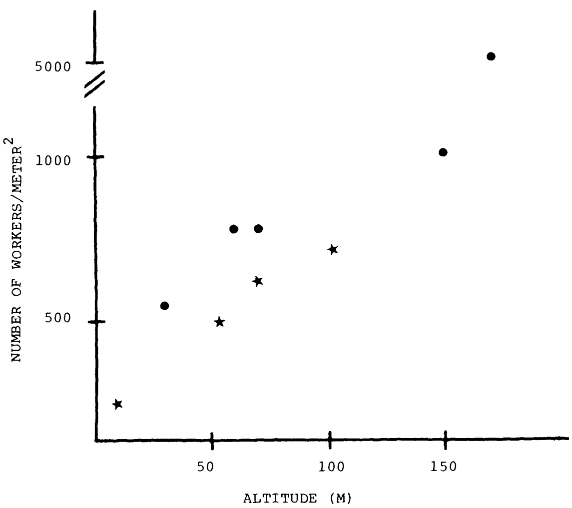

FIGURE 2. Relation between density of *Wasmannia auropunctata* workers and altitude on the south slope of Santa Cruz Island. Circles represent hot-season data, stars come from cool-season censuses.

nia, which uses honeydew, is unicolonial, and produces numerous small workers. In this case the principal displaced species (*Pogonomyrmex californicus* Buckley) was larger, had more specific food requirements, and formed smaller colonies than *I. humilis*. Erickson observed a steady displacement of *P. californicus* over a six-year period.

In Bermuda, *Pheidole megacephala* F. largely replaced the native ant fauna (Haskins and Haskins 1965). In the 1950's *Iridomyrmex humilis* appeared in Bermuda and began replacing *P. megacephala*, rapidly at first but later at markedly lower rate (Crowell 1968). In this case both species were unicolonial with small workers.

Hölldobler and Wilson (1977) suggest that tramp species like *W. auropunctata, P. megacephala*, and *I. humilis*, because they are unicolonial and support dense populations, must be generalists in food and nest-site requirements, a situation that was true for *Wasmannia* on Santa Cruz. Relative to most other species, *Wasmannia* tolerated a wide variety of environments. It foraged 24 hours a day, and so had a broader spectrum of foods available to it than species like *Camponotus macilentus* that were either diurnal or crepuscular/nocturnal. *Wasmannia* consumed a wide variety of foods, but because diet information for the other species is lacking it is not known whether *Wasmannia*'s diet is in fact broader than that of the other ants.

The baiting experiments demonstrated that in situations of interference competition for a concentrated resource *Wasmannia* is the best competitor on Santa Cruz. While suggestive, these data do not prove that *Wasmannia*'s dominance is due to superior interference competitive ability. Other possible explanations could be superior exploitative competitive ability, direct predation on other ants, or most probably some combination of these three processes. It would be possible to resolve the problem through careful observation of ant foraging at sharp boundary areas and in non-*Wasmannia* sites.

The ant fauna of Santa Cruz is in a state of transition. Two of the endemic species, *Camponotus planus* and *Pheidole williamsi*, have been devastated by *Wasmannia* (tables 1 and 2). The other two known endemics, *Cylindromyrmex williamsi* and *Camponotus macilentus*, have largely escaped the effects of *Wasmannia*, since both species are arid-zone specialists (table 1; Wheeler 1924). The effects of other species of introduced ants on the arid-zone endemics are not known.

The present data demonstrate that no ant now present on Santa Cruz can resist *Wasmannia* in areas of high *Wasmannia* density (tables 2 and 3). To the extent that a species' distribution overlaps with *Wasmannia*'s, therefore, that species must be considered endangered on Santa Cruz.

The long-term ecosystem effects of *Wasmannia* in the Galápagos are impossible to predict, primarily because comparative data on invertebrate density in *Wasmannia* and non-*Wasmannia* areas are not available. Given the observed density of *Wasmannia* and the catholic range of prey taken, it is very likely that in areas of high *Wasmannia* density, invertebrate density has been substantially reduced. A similar situation has apparently occurred in Hawaii, where according to Zimmerman (1970) the introduced predatory ant *Pheidole megacephala* has devastated the endemic insect fauna.

Wasmannia currently occurs on Santa Cruz, Floreana, San Cristóbal, Isabela, and Santiago Islands. It was introduced but successfully eradicated on the arid island of Santa Fe. Based on the Santa Cruz data, it appears that areas of maximum *Wasmannia* impact are the mesic zones, which occur only on the high islands of the Galápagos. It is especially vital that high islands which have not yet been infected (Pinta, Fernandina, some volcanoes of Isabela) be protected. Areas which are probably undergoing rapid change (like Santiago) should be studied.

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