Genetic Variation and Population Differentiation in the Rhytidoponera impressa Group, a Species Complex of Ponerine Ants (Hymenoptera: Formicidae)

P. S. Ward

Evolution, Volume 34, Issue 6 (Nov., 1980), 1060-1076.

Stable URL:
http://links.jstor.org/sici?sici=0014-3820%28198011%2934%3A6%3C1060%3AGVAPDI%3E2.0.CO%3B2-6

Evolution, 34(6), 1980, pp. 1060–1076

GENETIC VARIATION AND POPULATION DIFFERENTIATION IN THE *RHYTIDOPONERA IMPRESSA* GROUP, A SPECIES COMPLEX OF PONERINE ANTS (HYMENOPTERA: FORMICIDAE)

P. S. WARD[1]
Zoology Department, University of Sydney, N.S.W. 2006, Australia

Received November 11, 1979. Revised March 21, 1980

Insects of the order Hymenoptera possess an unusual genetic system known as haploid arrhenotoky, or haplodiploidy, in which males are haploid and arise parthenogenetically from unfertilized eggs, while females develop from diploid zygotes. Apart from being universal in the Hymenoptera, haplodiploidy is also known in monogonant rotifers, about a dozen families of mites (Acarina), and several families belonging to the insect orders Homoptera, Thysanoptera, and Coleoptera (Hartl and Brown, 1970; Oliver, 1977).

It has been suggested that haplodiploid species have reduced amounts of genetic variation relative to diploid species because of the exposure of alleles to selection at each generation in the male (White, 1945; Suomalainen, 1962). Most selection models indicate that haplodiploidy imposes more restrictive conditions for the maintenance of stable balanced polymorphisms than diploidy (Hartl, 1971; Lester and Selander, 1979; Pamilo and Crozier, unpubl.; cf. Crozier, 1970). As with sex-linked loci (Bennett, 1957; Mandel, 1959; Haldane and Jayakar, 1964), overdominance in females is neither a necessary nor sufficient condition for a stable polymorphism. When there is a correlation in fitness between sexes, a lower frequency of balanced polymorphisms is expected, relative to equivalent diploid species (Crozier, 1979).

Models based on neutral mutation theory predict lower levels of heterozygosity in haplodiploid species. This is due to a variety of factors associated with a smaller effective population size, including greater sampling variance, less pronounced associative overdominance, and a stronger "hitchhiking effect" (Lester and Selander, 1979).

It has been postulated that haplodiploidy leads to increased interpopulation variation (Helle and Overmeer, 1973). Hartl (1972) applied Fisher's fundamental theorem of natural selection to haplodiploidy and found (under certain assumptions) that haplodiploid species are expected to evolve one-third faster than similar diploid species.

Crozier (1977*a*) and Pamilo et al. (1978*b*) have reviewed available data on levels of polymorphism in Hymenoptera, and the pattern which emerges from most electrophoretic studies is one of reduced intrapopulation variation relative to diploid insects. Less attention has been paid to interpopulation variation, and as a result we lack detailed studies of population differentiation and genetic structure in haplodiploid species. Such studies are all the more relevant, given the burgeoning development of theory devoted to the evolution of social behavior, in which population (as well as colony) structure plays a prominent role (e.g., Hamilton, 1971; Wade, 1978; D. S. Wilson, 1980).

The present study is concerned with patterns of electrophoretically detectable genetic variation in the *Rhytidoponera impressa* group, a complex of closely-related ant species belonging to the subfamily Ponerinae. Thirty-five populations are examined in detail, with particular attention being focused on (i) levels of heterozygosity, (ii) differentiation between populations, and (iii) interspecific genetic differences. The results are compared

[1] Present address: Zoology Department, University of Texas at Austin, Austin, Texas 78712.

with those of other empirical studies and with theoretical expectations of reduced heterozygosity and increased population divergence. Patterns of genetic diversity and relatedness *within colonies* will be described elsewhere (Ward, unpubl.).

The *R. impressa* group consists of five morphologically very similar species (*chalybaea, confusa, enigmatica, impressa,* and *purpurea*) which are confined to mesic habitats, mostly rainforest, along the east coast of Australia, with one species also occurring in New Guinea (Ward, 1978, 1980). Colonies of these species are generally located in rotten logs and under stones. Both monogynous (single-queen) and polygynous colonies occur within a population, but a single colony usually does not occupy more than one nest-site, so the terms "colony" and "nest" are used equivalently in this paper. "Population" refers to an assemblage of colonies occupying a particular tract of suitable mesic forest, usually over an area of about 100–200 hectares. Most populations of the *R. impressa* group in eastern Australia occupy stable, spatially restricted patches of rainforest whose properties of discretenesss and temporal stability make them convenient units for examining intra- and interpopulation genetic diversity.

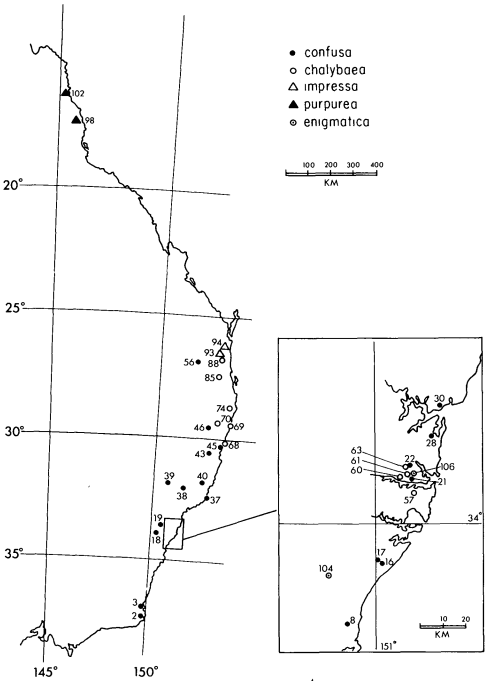

FIG. 1. Eastern Australia, showing location of 35 *R. impressa* group populations for which gene frequencies and average heterozygosities have been calculated. Numbers are population code numbers (see Table 1).

METHODS

Collection and Electrophoresis

Colonies belonging to the *R. impressa* group were collected in over 100 localities, from all major rainforest areas of New South Wales and southern Queensland, as well as from several sites in north Queensland and one in Papua New Guinea. Collection details are given in Ward (1978). Gene frequencies and heterozygosity were estimated in 35 populations, in which four or more colonies were collected (Fig. 1 and Table 1). Occasional reference is made to other, smaller population samples in which fewer than four nests were examined.

Ant workers (and other castes when present) were stored frozen at −25 C. For electrophoresis, whole worker ants were ground in distilled water. The crude homogenate was absorbed onto several filter paper circles, and subjected to polyacrylamide disc (tube) gel electrophoresis (Davis, 1964; Ornstein, 1964). All gels used in standard runs were 7% acrylamide, with one exception: for scoring esterases, 4.5% gels were used as they gave superior resolution. Two gel buffers were utilized: 0.375 M Tris-HCl, pH 8.9 (TH), and 0.02 M Tris-Borate, pH 8.9 (TB) (with 1 mM EDTA when used in 4.5% gels). The electrode (compartment) buffer was 5 mM Tris-Glycine, pH 8.3

The following systems were assayed, using standard histochemical stains (Shaw and Prasad, 1970; Harris and Hopkinson, 1976) (the gel buffer system and number of loci scored are also indicated): esterases (TB, 3), leucine aminopeptidase (TB, 1), amylase (TB, 1), glutamate oxaloacetate transaminase (TB, 1), phosphoglucomu-

TABLE 1. *List of 35* R. impressa *group populations for which gene frequencies and average heterozygosity have been estimated.* n *and* N *are the numbers of nests and worker genomes sampled per locus, respectively.* $\hat{H}$ *is the expected heterozygosity based on gene frequencies;* H *is the observed number of heterozygotes per locus, averaged over all 22 loci. SE is the inter-locus standard error.*

Population code no.	Locality	Species	*n, N*	Latitude °S	Longitude °E	Altitude	Habitat	$\hat{H}$	SE	*H*	SE
2	Naghi S.F.	*confusa*	35, 420	37°23′	149°46′	200 m	wet sclerophyll	.023	.019	.022	.018
3	Bellbird Crk.	*confusa*	6, 72	37°02′	149°55′	50 m	temperate rainfor.	.012	.012	.011	.011
8	Mt. Keira	*confusa*	24, 288	34°24′	150°51′	300 m	temperate rainfor.	.024	.014	.025	.015
16	Royal N.P.r.f.	*confusa*	62, 744	34°09′	151°01′	50 m	temperate rainfor.	.023	.014	.024	.016
17	Royal N.P.w.s.	*confusa*	7, 84	34°09′	151°01′	160 m	wet sclerophyll	.016	.016	.017	.017
18	Cox's R.	*confusa*	7, 84	33°52′	150°10′	150 m	temperate rainfor.	.006	.006	.006	.006
19	Blackheath	*confusa*	5, 60	33°38′	150°19′	550 m	temperate rainfor.	.032	.024	.035	.026
21	Lane Cove W.	*confusa*	13, 156	33°49′	151°09′	10 m	wet sclerophyll	.045	.031	.062	.043
22	Grosvenor Rd.	*confusa*	13, 156	33°47′	151°09′	10 m	temperate rainfor.	.035	.026	.038	.029
28	McCarrs Crk.	*confusa*	19, 228	33°40′	151°16′	30 m	temperate rainfor.	.028	.017	.031	.019
30	Pearl Beach	*confusa*	36, 432	33°33′	151°18′	30 m	wet sclerophyll	.072	.040	.074	.041
37	Seal Rocks	*confusa*	10, 120	32°26′	152°32′	10 m	littoral rainfor.	.020	.020	.023	.023
38	Up. Allyn R.	*confusa*	24, 288	32°08′	151°29′	400 m	temperate rainfor.	.024	.020	.023	.019
39	Sparkes Crk.	*confusa*	11, 132	31°50′	150°41′	700 m	temperate rainfor.	.043	.030	.048	.034
40	Wingham	*confusa*	8, 96	31°52′	152°22′	20 m	temperate rainfor.	.033	.022	.031	.020
43	Platypus Crk.	*confusa*	8, 96	30°29′	152°28′	500 m	temperate rainfor.	.035	.025	.035	.024
45	Bruxner Pk.	*confusa*	18, 216	30°15′	153°06′	150 m	subtrop. rainfor.	.043	.024	.042	.024
46	Gibraltar Ra.	*confusa*	9, 108	29°26′	152°23′	620 m	subtrop. rainfor.	.041	.023	.041	.023
56	Bunya Mtns.	*confusa*	4, 48	26°54′	151°37′	1,000 m	subtrop. rainfor.	.045	.031	.055	.039
57	Sydney Univ.	*chalybaea*	7, 84	33°53′	151°11′	30 m	urban parkland	.048	.033	.044	.032
60	East Ryde	*chalybaea*	4, 48	33°49′	151°08′	5 m	wet sclerophyll	.042	.032	.049	.038
61	Lane Cave W.	*chalybaea*	14, 168	33°49′	151°09′	10 m	wet sclerophyll	.047	.037	.043	.036
63	Grosvenor Rd.	*chalybaea*	5, 60	33°47′	151°09′	10 m	temperate rainfor.	.051	.032	.064	.061
68	Sapphire Beach	*chalybaea*	4, 48	30°14′	153°09′	10 m	littoral rainfor.	.047	.035	.053	.038
69	Iluka	*chalybaea*	10, 120	29°24′	153°12′	10 m	littoral rainfor.	.028	.020	.022	.015
70	Camira Crk.	*chalybaea*	6, 72	29°18′	152°50′	140 m	dry rainforest	.056	.034	.049	.031
74	Whian Whian S.F.	*chalybaea*	50, 600	28°39′	153°20′	200 m	subtrop. rainfor.	.050	.036	.052	.039
85	Mt. Glorious	*chalybaea*	6, 72	27°20′	152°46′	610 m	subtrop. rainfor.	.045	.034	.054	.043
88	Maleny	*chalybaea*	40, 480	26°47′	152°53′	400 m	subtrop. rainfor.	.043	.034	.045	.036
93	Mapleton Falls	*impressa*	4, 48	26°38′	152°51′	350 m	subtrop. rainfor.	.062	.040	.055	.038
94	Cooran Plat.	*impressa*	4, 48	26°17′	152°50′	370 m	subtrop. rainfor.	.043	.030	.038	.026
98	L. Eacham	*purpurea*	4, 48	17°17′	145°37′	760 m	tropical rainfor.	.010	.010	.011	.011
102	McDowall Ra.	*purpurea*	4, 48	16°05′	145°17′	550 m	tropical rainfor.	.000	.000	.000	.000
104	Appin	*enigmatica*	8, 96	34°12′	150°46′	180 m	wet sclerophyll	.033	.024	.030	.022
106	Lane Cove W.	*enigmatica*	12, 144	33°49′	150°09′	10 m	wet sclerophyll	.046	.031	.035	.023

tase (TB, 1), aldehyde oxidases (TB or TH, 3), malic enzyme (TB or TH, 1), malate dehydrogenase (TB or TH, 1), α-glycerophosphate dehydrogenase (TB, 1), lactate dehydrogenase (TB, 1), glucose-6-phosphate dehydrogenase (TH, 1), xanthine dehydrogenase (TH, 1), superoxide dismutases (TH, 1; TB, 1), hexokinase (TH, 1), fumarase (TH, 1), and nonenzymatic proteins (TB, 2).

Gel Interpretation and Genetic Analysis

A minimum of three standards was utilized per run of 24 gels, in addition to the bromphenol blue marker front. These standards consisted of workers from monogynous (single-queen) nests of known genotype(s). For every standard, two gels were run: one contained the standard alone, the other contained a mix of the standard and one of the samples. The latter sample was also run separately on a third gel.

The genetic basis of the observed isozyme variation was confirmed by examining the electromorphs of 1) haploid males (hemizygote pattern), and 2) offspring from monogynous nests, where the queen's isozyme pattern was known. The patterns of variation reported herein were consistent with a model of codominant alleles, obeying Mendelian inheritance. More than 1,100 males and 100 queen-typed monogynous colonies were examined electrophoretically, allowing considerable confidence to be placed in the genetic interpretation. Allozymes of variant loci were labeled according to relative mobility, with *1.00* being assigned to the commonest allele in *R. confusa*. In *confusa* the *0.78* allele of esterase-4 was sometimes obscured by an additional zone of esterase activity (esterase-2, not scored) which consisted of a single band of variable staining intensity. Therefore, the frequency of the *0.78* allele was estimated as $\sqrt{R}$, where R is the proportional frequency of individuals lacking the complementary (*1.00*) allelle (i.e., *0.78/0.78* homozygotes). All other gene frequencies were calculated directly from genotype frequencies.

Six workers (12 genomes) were analyzed per nest per locus, and at least four nests were examined per population, for the 35 populations in which gene frequencies were estimated. The justification for using worker gene frequencies to characterize population variation is that in the *Rhytidoponera impressa* group (as in probably all *Rhytidoponera*) workers have the potential to mate and reproduce (Ward, 1978); and in the populations with sufficiently large sample sizes for comparisons to be made, there were usually no significant gene frequency differences between queens and mated workers on the one hand, and unmated workers on the other. (There were also no gene frequency differences between the sexes.)

Since six workers were scored per nest, the true sample size for each population, as measured by the number of *nonduplicated* genes (cf. Cavalli-Sforza and Bodmer, 1971), will be less than the number of worker genomes examined. Given that the mean number of inseminated reproductive females in a nest is about three to four (Ward, 1978), the average number of nonduplicated genes sampled per nest (in a sample of six worker offspring) is about seven, rather than twelve. Taking into account a certain level of relatedness among the reproductive females, this figure drops closer to six. Therefore the true sample size (N') for each population is estimated to be approximately one-half the actual number of worker genomes sampled (i.e., $N' \approx N/2$). N' is used in all subsequent calculations involving sample size.

For each population, the intralocus heterozygosities (h_k) and mean heterozygosity ($\hat{H}$) were calculated from gene frequencies (Nei and Roychoudhury, 1974). Nei's (1972) standard genetic distance, D, was calculated between all possible pairs of 35 populations.

Departures from panmixia within local populations were assessed by Wright's (1922) inbreeding coefficient, F_i (see Crow and Kimura, 1970). The expected frequency of heterozygotes was corrected for small sample size using Levene's (1949) formula.

Wright's (1951, 1965) F-statistics, F_{IS},

TABLE 2. *Allele frequencies at seven loci in 19 populations of* R. confusa. *Some of the alleles listed are not present in* confusa *but occur in other members of the* impressa *group (see Table 3). Population code numbers are listed in Table 1. Calculations of percent polymorphic loci (%P) and estimated mean heterozygosity ($\hat{H}$) (based on gene frequencies) include 15 other monomorphic loci.* n *and* N *are the number of ant nests and worker genomes, respectively, sampled in each population, per locus.*

	#2	#3	#8	#16	#17	#18	#19	#21	#22	#28	#30	#37	#38	#39	#40	#43	#45	#46	#56
EST-3																			
1.00	.945	.847	.885	.832	.762	1.000	.883	.494	.603	.860	.157	.667	.691	.500	.698	.406	.801	.222	1.000
0.90	—	—	—	—	—	—	—	—	.295	—	—	—	—	—	—	—	—	—	—
0.81	.055	.153	.115	.168	.238	—	.117	.506	.103	.140	.336	.333	.309	.500	.302	.594	.199	.778	—
0.73	—	—	—	—	—	—	—	—	—	—	.507	—	—	—	—	—	—	—	—
0.66	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
EST-4																			
1.22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.031	—	—	—	—
1.00	.724	1.000	.856	.927	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.652	.969	1.000	.833	.864	1.000
0.78	.276	—	.144	.073	—	—	—	—	—	—	—	—	—	.348	—	—	.167	.136	—
null	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
AMY																			
1.23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.12	—	—	—	—	—	—	—	.103	.019	.026	.403	—	—	—	—	—	—	—	—
1.08	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.031	—	—	—	—
1.00	1.000	1.000	.986	.966	1.000	.929	.467	.673	.872	.838	.574	1.000	.955	1.000	.865	.833	.787	.796	.479
0.95	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.056	—	—
0.87	—	—	.014	.034	—	.071	.533	.224	.109	.136	.023	—	.045	—	.104	.167	.157	.204	.521
0.75	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.59	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
AO-2																			
1.08	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.00	1.000	1.000	.979	.992	1.000	1.000	1.000	1.000	1.000	.947	.366	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
0.92	—	—	.021	.008	—	—	—	—	—	.053	.634	—	—	—	—	—	—	—	—
0.83	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
MDH																			
1.19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.542
1.16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.458
0.82	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.72	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 2. *Continued.*

	#2	#3	#8	#16	#17	#18	#19	#21	#22	#28	#30	#37	#38	#39	#40	#43	#45	#46	#56
SOD-1																			
1.44	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
0.76	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
PGM																			
1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
0.81	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
n	35	6	24	62	7	7	5	13	13	19	36	10	24	11	8	8	18	9	4
N	420	72	288	744	84	84	60	156	156	228	432	120	288	132	96	96	216	108	48
% *P*	9.1	4.5	18.2	13.6	4.5	4.5	9.1	9.1	9.1	13.6	13.6	4.5	9.1	9.1	13.6	9.1	13.6	13.6	9.1
$\hat{H}$	.023	.012	.024	.023	.016	.006	.032	.045	.035	.072	.072	.030	.024	.043	.033	.035	.043	.041	.045

F_{IT}, and F_{ST} were calculated from genetic data on 19 local populations of *confusa* and ten of *chalybaea*. F_{IS} was obtained as a weighted mean F_i across all populations of interest (Workman and Niswander, 1970; Spielman et al., 1977). F_{IT} was calculated in a manner analogous to F_i, from the observed and expected (based on weighted mean gene frequencies) heterozygosities for the metapopulation.

A measure of population differentiation was provided by the standardized genetic variance, F_{ST}, which reflects the correlation between randomly chosen genes in a local population relative to the total population. For loci with multiple alleles, a weighted average F_{ST}, analogous to Nei's (1973) G_{ST}, was calculated. Very similar values of F_{ST} were obtained when multiallelic data were reduced to diallelic form by combining all of the less common alleles. The significance of observed F_{ST} was tested with heterogeneity χ^2 (Workman and Niswander, 1970).

RESULTS

Variation Within Populations

Fifteen out of 22 loci were found to be monomorphic and identical in all five species. The seven variant loci are: two esterases (*EST-3* and *EST-4*), amylase (*AMY*), malate dehydrogenase (*MDH*), an aldehyde oxidase (*AO-2*), a superoxide dismutase (*SOD-1*), and phosphoglucomutase (*PGM*). One of these (*PGM*) is not polymorphic, but shows substitution of an alternate allelle in *purpurea*. Allele frequencies at the seven variant loci are given in Tables 2 and 3.

Table 1 compares estimated ($\hat{H}$) and observed (H) levels of heterozygosity in the 35 populations. The two measures are very similar in most populations, and there is no evidence of marked heterozygote excess or deficiency. There is a slight but insignificant tendency towards excess heterozygosity ($H > \hat{H}$ in 18 populations; $H \approx \hat{H}$ in four populations; and, $H < \hat{H}$ in 13 populations).

$\hat{H}$ varies from .000 to .072, the unweighted mean for all 35 populations

TABLE 3. *Allele frequencies at 7 variant loci in 10 populations of* R. chalybaea *and 2 populations each of* impressa, purpurea *and* enigmatica. *Symbols as in Table 2.*

	chalybaea										*impressa*		*purpurea*		*enigmatica*	
	#57	#60	#61	#63	#68	#69	#70	#74	#85	#88	#93	#94	#98	#102	#104	#106
EST-3																
1.00	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.90	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.81	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.988	1.000	1.000	—	—	1.000	1.000
0.73	—	—	—	—	—	—	—	—	—	—	—	—	.875	1.000	—	—
0.66	—	—	—	—	—	—	—	—	—	.012	—	—	.125	—	—	—
EST-4																
1.22	.036	—	.006	—	—	—	.778	—	.056	—	—	—	—	—	—	.049
1.12	.964	1.000	.994	1.000	1.000	1.000	.222	1.000	.944	.938	.625	.625	—	—	1.000	.951
1.00	—	—	—	—	—	—	—	—	—	.062	.375	.375	—	—	—	—
0.78	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
null	—	—	—	—	—	—	—	—	—	—	—	—	1.000	1.000	—	—
AMY																
1.23	.083	.125	.083	.300	.250	.058	.056	.230	.056	.081	.188	.208	—	—	—	—
1.12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.375	.486
1.08	.024	.167	.149	.017	.083	.017	.111	.355	.333	.377	.333	.688	—	—	—	—
1.00	—	.042	.089	.067	—	.025	—	—	—	—	—	—	—	—	.625	.306
0.95	.250	—	.250	.050	—	—	.083	.015	.097	—	—	.104	—	—	—	—
0.87	.226	.188	.143	.050	.271	.858	.486	.343	.236	.240	.292	—	1.000	1.000	—	.208
0.75	.417	.479	.286	.517	.396	.042	.264	.057	.250	.190	.062	—	—	—	—	—
0.59	—	—	—	—	—	—	—	—	.027	.112	.125	—	—	—	—	—
AO-2																
1.08	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.125
1.00	.976	.917	.869	.817	.792	.242	.917	.003	.958	.988	1.000	1.000	—	—	1.000	.833
0.92	.024	.083	.131	.183	.208	.758	.083	.997	.042	.012	—	—	—	—	—	.042
0.83	—	—	—	—	—	—	—	—	—	—	—	—	1.000	1.000	—	—
MDH																
1.19	—	—	—	—	—	—	—	—	—	.010	.083	—	—	—	—	—
1.16	—	—	—	—	—	—	—	.007	—	—	—	—	—	—	—	—
1.00	.857	.958	1.000	.900	1.000	1.000	.972	.745	1.000	.983	.917	1.000	—	—	1.000	1.000
0.82	—	—	—	—	—	—	—	—	—	.006	—	—	1.000	1.000	—	—
0.72	.143	.042	—	.100	—	—	.028	.248	—	—	—	—	—	—	—	—

TABLE 3. *Continued.*

	chalybaea									*impressa*		*purpurea*		*enigmatica*	
	#57	#60	#61	#63	#68	#69	#70	#74	#85	#88	#93	#94	#98	#102	#104	#106
SOD-1																
1.44	—	—	—	—	—	—	—	—	.027	—	—	—	1.000	1.000	—	—
1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.973	1.000	1.000	1.000	—	—	.854	1.000
0.76	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.146	—
PGM																
1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	—	—	1.000	1.000
0.82	—	—	—	—	—	—	—	—	—	—	—	—	1.000	1.000	—	—
n	7	4	14	5	4	10	6	50	6	40	4	4	4	4	8	12
N	84	48	168	60	48	120	72	600	72	480	48	48	48	48	96	144
% *P*	18.2	13.6	9.1	13.6	9.1	9.1	18.2	9.1	18.2	22.7	13.6	9.1	4.5	0.0	9.1	13.6
$\hat{H}$	.048	.042	.047	.051	.047	.028	.056	.050	.045	.043	.062	.043	.010	.000	.033	.046

being .036 ± .003 SE. Population means for each species range from .005 (*purpurea*) to .052 (*impressa*) (Table 4). The mean $\hat{H}$ for all five species is .034 ± .008 SE. Within the species *confusa* and *chalybaea,* there is no significant association between latitude or altitude and heterozygosity. However, in *confusa* the regression of $\hat{H}$ on latitude approaches significance ($P = .054$).

Levels of heterozygosity were examined in relation to habitat. First, populations were categorized as inhabiting partially open habitat (wet sclerophyll, urban parkland) or closed forest (various rainforest types), and all 35 populations (five species) were considered. The mean heterozygosities of nine populations from open habitat (mean $\hat{H} = .041 \pm .005$ SE) are not significantly different (t-test) from those of 26 populations from closed forest (mean $\hat{H} = .034 \pm .003$ SE). An intraspecific comparison of *confusa* populations also revealed no significant differences.

One factor which "explains" some of the variation in heterozygosity is a species difference. The mean estimated ($\hat{H}$) heterozygosity of 19 *confusa* populations is significantly less than that of ten *chalybaea* populations (t-test, $P < .01$). Moreover, the available data suggest that the tropical species, *purpurea,* is less variable than the others. The $\hat{H}$ estimates for the two populations of *purpurea* lie below the 95% confidence limits of the mean $\hat{H}$ for *chalybaea.*

The results of the present study and others on haplodiploid species are summarized in the upper third of Figure 2 which is based on heterozygosity estimates for 53 species of Hymenoptera. There is a remarkable consistency among these data, with $\hat{H}$ ranging from 0.000 to 0.084 (mean .036 ± .004 SE). The *Rhytidoponera* data fall well within the range of values reported in other haplodiploid species.

By contrast, multilocus electrophoretic surveys of *Drosophila* and other insects have generally revealed higher levels of allozyme variation within species, and greater interspecific variation (Fig. 2). The mean heterozygosity estimates for 40

TABLE 4. *Expected* ($\hat{H}$) *and observed* (H) *heterozygosities, averaged over all populations for each species.*

Species	No. populations	$\hat{H}$ ± SE	H ± SE
confusa	19	.0316 ± .0034	.0338 ± .0040
chalybaea	10	.0457 ± .0023	.0475 ± .0034
impressa	2	.0525 ± .0095	.0465 ± .0085
purpurea	2	.0050 ± .0050	.0055 ± .0055
enigmatica	2	.0395 ± .0065	.0325 ± .0025
All populations	35	.0357 ± .0027	.0368 ± .0029

species of *Drosophila* and 17 species of other insects are 0.137 and 0.112, respectively (data from Powell [1975] and Nevo [1978]). Both of these groups show significantly greater heterozygosity than the Hymenoptera (one-tailed Mann-Whitney U-test, $P < .001$ for both comparisons). On the basis of the present data, then, haplodiploid insects show less genetic variability than diploid species.

Departures from Panmixia Within Local Populations

Wright's (1922) inbreeding coefficient, F_i, was calculated for the variable loci in all 34 populations. Testing with χ^2 (Li and Horvitz, 1953), there were only six instances out of 81 comparisons, where F_i was significantly ($P < .05$) greater than zero. In five of these six cases there were other variable loci in the population whose F_i values were not significantly different from zero, suggesting an alternative explanation to inbreeding (e.g., selection or sampling error) for the single positive F_i value. Of the 81 F_i estimates, 30 were positive and 51 were negative; this is significantly different from 50:50 (sign test, $P < .05$), suggesting a tendency towards heterosis. However, there were only two instances in which F_i was significantly ($P < .05$) less than zero. Weighted mean F_i estimates (i.e., F_{IS}) across all conspecific populations of *confusa* and *chalybaea* are given in Table 5.

These calculations suggest that populations of the *Rhytidoponera impressa* group are essentially outbred. However, much larger sample sizes are needed to detect *low* levels of inbreeding in local populations (cf. Brown, 1970; Ward and Sing, 1970), and to the extent that heterosis occurs, it would tend to counteract the effects of inbreeding on genotype frequencies. Evidence for infrequent inbreeding comes from the finding of a few males showing diploid (heterozygote) banding patterns in four out of 52 populations in which they were examined, such males presumably arising from homozygosity of sex alleles (cf. Crozier, 1971). The actual incidence of diploid males could be higher, and would be more accurately assessed from karyotype data.

Population Differentiation— Intraspecific Patterns

In *confusa*, the *EST-3* and *AMY* loci show geographical variation in gene frequencies, although the same predominant allele occurs in most populations (Table 2). The remaining loci tend to be fixed for one allele, but are polymorphic in some populations. In general, *confusa* populations display considerable homogeneity, with several notable exceptions: 1) population #22 (Grosvenor Rd., N.S.W.) possesses a unique *EST-3* allele, in moderate frequency, which is absent in all other *confusa* populations; 2) population #30 (Pearl Beach, N.S.W.) has medium to high frequencies of otherwise rare alleles at the *EST-3*, *AMY*, and *AO-2* loci; and 3) population #56 (Bunya Mtns., Qld.) is polymorphic for *MDH*, a locus uniformly fixed in all the other *confusa* populations. One might expect genetic divergence of the isolated Bunya Mountains population, but the local differentiation of Grosvenor Road and Pearl Beach populations in the Sydney region is more surprising.

Rhytidoponera chalybaea also shows

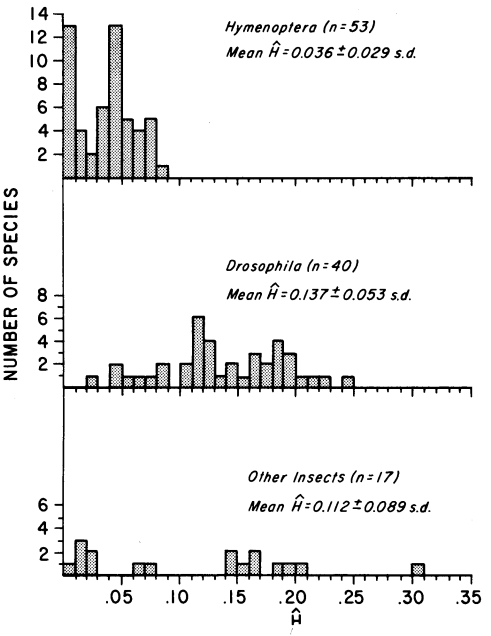

FIG. 2. Frequency distributions of heterozygosity ($\hat{H}$) in several insect taxa. Sources of data are as follows: for Hymenoptera, Snyder (1974), Metcalf et al. (1975), Pamilo et al. (1978*a*), Pamilo et al. (1978*b*), Halliday (1978), Lester and Selander (1979), and present study; for *Drosophila,* Nevo (1978); and for other insects, Powell (1975) and Nevo (1978). Most studies involved 12 or more loci. Mean numbers of loci studied in each group are: 14.2 ± 4.1 SD (Hymenoptera), 21.2 ± 6.9 SD (*Drosophila*), and 18.2 ± 4.5 SD (other insects).

moderate levels of differentiation for some loci and populations (Table 3). The *AMY* locus, in particular, shows high allelic diversity (seven alleles), and the commonest allele varies from population to population. At the other loci one allele is usually predominant in all populations (Table 3), but there are exceptions, for example, the *EST-4*$^{1.22}$ allele in population #70 (Camira Creek, N.S.W.), and the *AO-2*$^{0.92}$ allele in populations #69 (Iluka, N.S.W.) and #74 (Whian Whian State Forest, N.S.W.).

Little can be said about population differentiation in the remaining three species on the basis of the six populations listed in Table 3. However, additional, small samples (less than four nests/locality) of *impressa* from elsewhere in Queensland (Eungella National Park and north Queensland) suggest the frequent occurrence of allelic substitutions, and the possibility that *impressa* represents a composite of species.

By contrast, small samples of *purpurea* from other localities (Barron Falls, Qld.; Mt. Lewis, Qld.; Mt. Windsor Tableland, Qld.; and Wau, Papua New Guinea) were found to be identical and monomorphic at all loci. *Rhytidoponera purpurea* is absent from lowland rainforest in Cape York Peninsula and is more or less restricted to montane rainforest in New Guinea (Ward, 1980). Hence the lack of genetic differentiation between New Guinea and north Queensland populations is all the more striking, and contrasts with the population differentiation which occurs over very short distances in other members of the *impressa* group.

Population Structure and F-*Statistics*

An F-statistic analysis of the segregating loci confirms that there is a rather marked degree of population differentiation. Table 5 provides estimates of F_{IS}, F_{ST}, and F_{IT} for four loci in *confusa* and *chalybaea*. All of the F_{ST} values are large and highly significant (heterogeneity χ^2, $P < .001$) in contrast to the generally low values of F_{IS}. As expected, estimates of F_{IT} tend to mirror those of F_{ST}, although there is some discrepancy at the *AMY* locus probably due in part to an excess of heterozygotes within local populations, at least in *chalybaea*. There is considerable heterogeneity of F_{ST} values (from .102 to .815 among four loci in *chalybaea,* and from .143 to .550 in *confusa*).

The preceding calculations are based on population samples taken over the entire species range, but approximately the same level of differentiation occurs on a local scale in some areas (Table 6). The mean F_{ST} for nine *confusa* populations in the Sydney region ($\bar{F}_{ST} \approx .271$) is only slightly less than that which occurs over the entire range of the species ($\bar{F}_{ST} \approx .294$). Regional populations of *chalybaea* also appear to show high levels of differentiation (Table

TABLE 5. *F-statistics, calculated over all conspecific populations of* R. confusa *and* chalybaea. *Sample size is the total number of worker genomes sampled, corrected for duplicated genes (see text). Estimates of* F_{IS} *and* F_{IT} *at the* EST-4 *locus in* confusa *are lacking, because of ambiguity in scoring heterozygotes, as explained in text (under Methods).*

Species	No. populations	Sample size (N')	Locus	F_{IS}	F_{ST}	F_{IT}
confusa	19	1,914	*EST-3*	−.033	.265	.223
			EST-4	—	.143	—
			AMY	−.002	.215	.136
			AO-2	+.009	.550	.542
chalybaea	10	876	*EST-4*	+.038	.465	.511
			AMY	−.077	.102	.034
			AO-2	+.001	.815	.839
			MDH	+.031	.137	.195

6), with one interesting exception: the mean F_{ST} for four populations in the Sydney area is only .042 ± .023 SD. However, ecological evidence suggests that these populations are recently derived from a parental source farther north, especially in view of their restriction to anthropogenic habitats (parks, gardens, and wet forested gullies dominated by introduced vegetation) in the Sydney region (Ward, 1978, 1980). Hence, we would expect rather limited genetic divergence of these recent, adventive, urban populations of *chalybaea,* in comparison to populations of *confusa* which have presumably been present locally in natural habitats for much longer periods of time.

Interspecific Genetic Differences

Most species pairs show considerably more genetic differentiation than occurs between conspecific populations. The mean genetic distance (Nei's [1972] measure D) between conspecific populations is .015 ± .001 SE (219 comparisons), contrasting with a mean D between interspecific populations of .136 ± .005 SE (376 comparisons). Furthermore, whereas conspecific populations are not usually fixed for alternate alleles, several pairs of species show no overlap in allelic arrays at some loci.

Rhytidoponera purpurea is the most genetically distinct member of the *impressa* group. At all variant loci except *AMY,* this species contains alleles which are rare or absent in the remaining species.

Differences between the other species are less marked. *Rhytidoponera confusa* can be distinguished from *chalybaea,* from which it is morphologically little differentiated (Ward, 1980), on the basis of (i) substitution of alternate alleles at the *EST-4* locus (alleles *1.00* and *0.78* in *confusa*; *1.22* and *1.12* in *chalybaea*), and (ii) the presence of unique alleles at the *EST-3* and *AMY* loci. The same loci are useful for distinguishing *enigmatica* from *confusa* and *chalybaea.*

Rhytidoponera chalybaea and the two *impressa* populations (Mapleton Falls and Cooran Plateau, Qld.) appear to be similar in terms of allozyme frequencies, the only distinctive (but not "diagnostic," sensu Ayala and Powell, 1972) feature of these *impressa* populations being a moderate frequency of the *EST-4*$^{1.00}$ allele. This same allele is absent from all *chalybaea* populations except for one locality adjacent to the *impressa* populations. This suggests limited gene exchange between the two species, a hypothesis also supported by morphological evidence (Ward, 1980).

Genetic distances (Nei's measure) were calculated between all possible pair combinations of the 35 *impressa* group populations listed in Table 1. UPGMA clustering (Sneath and Sokal, 1973) was used to construct the dendrogram shown in Figure 3.

The clustering is in reasonable agreement with the accepted species categories. The dendrogram emphasizes the large dif-

TABLE 6. *Estimates of* F_{ST} *for several clusterings of* confusa *and* chalybaea *populations.*

Species, sample size (N')	Geographical region	No of populations	Approx. area	Latitudinal range (degrees)	Locus	F_{ST}*	$\bar{F}_{ST} \pm$ SD
confusa (486)	Sydney north to Hawkesbury River	4	500 km²	0.27	*EST-3*	.263	.230 ± .233
					EST-4	—†	
					AMY	.117	
					AO-2	.539	
confusa (1,116)	Sydney region (incl. Blue Mtns.)	9	10,000 km²	0.85	*EST-3*	.280	.271 ± .190
					EST-4	.063	
					AMY	.221	
					AO-2	.521	
confusa (1,914)	entire species range	19	100,000 km²	10.5	*EST-2*	.265	.294 ± .178
					EST-4	.143	
					AMY	.215	
					AO-2	.550	
chalybaea (180)	Sydney (urban areas)	4	100 km²	0.10	*EST-4*	.018	.042 ± .023
					AMY	.045	
					AO-2	.033	
					MDH	.072	
chalybaea (420)	northern N.S.W. (rainforest areas)	4	10,000 km²	1.58	*EST-4*	.810	.402 ± .385
					AMY	.083	
					AO-2	.653	
					MDH	.063	
chalybaea (876)	entire species range	10	50,000 km²	7.05	*EST-4*	.465	.380 ± .333
					AMY	.102	
					AO-2	.815	
					MDH	.137	

* All F_{ST} values highly significant ($P < .001$, heterogeneity χ^2), except for the following loci in Sydney populations of *chalybaea*: *EST-4* (n.s.), *AO-2* (n s.), *MDH* ($P < .01$).
† Invariant in these four populations.

ference between *purpurea* and the other species, as well as the distinction between *confusa* populations and populations belonging to *chalybaea, impressa,* and *enigmatica*. The last two are closely clustered to some *chalybaea* populations, and the dendrogram suggests the possibility that *chalybaea* is a paraphyletic entity. There is certainly considerable genetic heterogeneity among *chalybaea* populations, and the complex would appear to be in a state of evolutionary flux.

DISCUSSION

Heterozygosity and Haplodiploidy

The foregoing data suggest low levels of intrapopulation genic heterozygosity in *Rhytidoponera* (and other haplodiploid species) relative to diploid insects. Also suggestive of constraints on the maintenance of genetic variability is the limited range of $\hat{H}$ values among the 53 species of Hymenoptera for which information is available. The variance of $\hat{H}$ for this group is significantly less than the variance of $\hat{H}$ for the genus *Drosophila* ($F_S = 3.267$, $P < .01$), despite the greater taxonomic diversity encompassed in the Hymenoptera sample (12 families, 24 genera).

Drosophila appear to have exceptionally high levels of heterozygosity compared to other invertebrates (Nevo, 1978, p. 147), so a comparison of Hymenoptera with *Drosophila* may be inappropriate. The data on other diploid insects are still sparse, but the wide range and clumped distribution of $\hat{H}$ values (Fig. 3) suggest that heterozygosity levels may be characteristic of particular taxa. Indeed, the mean $\hat{H}$ for all orthopteroids ($N = 7$) is

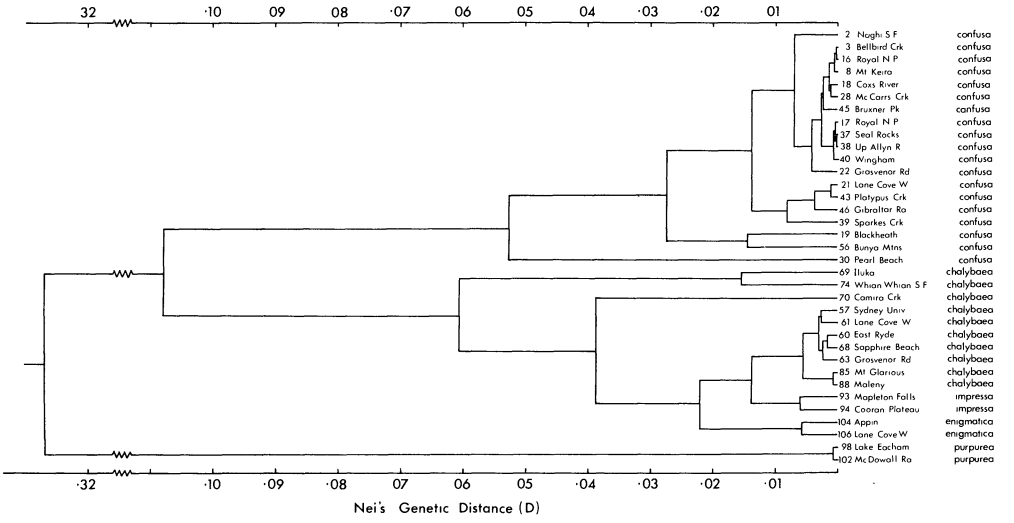

FIG. 3. Dendrogram of 35 *R. impressa* group populations, based on UPGMA cluster analysis of Nei's genetic distance coefficients (*D*). The number preceding each locality is the population code number (see Table 1).

0.038 ± .047 SD, not significantly different from that of the Hymenoptera!

Thus, the evidence supporting the hypothesis that haplodiploidy reduces genetic variability is rather weak. It seems desirable to obtain more data on diploid arthropods, and to extend the comparison to closely related haplodiploid and diploid species (e.g., certain mites). A different approach, involving the comparison of levels of variability at sex-linked and autosomal loci in diploid species, was attempted by Cooper et al. (1979) who found significantly less polymorphism at sex-linked loci in *Drosophila,* but no difference between the two classes of loci in man and kangaroos.

Even if we accept that haplodiploid species show inherently less intrapopulation variation than diploid organisms, the factors responsible for this remain difficult to disentangle, since low heterozygosity is predicted by both selectionist and neutralist models (Lester and Selander, 1979). However the ecological and taxonomic diversity among the 53 species of Hymenoptera thus far examined makes it seem likely that the sample includes a considerable range of values of N_e (effective population size). If so, the low mean and variance of $\hat{H}$ argue against a neutralist model in which heterozygosity levels are a function of N_e.

The ecological success of Hymenoptera and haplodiploid mites suggests no obvious constraints on adaptability arising from lower additive genetic variability. In the social Hymenoptera a sizable proportion of important adaptive traits may be female sex-limited. This is suggested, for example, by the much more extensive morphological and behavioral radiation among worker (and queen) ants, compared to males. Sex-limitation may allow the storage of considerable variability in haplodiploids.

For non-sex-limited loci in haplodiploids generally, low levels of intrapopulation variation may be partly a reflection of more efficacious selection. Given a selective environment which varies across the species range, the total pool of genic variability within a species may still be quite high.

Population Differentiation and Speciation

The allozyme data for the *Rhytidoponera impressa* group reveal no indication of significant departures from panmixia

within local populations occupying patches of rainforest or wet sclerophyll forest over several square kilometers ($F_{IS} \approx 0$). However, F-statistic analysis reveals a striking degree of differentiation *between* populations, even over limited geographical areas. The mean F_{ST} estimates for *confusa* (0.294) and *chalybaea* (0.380) are higher than those reported for most outbreeding animals, where $\bar{F}_{ST}$ ranges from .009 to .162 (reviewed in Eanes and Koehn, 1978).

Divergent allele frequencies in *Rhytidoponera* may be indicative of both stochastic processes and diversifying selection. Founder effects may have been important during initial colonizations and during population bottlenecks associated with habitat reduction, especially in view of the larger sampling variance of alleles in haplodiploid (as opposed to diploid) species. On the other hand, local population sizes of *confusa* and *chalybaea* appear to be high, on the order of 10^3 to 10^5 colonies (Ward, 1978). Moreover, the heterogeneity of F_{ST} estimates suggests that selective forces are acting on one or more loci.

While the high values of F_{ST} in *Rhytidoponera* favor the notion that haplodiploidy encourages population differentiation, a more appropriately controlled test would involve comparing the heterogeneity of allele frequencies at polymorphic sex-linked and autosomal loci in a diploid species. Such a comparison is provided in Table 7 for *Drosophila pseudoobscura,* where a relatively large number of sex-linked polymorphisms are known. The differences, while not significant (Mann-Whitney U-test), are in the direction expected, the mean F_{ST} for sex-linked loci being greater than that for autosomal loci. However interpretation is complicated by the great heterogeneity of F_{ST} values and by the association of some loci (particularly those on chromosome III) with inversions.

When measured over *all 22* loci, conspecific populations of *Rhytidoponera* are no more differentiated than those of most diploid species and interspecific differences are relatively small. (Data on genetic distances in diploid species are reviewed by Avise, 1976.) This is perhaps not too surprising, given the strong morphological similarity between members of the *impressa* group (Ward, 1980). Limited genetic differentiation was found between ant species in the *Formica rufa* group (Pamilo and Vepsalainen, 1977) and the *Aphaenogaster rudis* complex (Crozier, 1977*b*).

TABLE 7. *Mean* F_{ST} *values for polymorphic autosomal and sex-linked loci of* Drosophila pseudoobscura, *calculated from gene frequency data for five populations (Strawberry Canyon, Mesa Verde, Austin, Guatemala, and Bogotá). Source of data: Prakash et al. (1969); Prakash, Lewontin and Crumpacker in Lewontin (1974); and Prakash (1977).*

Class of loci	No. loci	$\bar{F}_{ST} \pm$ SD
Autosomal (excl. chromosome III)	13	.071 ± .067
Autosomal (incl. chromosome III)	19	.119 ± .165
Sex-linked	7	.181 ± .235

The cluster of sibling species in the *Rhytidoponera impressa* group is paralleled by other examples in the Hymenoptera, and Crozier (1977*a,* 1980) has suggested that sibling species are common in this order. Ants are notorious for showing geographical variation in morphology (e.g., Wilson, 1955, 1958; Brown, 1958) and many probable cases of sibling species complexes can be found in conventional taxonomic treatments of various formicid genera (e.g., Wilson, 1955; Taylor, 1967; Cole, 1968; Francoeur, 1973). Recent studies of allozyme and karyotype variation by Crozier (1975, 1977*b,* 1980), Halliday (1975, 1978), Imai et al. (1977), and Pressick (1972) have confirmed the trend and extended the evidence.

The family Formicidae is known from the Cretaceous (Wilson et al., 1967; Dlussky, 1975) yet some of the most species-rich contemporary genera (e.g., *Pheidole, Tetramorium* and *Crematogaster,* each with hundreds of species) are unknown before the Miocene, and must have undergone an explosive radiation since the mid-Tertiary (Brown, 1973). Crozier (1977*a*)

reviews evidence of rapid speciation in some symphytan and parasitic Hymenoptera, including the pteromalid housefly parasitoid, *Muscidifurax raptor,* which appears to have radiated into a complex of four species since its introduction into the Americas in Columbian times (Legner, 1969).

Evidence of rapid differentiation and speciation in the Hymenoptera is consistent with theoretical expectations for haplodiploidy. As with heterozygosity comparisons, however, it is difficult to know which taxa constitute an appropriate "control" group with which to compare the haplodiploid Hymenoptera. Certainly, comparable examples of rapid speciation among diploid insects can be cited, for example, the Hawaiian *Drosophila* (Carson et al., 1970), gelechiid moths of the genus *Hyposmocoma* (Zimmerman, 1978), and some tephritid fruit flies (Bush, 1969, 1975).

Summary

An electrophoretic survey of 22 loci in the *Rhytidoponera impressa* group revealed seven variant loci. Gene frequencies and average heterozygosity have been estimated for 35 populations (five species) occurring in tracts of mesic forest (mostly rainforest and wet sclerophyll) along the east coast of Australia. Estimated heterozygosity ($\hat{H}$) per population varies from .000 to .072 (mean .036 ± .003 SE). This is consistent with low values reported for other species of Hymenoptera, and contrasts with higher levels of allozyme variability reported in most diploid insects. However the evidence supporting the hypothesis that *haplodiploidy* is responsible for the reduced variation is still weak.

Local populations show no evidence of inbreeding, insofar as there are no detectable departures from panmixia ($F_{IS} \approx 0$). When considered over *all* loci, most populations are only moderately differentiated, the mean genetic distance (Nei's measure, D) between conspecific populations being 0.015 ± 0.001 SE ($N = 219$ comparisons). Nevertheless, there is marked heterogeneity of gene frequencies at the *segregating* loci. Mean estimates of F_{ST} (based on four loci) in *Rhytidoponera confusa* (*.294*) and *chalybaea* (*.380*) are larger than F_{ST} values reported for most outbreeding species. Divergent gene frequencies may be a reflection of both stochastic processes (founder effect and a high sampling variance) and selection, since contemporary population sizes appear to be quite high. These findings are consistent with theoretical expectations of rapid population differentiation under haplodiploidy, although the habitat requirements of the *impressa* group are also conducive to population divergence.

The mean genetic distance between all interspecific populations is 0.136 ± 0.005 SE ($N = 376$). Genetic distance data suggest the possibility that two species (*impressa* and *enigmatica*) are recently derived from divergent populations of a third, paraphyletic species (*chalybaea*). The occurrence of sibling species in the *Rhytidoponera impressa* group is paralleled by numerous other examples in the Hymenoptera, and lends support to the notion that speciation is a potentially rapid process in this group of insects.

Acknowledgments

For critical comments and discussion I thank L. C. Birch, G. L. Bush, R. H. Crozier, L. J. Lester, P. Pamilo, and W. D. Hamilton. R. W. Taylor kindly supplied several collections of ant colonies from north Queensland. This work was supported by a Commonwealth Scholarship administered by the Australian Department of Education, and forms part of a Ph.D. dissertation submitted to the University of Sydney. Additional financial support from L. C. Birch and the University of Sydney is gratefully acknowledged.

Literature Cited

Avise, J. C. 1976. Genetic differentiation during speciation, p. 106–122. *In* F. Ayala (ed.), Molecular Evolution. Sinaeur Associates, Sunderland, Mass.

Ayala, F. J., and J. R. Powell. 1972. Allozymes as diagnostic characters of sibling species of *Drosophila*. Proc. Nat. Acad. Sci. 69:1094–1096.

BENNETT, J. H. 1957. Selectively balanced polymorphism at a sex-linked locus. Nature 180: 1363–1364.

BROWN, A. H. D. 1970. The estimation of Wright's fixation index from genotypic frequencies. Genetica 41:399–406.

BROWN, W. L. 1958. Contributions towards a reclassification of the Formicidae, II. Tribe Ectatommini (Hymenoptera). Bull. Mus. Comp. Zool. 118:175–362.

———. 1973. A comparison of the Hylean and Congo-West African rain forest ant faunas, p. 161–185. *In* B. H. Meggers, E. S. Ayensu, and W. D. Duckworth (eds.), Tropical Forest Ecosystems in Africa and South America, a Comparative Review. Smithsonian Inst. Press, Washington, D.C.

BUSH, G. L. 1969. Sympatric host formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). Evolution 23:273–351.

———. 1975. Modes of animal speciation. Ann. Rev. Ecol. Syst. 6:339–364.

CARSON, H. L., O. E. HARDY, H. T. SPIETH, AND W. S. STONE. 1970. The evolutionary biology of the Hawaiian Drosophilidae, p. 437–543. *In* M. K. Hecht and W. C. Steere (eds.), Essays in Evolution and Genetics in Honor of Theodosius Dobzhansky. Appleton-Century-Crofts, N.Y.

CAVALLI-SFORZA, L. L., AND W. F. BODMER. 1971. The Genetics of Human Populations. W. H. Freeman, San Francisco.

COLE, A. C. 1968. Pogonomyrmex harvester ants: a study of the genus in North America. Univ. of Tenn. Press, Knoxville.

COOPER, D. W., P. G. JOHNSTON, J. L. VANDERBERG, G. M. MAYNES, AND G. K. CHEW. 1979. A comparison of genetic variability at X-linked and autosomal loci in kangaroos, man, and *Drosophila*. Genet. Res. 33:243–252.

CROW, J. F., AND M. KIMURA. 1970. Introduction to Population Genetics Theory. Harper and Row, N.Y.

CROZIER, R. H. 1970. On the potential for genetic variability in haplo-diploidy. Genetica 14:551–556.

———. 1971. Heterozygosity and sex determination in haplodiploidy. Amer. Natur. 105:339–412.

———. 1975. Animal Cytogenetics 3. Insects 7. Hymenoptera. Gebrüder Borntraeger, Berlin.

———. 1977*a*. Evolutionary genetics of the Hymenoptera. Ann. Rev. Entomol. 22:263–288.

———. 1977*b*. Genetic differentiation between populations of the ant *Aphaenogaster "rudis"* in the southeastern United States. Genetica 47: 17–36.

———. 1979. Genetics of sociality, p. 223–286. *In* H. R. Hermann (ed.), Social Insects, Vol. I. Academic Press, N.Y.

———. 1980. Genetic aspects of ant evolution. *In* W. R. Atchley and D. S. Woodroff (eds.), Essays on Evolution and Speciation in Honor of M. J. D. White. Cambridge Univ. Press. *In press.*

DAVIS, B. J. 1964. Disc electrophoresis, II. Method and application to human serum proteins. Ann. N.Y. Acad. Sci. 121:404–427.

DLUSSKY, G. M. 1975. Family Formicidae Latreille, 1802, p. 114–121. *In* A. Rasnitzyn (ed.), Mesozoic Apocryta. Trans. Paleontol. Inst. Acad. Sci. U.S.S.R., Volume 147. (In Russian)

EANES, W. R., AND R. K. KOEHN. 1978. An analysis of genetic structure in the monarch butterfly, *Danaus plexippus* L. Evolution 32:784–797.

FRANCOEUR, A. 1973. Révision taxonomique des espèces néarctiques du groupe *fusca,* genre *Formica* (Formicidae, Hymenoptera). Mem. Soc. Entomol. Québec 3:1–316.

HALDANE, J. B. S., AND S. D. JAYAKAR. 1964. Equilibria under natural selection at a sex-linked locus. J. Genet. 59:29–36.

HALLIDAY, R. B. 1975. Electrophoretic variation of amylase in meat ants, *Iridomyrmex purpureus,* and its taxonomic significance. Aust. J. Zool. 23:271–276.

———. 1978. Genetic studies of meat ants. Ph.D. Thesis. Univ. of Adelaide.

HAMILTON, W. D. 1971. Selection of selfish and altruistic behavior in some extreme models, p. 57–91. *In* J. F. Eisenberg and W. S. Dillon (eds.), Man and Beast: Comparative Social Behavior. Smithsonian Inst. Press, Washington, D.C.

HARRIS, H., AND D. A. HOPKINSON. 1976. Handbook of Enzyme Electrophoresis in Human Genetics. American Elsevier Publ. Co., N.Y.

HARTL, D. L. 1971. Some aspects of natural selection in arrhenotokous populations. Amer. Zool. 11:309–325.

———. 1972. A fundamental theorem of natural selection for sex linkage or arrhenotoky. Amer. Natur. 106:516–524.

HARTL, D. L., AND S. W. BROWN. 1970. The origin of male haploid genetic systems and their expected sex ratio. Theoret. Pop. Biol. 1:165–190.

HELLE, W., AND W. P. J. OVERMEER. 1973. Variability in tetranychid mites. Ann. Rev. Entomol. 18:97–120.

IMAI, H. T., R. H. CROZIER, AND R. W. TAYLOR. 1977. Karyotype evolution in Australian ants. Chromosoma 59:341–393.

LEGNER, E. G. 1969. Reproductive isolation and size variation in the *Muscidifurax raptor* complex. Ann. Entomol. Soc. Amer. 62:382–385.

LESTER, L. J., AND R. K. SELANDER. 1979. Population genetics of haplodiploid insects. Genetics 92:1329–1345.

LEVENE, H. 1949. On a matching problem arising in genetics. Ann. Math. Stat. 20:91–94.

LEWONTIN, R. C. 1974. The Genetic Basis of Evolutionary Change. Columbia Univ. Press, N.Y.

LI, C. C., AND D. G. HORVITZ. 1953. Some methods of estimating the inbreeding coefficient. Amer. J. Human Genet. 95:107–117.

MANDEL, S. P. H. 1959. Stable equilibrium at a sex-linked locus. Nature 183:1347–1348.

METCALF, O. A., J. C. MARLIN, AND G. S.

WHITT. 1975. Low levels of genetic heterozygosity in Hymenoptera. Nature 257:792–794.

NEI, M. 1972. Genetic distance between populations. Amer. Natur. 106:283–292.

———. 1973. Analysis of gene diversity in subdivided populations. Proc. Nat. Acad. Sci. 70:3321–3323.

NEI, M., AND A. K. ROYCHOUDHURY. 1974. Sampling variances of heterozygosity and genetic distance. Genetics 76:379–390.

NEVO, E. 1978. Genetic variation in natural populations: patterns and theory. Theoret. Pop. Biol. 13:121–177.

OLIVER, J. H. 1977. Cytogenetics of mites and ticks. Ann. Rev. Entomol. 22:407–429.

ORNSTEIN, L. 1964. Disc electrophoresis, I. Background and theory. Ann. N.Y. Acad. Sci. 121:321–349.

PAMILO, P., R. ROSENGREN, K. VEPSÄLÄINEN, S. VARVIO-AHO, AND B. PISARSKI. 1978*a*. Population genetics of *Formica* ants, I. Patterns of enzyme gene variation. Hereditas 89:233–248.

PAMILO, P., S. VARVIO-AHO, AND A. PEKKARINEN. 1978*b*. Low enzyme gene variability in Hymenoptera as a consequence of haplodiploidy. Hereditas 88:93–99.

PAMILO, P., AND K. VEPSÄLÄINEN. 1977. Heretical notes on the taxonomy of *Formica* s. str. (Hym.). Proc. VIII. Int. Congr. IUSSI. p. 128–129.

POWELL, J. R. 1975. Protein variation in natural poulations of animals. Evol. Biol. 8:79–119.

PRAKASH, S. 1977. Further studies on gene polymorphism in the mainbody and geographically isolated populations of *Drosophila pseudoobscura*. Genetics 85:713–719.

PRAKISH, S., R. C. LEWONTIN, AND J. L. HUBBY. 1969. A molecular approach to the study of genic heterozygosity in natural populations, IV. Patterns of genic variation in central, marginal, and isolated populations of *Drosophila pseudoobscura*. Genetics 61:841–858.

PRESSICK, M. L. 1972. Competition and coexistence of ant populations on St. John, Virgin Islands. Ph.D. Thesis, Univ. of Kansas, Lawrence.

SHAW, C. R., AND R. PRASAD. 1970. Starch gel electrophoresis of enzymes—a compilation of recipes. Biochem. Genet. 4:297–320.

SNEATH, P. H., AND R. R. SOKAL. 1973. Numerical Taxonomy. W. H. Freeman, San Francisco.

SNYDER, T. P. 1974. Lack of allozymic variability in three bee species. Evolution 28:687–689.

SUOMALAINEN, E. 1962. Significance of parthenogenesis in the evolution of insects. Ann. Rev. Entomol. 7:349–366.

SPIELMAN, R. S., J. V. NEEL, AND F. H. LI. 1977. Inbreeding estimation from population data: models, procedures, and implications. Genetics 85:355–371.

TAYLOR, R. W. 1967. A monographic revision of the ant genus *Ponera* Latreille (Hymenoptera: Formicidae). Pac. Ins. Monogr. 13:1–112.

WADE, M. J. 1978. A critical review of the models of group selection. Quart. Rev. Biol. 53:101–114.

WARD, P. S. 1978. Genetic variation, colony structure, and social behaviour in the *Rhytidoponera impressa* group, a species complex of ponerine ants. Ph.D. Thesis. Univ. of Sydney.

———. 1980. A systematic revision of the *Rhytidoponera impressa* group (Hymenoptera: Formicidae) in Australia and New Guinea. Aust. J. Zool. *In press*.

WARD, R. H., AND C. F. SING. 1970. A consideration of the power of the χ^2 test to detect inbreeding effects in natural populations. Amer. Natur. 104:335–365.

WHITE, M. 1945. Animal Cytology and Evolution, 1st ed. Cambridge Univ. Press.

WILSON, D. S. 1980. The natural selection of populations and communities. Benjamin/Cummings, Menlo Park.

WILSON, E. O. 1955. A monographic revision of the ant genus *Lasius*. Bull. Mus. Comp. Zool. 113:1–201.

WILSON, E. O. 1958. Studies on the ant fauna of Melanesia, I. The tribe Leptogenyini, II. The tribes Amblyoponini and Platythyreini, III. *Rhytidoponera* in western Melanesia and the Moluccas, IV. The tribe Ponerini, V. The tribe Odontomachini. Bull. Mus. Comp. Zool. 118:101–153; 119:303–371; 120:483–510.

WILSON, E. O., F. M. CARPENTER, AND W. L. BROWN. 1967. The first Mesozoic ants, with the description of a new subfamily. Psyche 74:1–19.

WORKMAN, P. L., AND J. D. NISWANDER. 1970. Population studies on southwestern Indian tribes, II. Local genetic differentiation in the Papago. Amer. J. Human Genet. 22:24–49.

WRIGHT, S. 1922. Coefficients of inbreeding and relationship. Amer. Natur. 56:330–338.

———. 1951. The genetical structure of populations. Ann. Eugen. 15:323–354.

———. 1965. The interpretation of population structure by F-statistics, with special regard to systems of mating. Evolution 19:395–420.

ZIMMERMAN, E. C. 1978. Insects of Hawaii, Vol. 9. Microleptidoptera, Part II. Gelechioidea. Univ. Press of Hawaii, Honolulu.

Corresponding Editor: J. R. Powell