

GENE DIVERSITY IN HYMENOPTERA

DAN GRAUR

Center for Demographic and Population Genetics, The University of Texas Health Science Center
at Houston, P.O. Box 20334, Houston, TX 77225

Received July 28, 1983. Accepted November 16, 1983

Hymenopteran species display levels of electrophoretic variation significantly lower than most other insects, and a few of them lack variation altogether. These observations are variably explained by reduced heterozygote advantage, inbreeding, eusociality, environmental stability conferred by the nest microhabitat, facilitation of exposure of deleterious genes in the haploid sex, reproduction by arrhenotokous parthenogenesis with balancing selection, and small effective population size resulting in a reduction in the amount of neutral polymorphism (Suomalainen, 1962; Crozier, 1970; Hartl, 1971, 1972; Snyder, 1974; Metcalf et al., 1975; Pamilo et al., 1978a, 1978b; Pamilo and Crozier, 1981; Wagner and Briscoe, 1983). Recently, Berkelhamer (1983) tested several hypotheses concerning the low levels of intraspecific genetic variability in Hymenoptera. Her conclusions were: (1) Hymenopterans have significantly lower variability than other insects due to their haplodiploidy. (2) Primitively eusocial insects are less variable than either solitary or advanced social species, implying that eusociality arises as a consequence of inbreeding. (3) Polygynous and monogynous species have similar levels of variability, challenging the expectations derived from both the neutral theory of evolution (Kimura, 1968) and Hamilton's (1964) hypothesis. Hamilton's hypothesis is later rescued by assuming that the increased effective population size provided by polygyny is balanced by a more severe regime of inbreeding than in monogynous species. Unfortunately, three major errors and several minor ones in the analysis raise doubts as to the validity of these conclusions.

The first error concerns the interchangeable use of observed heterozygosity, H_{obs} (the average proportion of heterozygous loci per individual) and expected heterozygosity or average gene diversity, H_{exp} , defined as the mean of h over all loci, where $h = 1 - \sum x_i^2$, and x_i is the frequency of the i th allele at a locus (Nei, 1975). In her Procedures section, Berkelhamer (1983) claims to have used H_{obs} , but her data contain both H_{obs} and H_{exp} . For example, in the case of *Opius juglandis* and other species from Lester and Selander (1979), she uses H_{exp} , whereas, when given a choice between H_{exp} and H_{obs} , as in the case of *Rhytidoponera impressa* (Ward, 1980), she chooses H_{obs} . H_{obs} is very sensitive to the mating structure of a population and the amount of inbreeding. When inbreeding is strong,

H_{obs} can be very low, while H_{exp} is not affected. In extreme cases such as selfing species (e.g., Selander and Hudson, 1976) H_{obs} is effectively 0, yet H_{exp} can be large. We also note that haploid organisms, which, by definition, have $H_{obs} = 0$, are among the species with the highest gene diversity (Spieth, 1975; Krzakowa and Szweykowski, 1979; Selander and Levin, 1980; Gaur et al., 1981; Yamazaki, 1981). For comparative purposes, H_{exp} rather than H_{obs} should be used as a measure of genetic variability (for further details see Nei, 1975; Nei and Graur, 1984). In Hymenoptera, where mating structure can assume diverse forms, the distinction between H_{obs} and H_{exp} is particularly important. While it may be difficult to ascertain which species are inbred, the fact is that, in almost all cases, H_{obs} is less than H_{exp} , such that using H_{obs} will introduce a unidirectional bias. In *Heliothis zea*, for instance, the difference is 21%. It should be noted that other compilations of protein polymorphism (e.g., Soulé, 1976; Nevo, 1978) often include a mixture of H_{obs} and H_{exp} .

The second problem concerns the number of loci used to determine gene diversity. In Table 2 of Berkelhamer (1983), 51 hymenopteran species are listed, but the number of loci in the majority of them is very low. Presumably, the same is true for non-hymenopterans. Since genetic diversity is known to have a huge standard error (Nei and Roychoudhury, 1974b), it is advisable to use estimates based on at least 20 loci. This is especially true when genetic variability is low. When different groups of species are compared by pooling many species within each group, fewer than 20 loci may be used, provided that we examine the same set of loci. This stipulation derives from the fact that different loci have different levels of heterozygosity (for reasons see Zouros, 1976; Harris et al., 1977; Koehn and Eanes, 1977, 1978; Ward, 1977; Nei et al., 1978; Turner et al., 1979). Moreover, since students of genetic diversity tend to study the more polymorphic loci first, using a small number of loci tends to introduce an additional bias in H_{exp} . This sometimes has dramatic effects on estimates of gene diversity. For example, in humans, estimates of H_{exp} for blood groups are 0.264, 0.197, 0.130, and 0.114 when calculated in chronological order, on the basis of 21, 34, 57, and 67 loci respectively (Nei and Roychoudhury, 1974a, 1982). In the case of *Drosophila pseudoobscura*, H_{exp} was estimated to be 0.136 based on 46 loci (Fuerst et al., 1977), while

TABLE 1. H_{exp} for insect populations.

Order, suborder, category	Organism*	Loci**	H_{exp}	Reference
Orthoptera	<i>Allonemobius allardi</i>	18	0.130	Howard, 1983
	<i>A. tinnulus</i>	18	0.107	Howard, 1983
	<i>A. sp. Z</i>	18	0.071	Howard, 1983
	<i>A. sp. Y</i>	18	0.094	Howard, 1983
	<i>A. fasciatus</i>	18	0.110	Howard, 1983
	<i>A. socius</i>	18	0.148	Howard, 1983
	<i>A. griseus</i>	18	0.043	Howard, 1983
	<i>A. maculatus</i>	18	0.017	Howard, 1983
	<i>Ceuthophilus gracilipes</i>	26	0.030	Cockley et al., 1977
	<i>Gryllus integer</i>	20	0.145	Nevo, 1978
	<i>G. bimaculatus</i>	25	0.063	Nevo, 1978
	<i>G. veletis</i>	18	0.119	Harrison, 1979
	<i>G. pennsylvanicus</i>	18	0.068	Harrison, 1979
	<i>G. rubens</i>	18	0.073	Harrison, 1979
	<i>G. firmus</i>	18	0.050	Harrison, 1979
	<i>G. ovisopis</i>	18	0.092	Harrison, 1979
	<i>G. sp. 1</i>	18	0.042	Harrison, 1979
	<i>G. sp. 2</i>	18	0.057	Harrison, 1979
	<i>Periplaneta americana</i>	20	0.018	Nevo, 1978
	<i>Blatella germanica</i>	16	0.015	Nevo, 1978
	<i>Gryllodes hebraeus</i>	26	0.020	Nevo, 1978
	<i>Gryllotalpa gryllotalpa</i>	21	0.029	Nevo, 1978
	<i>Troglophilus cavicola</i>	16	0.082	Sbordoni et al., 1981
<i>T. andreinii</i> ¹	16	0.169	Sbordoni et al., 1981	
<i>Caledia captiva</i> ²	18-20	0.112	Daly et al., 1981	
Hemiptera				
Homoptera	<i>Magicicada tredecassini</i>	15	0.174	Krepp and Smith, 1974
	<i>M. tredecula</i>	15	0.153	Krepp and Smith, 1974
	<i>Philaenus spumarius</i>	23	0.076	Saura et al., 1973
	<i>Myzus persicae</i>	19	0.000	May and Holbrook, 1978
	<i>Macrosiphum euphorbiae</i>	18	0.070	May and Holbrook, 1978
	<i>Enchenopa binotata</i> ³	15	0.113	Guttman et al., 1981
Heteroptera	<i>Limnoporus caniculatus</i>	16	0.219	Zera, 1981
	<i>Gerris remigis</i>	18	0.109	Zera, 1981
	<i>G. argentatus</i>	15	0.053	Varvio-Aho, 1981
	<i>G. lacustris</i>	16	0.165	Varvio-Aho, 1981
	<i>G. lateralis</i>	16	0.055	Varvio-Aho, 1981
	<i>G. najas</i>	16	0.000	Varvio-Aho, 1981
	<i>G. odontogaster</i>	16	0.146	Varvio-Aho, 1981
	<i>G. paludum</i>	16	0.080	Varvio-Aho, 1981
	<i>G. rufoscutellatus</i>	16	0.044	Varvio-Aho, 1981
	<i>Oncopeltus fasciatus</i>	18	0.024	Leslie and Dingle, 1983
	<i>O. aulicus</i>	18	0.000	Leslie and Dingle, 1983
	<i>O. longirostris</i>	18	0.040	Leslie and Dingle, 1983
	<i>O. sandarachatus</i>	18	0.021	Leslie and Dingle, 1983
	<i>O. cingulifer</i>	18	0.029	Leslie and Dingle, 1983
	<i>Lygus hesperus</i>	17	0.256	Sluss et al., 1982
	<i>L. lineolaris</i>	17	0.212	Sluss et al., 1982
<i>L. desertinus</i>	17	0.212	Sluss et al., 1982	
<i>L. elisus</i>	17	0.255	Sluss et al., 1982	
Coleoptera	<i>Otiorrhynchus scaber</i>	25	0.309	Suomalainen and Saura, 1973
	<i>Strophosomus capitatus</i>	25	0.170	Suomalainen and Saura, 1973
	<i>Dendroctonus jeffreyi</i>	17	0.131	Higby and Stock, 1982
	<i>D. ponderosae</i>	17	0.143	Higby and Stock, 1982
	<i>Agonum deocrum</i>	15-17	0.204	Liebherr, 1983

TABLE 1. Continued.

Order, suborder, category	Organism*	Loci**	H_{exp}	Reference
Lepidoptera	<i>Solenobia triquetrella</i> ⁴	16	0.230	Lokki et al., 1975
	<i>S. t.</i> ⁵	16	0.250	Lokki et al., 1975
	<i>S. t.</i> ⁶	16	0.200	Lokki et al., 1975
	<i>Pectinophora gossypiella</i>	31	0.324	Bartlett, 1981
	<i>Archips argyrospilus</i>	15	0.112	Pashley, 1983
	<i>Argyrotaenia quercifoliana</i>	15	0.155	Pashley, 1983
	<i>Clepsis clemensiana</i>	15	0.131	Pashley, 1983
	<i>C. persicana</i>	15	0.155	Pashley, 1983
	<i>Cydia caryana</i>	15	0.101	Pashley, 1983
	<i>C. lautiscula</i>	15	0.031	Pashley, 1983
	<i>C. membrosa</i>	15	0.052	Pashley, 1983
	<i>C. pomonella</i>	15	0.145	Pashley, 1983
	<i>Ecdytophpa mana</i>	15	0.000	Pashley, 1983
	<i>Melissopus latiferreanus</i>	15	0.125	Pashley, 1983
	<i>Ptycholoma peritana</i>	15	0.118	Pashley, 1983
	<i>P. virescana</i>	15	0.189	Pashley, 1983
	<i>Choristoneura retiniana</i>	18	0.164	Stock and Castroville, 1981
	<i>C. occidentalis</i> ⁷	15-18	0.136	Stock and Castroville, 1981; Willhite and Stock, 1983; Pashley, 1983
	<i>C. fumiferana</i>	18	0.171	Stock and Castroville, 1981
	<i>C. biennis</i>	18	0.134	Stock and Castroville, 1981
	<i>C. lambertiana</i>	15	0.199	Stock and Castroville, 1981
	<i>Heliothis virescens</i>	19	0.389	Sluss et al., 1978; Sluss and Graham, 1979
	<i>H. zea</i> ⁸	21	0.327	Sluss et al., 1978
	<i>Speyeria adiastra</i>	16	0.084	Brittnacher et al., 1978
	<i>S. atlantis</i>	16	0.089	Brittnacher et al., 1978
	<i>S. callippe</i> ⁹	16	0.137	Brittnacher et al., 1978
	<i>S. cybele</i>	16	0.087	Brittnacher et al., 1978
	<i>S. coronis</i> ¹⁰	16	0.109	Brittnacher et al., 1978
	<i>S. egleis</i>	16	0.126	Brittnacher et al., 1978
	<i>S. hydaspe</i>	16	0.113	Brittnacher et al., 1978
	<i>S. mormonia</i>	16	0.136	Brittnacher et al., 1978
	<i>S. nokomis</i>	16	0.029	Brittnacher et al., 1978
<i>S. zereine</i> ¹¹	16	0.106	Brittnacher et al., 1978	
<i>Lymantria dispar</i>	20	0.061	Harrison et al., 1983	
Diptera	<i>Aedes aegypti</i> ¹²	23	0.152	Tabachnick et al., 1979
	<i>A. atropalpus</i>	17	0.033	Munstermann, 1980
	<i>A. epactius</i> ¹³	17	0.075	Munstermann, 1980
	<i>A. triseriatus</i>	17-18	0.228	Matthews and Craig, 1980; Munstermann et al., 1982
	<i>A. hendersonii</i>	18	0.154	Matthews and Munstermann, 1983
	<i>Anopheles marshalli</i> sp. A	16	0.139	Lambert, 1983
	<i>A. m.</i> sp. B	16	0.142	Lambert, 1983
	<i>A. m.</i> sp. C	16	0.144	Lambert, 1983
	<i>A. m.</i> sp. E	16	0.112	Lambert, 1983
	<i>A. malayensis</i>	19	0.181	Hilburn and Rai, 1981
	<i>A. alcasidi</i>	19	0.163	Hilburn and Rai, 1981
	<i>A. polynesiensis</i>	19	0.113	Hilburn and Rai, 1981
	<i>A. kesseli</i>	19	0.138	Hilburn and Rai, 1981
	<i>A. calceatus</i>	17	0.156	Lounibos and Munstermann, 1981
	<i>A. soleatus</i>	17	0.090	Lounibos and Munstermann, 1981

TABLE 1. Continued.

Order, suborder, category	Organism*	Loci**	H_{exp}	Reference
	<i>A. ledgeri</i>	15	0.154	Lounibos and Munstermann, 1981
	<i>A. mariae</i>	26	0.071	Cianchi et al., 1978
	<i>A. zammitii</i>	26	0.058	Cianchi et al., 1978
	<i>Discochaeta hyponomutae</i>	16	0.096	Menken, 1982
	<i>Rhagoletis pomonella</i>	15	0.182	Berlocher and Bush, 1982
	<i>R. mendax</i>	15	0.205	Berlocher and Bush, 1982
	<i>R. zephyria</i>	15	0.101	Berlocher and Bush, 1982
	<i>R. cornivora</i>	15	0.105	Berlocher and Bush, 1982
	<i>R. cingulata</i>	15	0.071	Berlocher and Bush, 1982
	<i>R. indifferens</i>	15	0.060	Berlocher and Bush, 1982
	<i>R. suavis</i>	15	0.061	Berlocher and Bush, 1982
	<i>R. completa</i>	15	0.075	Berlocher and Bush, 1982
	<i>R. juglandis</i>	15	0.087	Berlocher and Bush, 1982
	<i>R. boycei</i>	15	0.062	Berlocher and Bush, 1982
	<i>R. fausta</i>	15	0.107	Berlocher and Bush, 1982
	<i>R. tabellaria</i>	15	0.090	Berlocher and Bush, 1982
	<i>R. juniperina</i>	15	0.241	Berlocher and Bush, 1982
	<i>R. ribicola</i>	15	0.095	Berlocher and Bush, 1982
	<i>R. basiola</i>	15	0.199	Berlocher and Bush, 1982
	<i>R. cerasi</i>	15	0.105	Berlocher and Bush, 1982
	<i>R. berberides</i>	15	0.023	Berlocher and Bush, 1982
	<i>Zonosemata electa</i>	15	0.043	Berlocher and Bush, 1982
	<i>Oedicarena latrifons</i>	15	0.056	Berlocher and Bush, 1982
	<i>Epochra canadensis</i>	15	0.118	Berlocher and Bush, 1982
Drosophila spp.	<i>Drosophila mercaptorum</i>	21	0.124	Fuerst et al., 1977
	<i>D. heteronura</i>	25	0.162	Fuerst et al., 1977
	<i>D. silvestris</i>	25	0.151	Fuerst et al., 1977
	<i>D. engyochracea</i>	20	0.127	Steiner, 1979b
	<i>D. paulistorum</i>	33	0.177	Powell, 1975
	<i>D. nebulosa</i>	30	0.188	Powell, 1975
	<i>D. pseudoobscura</i>	63	0.009	Cabrera et al., 1983
	<i>D. persimilis</i>	43	0.107	Fuerst et al., 1977
	<i>D. miranda</i>	43	0.085	Fuerst et al., 1977
	<i>D. melanogaster</i>	25	0.154	Powell, 1975
	<i>D. robusta</i>	40	0.123	Prakash, 1973
	<i>D. buzzatii</i>	29	0.068	Fuerst et al., 1977
	<i>D. mimica</i>	21	0.222	Steiner, 1979a
	<i>D. busckii</i>	30	0.039	Prakash, 1973
	<i>D. parabipectinata</i>	23	0.111	Yang et al., 1972
	<i>D. bipectinata</i>	23	0.199	Yang et al., 1972
	<i>D. malerkotliana</i> ¹⁴	23	0.195	Yang et al., 1972
	<i>D. obscura</i>	33	0.109	Lakovaara and Saura, 1971
	<i>D. equinoxialis</i>	31	0.165	Ayala et al., 1974
	<i>D. willistoni</i>	36	0.192	Powell, 1975
	<i>D. subobscura</i>	67	0.084	Cabrera et al., 1983
	<i>D. bifasciata</i>	21	0.242	Saura, 1974
	<i>D. tropicalis</i>	34	0.198	Powell, 1975
	<i>D. adiostola</i>	31	0.142	Fuerst et al., 1977
	<i>D. nigra</i>	31	0.160	Fuerst et al., 1977
	<i>D. crassifemur</i>	31	0.204	Fuerst et al., 1977
	<i>D. simulans</i>	53	0.064	Cabrera et al., 1983
	<i>D. guanche</i>	68	0.066	Cabrera et al., 1983
	<i>D. madreinsis</i>	67	0.103	Cabrera et al., 1983
	<i>D. ambigua</i>	56	0.032	Cabrera et al., 1983
	<i>D. pavani</i>	24	0.192	Nair et al., 1971

TABLE 1. Continued.

Order, suborder, category	Organism*	Loci**	H_{exp}	Reference
Hymenoptera				
Solitary				
Bees	<i>Megachile pacifica</i>	15-19	0.033	Lester and Selander, 1979
	<i>Nomia heteropoda</i>	15	0.070	Metcalf et al., 1975
	<i>Savastra obliqua</i>	16	0.038	Metcalf et al., 1975
Sawflies	<i>Pontania vesicator</i>	18	0.021	Pamilo et al., 1978b
Wasps	<i>Stictia carolina</i>	17	0.056	Metcalf et al., 1975
	<i>Chalybion californicum</i>	16	0.073	Metcalf et al., 1975
	<i>Scolia dubia dubia</i>	15	0.051	Metcalf et al., 1975
	<i>Trypargilum politum</i>	19	0.059	Metcalf et al., 1975
	<i>Diadegma armillata</i>	19	0.048	Menken, 1982
	<i>Pimpla turionellae</i>	29	0.038	Menken, 1982
	<i>Triclistus yponomeutae</i>	20	0.020	Menken, 1982
	<i>Tetrastichus evonymellae</i>	20	0.055	Menken, 1982
	<i>Ageniaspis fuscicollis</i>	25	0.019	Menken, 1982
	<i>Itoplectis maculata</i>	20	0.056	Menken, 1982
Eusocial				
Primitive				
Bees	<i>Bombus terrestris</i>	15	0.037	Pamilo et al., 1978b
	<i>B. lapidarius</i>	16	0.007	Pamilo et al., 1978b
Wasps	<i>Lasioglossum zephyrum</i>	24	0.000	Snyder, 1974
	<i>Polistes exclamans</i>	15-16	0.039	Lester and Selander, 1979
	<i>P. annularis</i>	15	0.053	Lester and Selander, 1979
Advanced				
Ants	<i>Iridomyrmex purpureus</i> sp. P	15	0.039	Halliday, 1981
	<i>I. p.</i> sp. B	15	0.052	Halliday, 1981
	<i>I. p.</i> sp. V	15	0.010	Halliday, 1981
	<i>Rhytidoponera impressa</i>	22	0.053	Ward, 1980
	<i>R. confusa</i>	22	0.032	Ward, 1980
	<i>R. chalybaea</i>	22	0.046	Ward, 1980
	<i>R. purpurea</i>	22	0.005	Ward, 1980
	<i>R. enigmatica</i>	22	0.040	Ward, 1980
	<i>Nothomyrmecia macrops</i>	16	0.032	Ward and Taylor, 1981
Bees	<i>Trigona carbonaria</i>	20	0.000	Wagner and Briscoe, 1983
	<i>T. australis</i>	20	0.000	Wagner and Briscoe, 1983

*¹ The population from Castelana caves, designated CAS (Sbordoni et al., 1981) is ignored since only seven individuals were examined for 14 loci.

² Average for Torresian, Daintree, Moreton, South-East Australian, and hybrid zones' chromosomal taxa.

³ Average of six host races (*Ptelea trifoliata*, *Celastrus scandens*, *Robinia pseudoacacia*, *Cercis canadensis*, *Juglans nigra*, and *Viburnum* sp.).

⁴ Sexual.

⁵ Parthenogenetic XY.

⁶ Parthenogenetic XO.

⁷ Average for three populations (Stock and Castroville, 1981; Pashley, 1983; Willhite and Stock, 1983).

⁸ The laboratory population was ignored (Sluss et al., 1978).

⁹ Average for *callippe* and *liliana* subspecies.

¹⁰ Average for *coronis* and *snyderi* subspecies.

¹¹ Average for *zerene*, *bremneri*, *conchylatus*, and *malcolmi* subspecies.

¹² Average for domestic and feral (sylvan) populations.

¹³ Average for *epactius*, *nielsenii*, and *perichardes* subspecies.

¹⁴ Average for *malerkotliana* and *pallens* subspecies.

** In all species with $H_{exp} = 0.000$, the number of loci was determined tentatively by comparing the enzyme systems with related polymorphic insect species (e.g., Wagner and Briscoe, 1983).

TABLE 2. Mean H_{exp} values for insects.

Insect category	No. of species	$H_{exp} \pm SE$
All insects	188	0.107 \pm 0.005
Excluding		
<i>Drosophila</i>	157	0.101 \pm 0.006
Diploid	158	0.120 \pm 0.006
Excluding		
<i>Drosophila</i>	127	0.116 \pm 0.006
Orthoptera	25	0.076 \pm 0.009
Hemiptera	24	0.104 \pm 0.017
Homoptera	6	0.098 \pm 0.026
Heteroptera	18	0.107 \pm 0.022
Coleoptera	5	0.191 \pm 0.032
Lepidoptera	34	0.145 \pm 0.014
Diptera	70	0.124 \pm 0.007
<i>Drosophila</i>	31	0.135 \pm 0.011
Other Diptera	39	0.115 \pm 0.009
Haplodiploid		
(Hymenoptera)	30	0.036 \pm 0.004
Solitary	14	0.045 \pm 0.005
Wasps	10	0.048 \pm 0.005
Bees	3	0.047 \pm 0.012
Sawflies	1	0.021
Eusocial	16	0.028 \pm 0.005
Primitive	5	0.027 \pm 0.010
Wasps	3	0.031 \pm 0.016
Bees	2	0.022 \pm 0.015
Advanced	11	0.031 \pm 0.006
Bees	2	0.000 \pm 0.000
Ants	9	0.034 \pm 0.006
All wasps	13	0.044 \pm 0.006
All bees	7	0.026 \pm 0.010

subsequent studies with 63 loci have lowered the estimate to 0.009 (Cabrera et al., 1983). (The second value may be a little underestimated because of the use of two laboratory strains recently derived from natural populations instead of natural populations directly.)

The third problem concerns several assumptions on the effective population size (N_e). First, it is important to note that we do not know the present population sizes for the species in question. The differences found between groups of species may tell us nothing about the effects of haplodiploidy, degrees of eusociality, and polygyny, but may simply reflect differences in absolute population sizes and past bottleneck effects which last for long periods of time (Nei et al., 1975). In order to attribute the differences to factors other than effective population size, one must make explicit the assumption that all known catastrophic events in the last million years (Rensch, 1959; Martin and Wright, 1976; for an extensive bibliography, see Brain, 1981) and their expected effects on gene diversity (Wright, 1938; Nei et al., 1975) are ignored. This would be justifiable only if past values of N_e were positively correlated with present N_e values. Since neither set

of values is known, however, this assumption is unwarranted. In addition, the relative importance of actual population size versus mating pattern is not properly presented. The present effective population size for a haplodiploid population is given by $N_e = 9N_mN_f/(4N_m + 2N_f)$ (Wright, 1933; for other properties, see Yokoyama and Nei, 1979), where N_m and N_f are the numbers of males and females, respectively. One can see from the formula that the ratio between males and females is a minor factor compared to the total population size. An increase in population size will result in an increase of the same magnitude in N_e . On the other hand, changing the ratio of males to females will have a lesser effect on N_e . For example, changing the ratio of males to females by one order of magnitude will result in some cases in a change of only a factor of 3-4 in N_e . In addition, the number of males cannot be ignored. Hence, polygynous species may, in principle, have smaller effective population sizes than monogynous species, if the monogynous species have more males taking part in reproduction, or than monogynous species with larger population sizes. Consequently, all comparisons between mono- and polygynous species must first be adjusted by the absolute number of mating individuals. The available data, unfortunately, do not permit this kind of adjustment, although some data on multiple mating do exist (Adams et al., 1977; Page and Metcalf, 1982).

I have, therefore, reanalyzed the data by using H_{exp} calculated from at least 15 loci. In *Drosophila* there are many species for which more than 20 loci were studied, so that I did not relax this criterion. In addition to including new data and removing all species for which fewer than 15 loci were studied, several other modifications to Berkelhamer (1983) were made: (1) *Apis mellifera*, listed twice in her table, was removed from the analysis, because it was subjected in the past to domestication and genetic manipulation with unknown effects on genetic diversity. (2) *Rhytidoponera impressa* was divided into five different species (Ward, 1980). Similarly, *Anopheles marshalli* and *Iridomyrmex purpureus* were divided into four and three species, respectively. (3) *Polistes* species were reclassified as primitively eusocial, since they are generally regarded as less advanced than *Vespa*, considered as "primitively eusocial" in Berkelhamer (1983). In general, I adopted a suggestion by Pamilo (pers. comm.) to classify by perennial versus annual colonies regardless of nest size and behavioral differentiation. (4) *Bombus lucorum* was removed from the analysis, since it may consist of two sibling species (Scholl and Obrecht, 1983; Pamilo, pers. comm.). (5) The number of loci in *Iridomyrmex* species and *LasioGLOSSUM zephyrum* was modified to 15 and 24, respectively. The same statistical analysis used by Berkelhamer (1983) was performed. With the available data, I could test all but one of her hypotheses. The question of whether or not genetic variation is

related to the degree of polygyny cannot be answered at present.

H_{exp} values for 188 species are listed in Table 1. A summary by insect category appears in Table 2. Clearly, hymenopterans have significantly lower H_{exp} on average, than most insects. Even when *Drosophila* species are excluded, the difference remains highly significant. However, solitary hymenopterans do not differ significantly from Heteroptera (Mann-Whitney U test, one tailed, $0.08 < P < 0.09$; Zar, 1974), and the difference between solitary Hymenoptera and Orthoptera is significant but very small ($0.02 < P < 0.03$). Homoptera and Heteroptera were analyzed separately, since their status as either orders or suborders of Hemiptera is not consensual. No difference was found between them ($0.46 < P < 0.49$). Since none of the heteropterans or the orthopterans in this study is haplodiploid, I can conclude that haplodiploidy per se does not reduce genetic variability. For studying the effects of haplodiploidy independently of the peculiarities of Hymenoptera it would be worthwhile to examine non-hymenopteran haplodiploids, such as mites, thrips, aleurodid whiteflies, iceryine scale insects, and beetles of the genera *Xyleborus* and *Micromalthus*. Nevo (1978) concluded that *Drosophila* species have unusually high levels of variability. This compilation shows, in agreement with Berkelhamer (1983), that *Drosophila* are not exceptional. In fact, there is no difference in H_{exp} between *Drosophila* and the rest of the Diptera ($0.14 < P < 0.16$), and, as seen from Table 2, *Drosophila* species are less variable than Coleoptera and Lepidoptera, although not significantly so ($P > 0.05$). Interestingly, the three most prosperous orders of insects in nature, in terms of number of species and population sizes (i.e., Diptera, Coleoptera, and Lepidoptera), are also the most variable genetically, an indication that neutral variation, constrained by effective population size, may be the most important factor in determining heterozygosity (also see Nei and Graur, 1984).

Within the Hymenoptera, a small difference is detected between solitary and eusocial hymenopterans ($P = 0.01$) in agreement with Pamilo et al. (1978b). The comparison made by Berkelhamer (1983) between her data and those of Pamilo et al. (1978b) and her subsequent rejection of Pamilo et al.'s (1978b) findings are illegitimate since these two studies use different statistics, namely, H_{obs} and H_{exp} . Berkelhamer (1983) claimed that primitive eusocial species are less variable than either solitary or advanced eusocial species. The data presented here show that no difference exists either between primitive and advanced eusocial species ($0.41 < P < 0.46$) or between primitive eusocials and solitary species ($0.38 < P < 0.45$). Advanced eusocial species are less variable than solitary species ($P < 0.05$). These results are compatible with the neutral theory (Kimura, 1968), since in solitary species the number of reproducing individuals is potentially the same as the observed total number of adult insects, whereas it is expected to be a tiny fraction in advanced eusocial species. The reduction in effective

population size is expected to be less dramatic in primitive eusocials, and, hence, it would be statistically more difficult to detect a difference. The bees are the only group common to both the solitary and the two eusocial groups, and, interestingly, their genetic diversity decreases in the same order as their expected effective population size, from solitary through primitive- to advanced-eusocial. In wasps, too, the same tendency is detected in solitary and primitive eusocials. The number of species, however, is so small that statistical significance is precluded.

The conclusions of this analysis are that Hymenoptera are genetically less variable than most species of insects, and that an important factor in determining gene diversity is the degree of sociality via its influence on reducing the effective population size and the amount of neutral polymorphism that can be sustained by a species. Haplodiploidy per se has probably only a very minor effect in determining gene diversity. These conclusions, obviously, are conditional upon further data on electrophoretic polymorphism from non-hymenopteran social species such as Isoptera.

ACKNOWLEDGMENTS

I wish to thank Dr. Masatoshi Nei for valuable comments. Dr. Pekka Pamilo and an anonymous reviewer greatly improved and clarified the presentation. I am grateful to Dr. Pamilo for introducing me to sets of data considered in this paper. This study was supported by research grants NIH GM-20293 and NSF BSF-8315115 to Dr. M. Nei.

LITERATURE CITED

- ADAMS, J., E. D. ROTHMAN, W. E. KERR, AND Z. L. PAULINO. 1977. Estimation of the number of sex alleles and queen mating from diploid male frequencies in a population of *Apis mellifera*. *Genetics* 86:583-596.
- AYALA, F. J., M. L. TRACEY, L. G. BARR, J. F. McDONALD, AND S. PEREZ-SALAS. 1974. Genetic variation in natural populations of five *Drosophila* species and the hypothesis of the selective neutrality of protein polymorphisms. *Genetics* 77:343-384.
- BARTLETT, A. C. 1981. Isozyme polymorphism in populations of the pink bollworm. *Ann. Entomol. Soc. Amer.* 74:9-13.
- BERKELHAMER, R. C. 1983. Intraspecific genetic variation and haplodiploidy, eusociality, and polygyny in the Hymenoptera. *Evolution* 37:540-545.
- BERLOCHER, S. H., AND G. L. BUSH. 1982. An electrophoretic analysis of *Rhagoletis* (Diptera: Tephritidae) phylogeny. *Syst. Zool.* 31:136-155.
- BRAIN, C. K. 1981. The evolution of man in Africa: was it a consequence of Cenozoic cooling? *Annex. Geol. Soc. S. Afr.* 84:1-19.
- BRITTNACHER, J. G., S. R. SIMS, AND F. J. AYALA. 1978. Genetic differentiation between species

- of the genus *Speyeria* (Lepidoptera: Nymphalidae). *Evolution* 32:199-210.
- CABRERA, V. M., A. M. GONZÁLEZ, J. M. LARRUGA, AND A. GULLÓN. 1983. Genetic distance and evolutionary relationships in the *Drosophila obscura* group. *Evolution* 37:675-689.
- CIANCHI, R., S. URBANELLI, M. COLUZZI, AND L. BULLINI. 1978. Genetic distance between two sibling species of the *Aedes mariaae* complex (Diptera, Culicidae). *Parasitol.* 20:39-46.
- COCKLEY, D. E., J. L. GOOCH, AND D. P. WESTON. 1977. Genetic diversity in cave dwelling crickets (*Ceuthophilus gracilipes*). *Evolution* 31:313-318.
- CROZIER, R. H. 1970. On the potential for genetic variability in haplodiploidy. *Genetica* 41:551-556.
- DALY, J. C., P. WILKINSON, AND D. D. SHAW. 1981. Reproductive isolation in relation to allozymic and chromosomal differentiation in the grasshopper *Caledia captiva*. *Evolution* 35:1164-1179.
- FUERST, P. A., R. CHAKRABORTY, AND M. NEL. 1977. Statistical studies on protein polymorphism in natural populations. I. Distribution of single locus heterozygosity. *Genetics* 86:455-483.
- GAUR, P. K., R. W. LICHTWARDT, AND J. L. HARRICK. 1981. Isozyme variation among soil isolates of *Histoplasma capsulatum*. *Exp. Mycol.* 5:69-77.
- GUTTMAN, S. I., T. K. WOOD, AND A. A. KARLIN. 1981. Genetic differentiation along host plant lines in the sympatric *Enchenopa binotata* Say complex (Homoptera: Membracidae). *Evolution* 35:205-217.
- HALLIDAY, R. B. 1981. Heterozygosity and genetic distance in sibling species of meat ants (*Iridomyrmex purpureus* group). *Evolution* 35:234-242.
- HAMILTON, W. D. 1964. The genetical theory of social behavior. I and II. *J. Theoret. Biol.* 7:1-52.
- HARRIS, H., D. A. HOPKISON, AND Y. H. EDWARDS. 1977. Polymorphism and the subunit structure of enzymes: a contribution to the neutralist-selectionist controversy. *Proc. Nat. Acad. Sci. USA* 74:698-701.
- HARRISON, R. G. 1979. Speciation in north American field crickets: evidence from electrophoretic comparisons. *Evolution* 33:1009-1023.
- HARRISON, R. G., S. F. WINTERMEYER, AND T. M. ODELL. 1983. Patterns of genetic variation within and among gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations. *Ann. Entomol. Soc. Amer.* 76:652-656.
- 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.
- HIGBY, P. K., AND M. W. STOCK. 1982. Genetic relationship between two sibling species of bark beetle (Coleoptera: Scolytidae), Jeffrey pine beetle and mountain pine beetle, in Northern California. *Ann. Entomol. Soc. Amer.* 75:668-674.
- HILBURN, L. R., AND K. S. RAI. 1981. Electrophoretic similarities and mating compatibility among four species of *Aedes* (*Stegomyia*) *scutellaris* complex. *J. Med. Entomol.* 18:401-408.
- HOWARD, D. J. 1983. Electrophoretic survey of eastern north American *Allonemobius* (Orthoptera: Gryllidae): evolutionary relationships and the discovery of three new species. *Ann. Entomol. Soc. Amer.* 76:1014-1021.
- KIMURA, M. 1968. Genetic variability maintained in a finite population due to mutational production of neutral and nearly neutral isoalleles. *Genet. Res.* 11:247-269.
- KOEHN, R. K., AND W. F. EANES. 1977. Subunit size and genetic variation of enzymes in natural populations of *Drosophila*. *Theoret. Popul. Biol.* 11:330-341.
- . 1978. Molecular structure and protein variation within and among populations. *Evol. Biol.* 11:39-100.
- KREPP, S. R., AND M. H. SMITH. 1974. Genetic heterozygosity in the 13-year cicada, *Magicicada*. *Evolution* 28:396-401.
- KRZAKOWA, M., AND J. SZWEYKOWSKI. 1979. Isozyme polymorphism in a natural population of liverwort, *Plagiochilla asplenoides*. *Genetics* 93:711-719.
- LAKOVAARA, S., AND A. SAURA. 1971. Genetic variation in natural populations of *Drosophila obscura*. *Genetics* 69:377-384.
- LAMBERT, D. M. 1983. A population genetical study of the African mosquito *Anopheles marshalli*. *Evolution* 37:484-495.
- LESLIE, J. F., AND H. DINGLE. 1983. Interspecific hybridization and genetic divergence in milkweed bugs (*Oncopeltus*: Hemiptera: Lygaeidae). *Evolution* 37:583-591.
- LESTER, L. J., AND R. K. SELANDER. 1979. Population genetics of haplodiploid insects. *Genetics* 92:1329-1345.
- LIEBHERR, J. K. 1983. Genetic basis for polymorphism in the ground beetle, *Agonum decorum* (Say) (Coleoptera: Carabidae). *Ann. Entomol. Soc. Amer.* 76:349-358.
- LOKKI, J., E. SUOMALAINEN, A. SAURA, AND P. LANKINEN. 1975. Genetic polymorphism and evolution in parthenogenetic animals II. Diploid and polyploid *Solenobia triquetrella* (Lepidoptera: Psychidae). *Genetics* 79:513-525.
- LOUNIBOS, L. P., AND L. E. MUNSTERMANN. 1981. Ecological and genetic separation of three sympatric species of *Aedes* (Diptera: Culicidae) from the Kenya coast. *Bull. Entomol. Res.* 71:639-648.
- MARTIN, P. S., AND H. E. WRIGHT. 1976. Pleistocene Extinctions. Yale Univ. Press, New Haven.
- MATTHEWS, T. C., AND G. B. CRAIG. 1980. Genetic heterozygosity in natural populations of the tree-hole mosquito *Aedes triseriatus*. *Ann. Entomol. Soc. Amer.* 73:739-743.
- MATTHEWS, T. C., AND L. E. MUNSTERMANN. 1983.

- Genetic diversity and differentiation in northern populations of the tree-hole mosquito *Aedes hendersoni* (Diptera: Culicidae). *Ann. Entomol. Soc. Amer.* 76:1005-1010.
- MAY, B., AND F. R. HOLBROOK. 1978. Absence of genetic variability in the green peach aphid, *Myzus persicae* (Hemiptera: Aphididae). *Ann. Entomol. Soc. Amer.* 71:809-812.
- MENKEN, S. B. J. 1982. Enzymatic characterization of nine endoparasite species of small ermine moths (Yponomeutidae). *Experientia* 38:1461-1462.
- METCALF, R. A., J. C. MARLIN, AND G. S. WHITT. 1975. Low levels of genetic heterozygosity in Hymenoptera. *Nature* 257:792-794.
- MUNSTERMANN, L. E. 1980. Distinguishing geographic strains of *Aedes atropalpus* group (Diptera: Culicidae) by analysis of enzyme variation. *Ann. Entomol. Soc. Amer.* 73:699-704.
- MUNSTERMANN, L. E., D. B. TAYLOR, AND T. C. MATTHEWS. 1982. Population genetics and speciation in the *Aedes triseriatus* group, p. 433-453. In W. W. M. Steiner, W. J. Tabachnick, K. S. Rai and S. Narang (eds.), *Recent Developments in the Genetics of Insect Disease Vectors*. Stipes, Champaign, IL.
- NAIR, P. S., D. BRNIC, AND K. KOJIMA. 1971. Isozyme variation and evolutionary relationships in the *mesophragmatica* species group of *Drosophila*. *Univ. Texas Publ.* 7103:17-28.
- NEI, M. 1975. Molecular Population Genetics and Evolution. North-Holland, Amsterdam.
- NEI, M., P. A. FUERST, AND R. CHAKRABORTY. 1978. Subunit molecular weight and genetic variability of proteins in natural populations. *Proc. Nat. Acad. Sci. USA* 75:3359-3362.
- NEI, M., AND D. GRAUR. 1984. Extent of protein polymorphism and the neutral mutation theory. *Evol. Biol.* 17:73-118.
- NEI, M., T. MARUYAMA, AND R. CHAKRABORTY. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29:1-10.
- NEI, M., AND A. K. ROYCHOUDHURY. 1974a. Genetic variation within and between the three major races of man, Caucasoids, Negroids and Mongoloids. *Amer. J. Hum. Genet.* 26:421-443.
- . 1974b. Sampling variances of heterozygosity and genetic distance. *Genetics* 76:379-390.
- . 1982. Genetic relationship and evolution of human races. *Evol. Biol.* 14:1-59.
- NEVO, E. 1978. Genetic variation in natural populations: patterns and theory. *Theoret. Popul. Biol.* 13:121-177.
- PAGE, R. E., AND R. A. METCALF. 1982. Multiple mating, sperm utilization, and social evolution. *Amer. Natur.* 119:263-281.
- PAMILO, P., AND R. H. CROZIER. 1981. Genetic variation in male haploids under deterministic selection. *Genetics* 98:199-214.
- PAMILO, P., R. ROSENGREN, K. VEPSÄLÄINEN, S.-L. VARVIO-AHO, AND B. PISARSKI. 1978a. Population genetics of *Formica* ants. I. Patterns of enzyme gene variation. *Hereditas* 89:233-248.
- PAMILO, P. S., S.-L. VARVIO-AHO, AND A. PEKKARINEN. 1978b. Low enzyme gene variability in Hymenoptera as a consequence of haplodiploidy. *Hereditas* 88:93-99.
- PASHLEY, D. P. 1983. Biosystematic study of Tortricidae (Lepidoptera), with a note on evolutionary rates of allozymes. *Ann. Entomol. Soc. Amer.* 76:139-148.
- POWELL, J. R. 1975. Protein variation in natural populations of animals. *Evol. Biol.* 8:79-119.
- PRAKASH, S. 1973. Patterns of gene variation in central and marginal populations of *Drosophila robusta*. *Genetics* 75:347-369.
- RENSCH, B. 1959. *Evolution Above the Species Level*. Columbia Univ. Press, N.Y.
- SAURA, A. 1974. Genic variation in Scandinavian populations of *Drosophila bifasciata*. *Hereditas* 76:161-172.
- SAURA, A., O. HALKKA, AND J. LOKKI. 1973. Enzyme gene heterozygosity in small island populations of *Philaenus spumarius* (L.) (Homoptera). *Genetica* 44:459-473.
- SBORDONI, V., G. ALLEGRUCCI, A. CACCONI, D. CESARONI, M. C. SBORDONI, AND E. DEMATTHAEIS. 1981. Genetic variability and divergence in cave populations of *Troglophilus cavicola* and *T. andreinii* (Orthoptera, Rhaphidophoridae). *Evolution* 35:226-233.
- SCHOLL, A., AND E. OBRECHT. 1983. Enzymelektrophoretische untersuchungen zur atrabgrenzung im *Bombus lucorum*-komplex (Apidae, Bombini). *Apidiologie* 14:65-78.
- SELANDER, R. K., AND R. O. HUDSON. 1976. Animal population structure under close inbreeding: the landsnail *Rumina* in Southern France. *Amer. Natur.* 110:695-718.
- SELANDER, R. K., AND B. R. LEVIN. 1980. Genetic diversity and structure in *Escherichia coli* populations. *Science* 210:545-547.
- SLUSS, T. P., AND H. M. GRAHAM. 1979. Allozyme variation in natural populations of *Heliothis virescens*. *Ann. Entomol. Soc. Amer.* 72:317-322.
- SLUSS, T. P., H. M. GRAHAM, AND E. S. SLUSS. 1982. Morphometric, allozyme, and hybridization comparisons of four *Lygus* species (Hemiptera: Miridae). *Ann. Entomol. Soc. Amer.* 75:448-456.
- SLUSS, T. P., E. S. SLUSS, H. M. GRAHAM, AND M. DUBOIS. 1978. Allozyme differences between *Heliothis virescens* and *H. zea*. *Ann. Entomol. Soc. Amer.* 71:191-195.
- SNYDER, T. P. 1974. Lack of allozymic variability in three bee species. *Evolution* 28:687-688.
- SOULÉ, M. 1976. Allozyme variation: its determinants in space and time, p. 60-77. In F. J. Ayala (ed.), *Molecular Evolution*. Sinauer, Sunderland, MA.
- SPIETH, P. T. 1975. Population genetics of allozyme variation in *Neurospora intermedia*. *Genetics* 80:785-805.
- STEINER, W. W. M. 1979a. Genetic variation in Hawaiian *Drosophila*. VII. Seasonally-dependent gene changes in *Drosophila mimica*. *Evolution* 33:543-562.

- . 1979b. Genetic variation in Hawaiian *Drosophila*. VIII. Heterozygosity and genetic changes in isolated populations of *D. engyochracea*. *Biochem. Genet.* 17:645-664.
- STOCK, M. W., AND P. J. CASTROVILLO. 1981. Genetic relationship among representative populations of five *Choristoneura* species: *C. occidentalis*, *C. retiniana*, *C. biennis*, *C. lambertiana* and *C. fumiferana* (Lepidoptera: Tortricidae). *Can. Entomol.* 113:857-865.
- SUOMALAINEN, E. 1962. Significance of parthenogenesis in the evolution of insects. *Ann. Rev. Entomol.* 7:349-366.
- SUOMALAINEN, E., AND A. SAURA. 1973. Genetic polymorphism and evolution in parthenogenetic animals. I. Polyploid curculionidae. *Genetics* 74:489-508.
- TABACHNICK, W. J., L. E. MUNSTERMANN, AND J. R. POWELL. 1979. Genetic distinctness of sympatric forms of *Aedes aegypti* in East Africa. *Evolution* 33:287-295.
- TURNER, J. R. G., M. S. JOHNSON, AND W. F. EANES. 1979. Contrasted models of evolution in the same genome: allozymes and adaptive change in *Heliconius*. *Proc. Nat. Acad. Sci. USA* 76: 1924-1928.
- VARVIO-AHO, S.-L. 1981. The effects of ecological differences on the amount of enzyme gene variation in Finnish water-strider (*Gerris*) species. *Hereditas* 94:35-39.
- WAGNER, A. E., AND D. A. BRISCOE. 1983. An absence of enzyme variability within two species of *Trigona* (Hymenoptera). *Heredity* 50:97-103.
- WARD, P. S. 1980. Genetic variation and population differentiation in the *Rhytidoponera impressa* group, a species complex of ants (Hymenoptera: Formicidae). *Evolution* 34:1060-1076.
- WARD, P. S., AND R. W. TAYLOR. 1981. Allozyme variation, colony structure and genetic relatedness in the primitive ant *Nothomyrmecia macrops* Clark (Hymenoptera: Formicidae). *J. Austral. Entomol. Soc.* 20:177-183.
- WARD, R. D. 1977. Subunit size of enzymes and genetic heterozygosity in vertebrates. *Biochem. Genet.* 15:123-135.
- WILLHITE, E. A., AND M. W. STOCK. 1983. Genetic variation among western spruce budworm (*Choristoneura occidentalis*) (Lepidoptera: Tortricidae) outbreaks in Idaho and Montana. *Can. Entomol.* 115:41-54.
- WRIGHT, S. 1933. Inbreeding and homozygosity. *Proc. Nat. Acad. Sci. USA* 19:411-420.
- . 1938. Size of population and breeding structure in relation to evolution. *Science* 87: 430-431.
- YAMAZAKI, T. 1981. Genetic variabilities in natural populations of haploid plant, *Conocephalum conicum*. I. The amount of heterozygosity. *Japan. J. Genet.* 56:373-383.
- YANG, S. Y., L. L. WHEELER, AND I. R. BOCK. 1972. Isozyme variations and phylogenetic relationships in the *Drosophila bipectinata* species complex. *Univ. Texas Publ.* 7213:213-227.
- YOKOYAMA, S., AND M. NEI. 1979. Population dynamics of sex-determining alleles in honey bees and self-incompatibility alleles in plants. *Genetics* 91:609-626.
- ZAR, J. H. 1974. *Biostatistical Analysis*. Prentice-Hall, Engelwood Cliffs, N.J.
- ZERA, A. J. 1981. Genetic structure of two species of water striders (Gerridae: Hemiptera) with differing degrees of winglessness. *Evolution* 35:218-225.
- ZOUROS, E. 1976. Hybrid molecules and the superiority of the heterozygote. *Nature* 269:227-229.

Corresponding Editor: D. Futuyma