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(Hymenoptera: Halictidae)

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DIPLOID MALES IN A PRIMITIVELY EUSOCIAL BEE,  
*LASIOGLOSSUM (DIALICTUS) ZEPHYRUM*  
(HYMENOPTERA: HALICTIDAE)

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**Abstract.**—Hymenoptera are characterized by a haplo-diploid mechanism of sex determination. Females are diploid and males are haploid. However, in many species diploid males may occur if individuals are homozygous at a sex determining locus. Diploid males were found in three out of four populations (nest aggregations) of the primitively eusocial, halictine bee *Lasioglossum zephyrum* for which samples of males were examined electrophoretically. The frequency of diploid males was greater in a small, geographically isolated population (the “Robinson” nest aggregation) than in a large population that had nearby neighboring populations (the “Salmon Creek A” nest aggregation). In addition, the proportion of polymorphic loci was lower in the Robinson nest aggregation suggesting that a bottleneck event or loss of alleles due to small population size occurred in the Robinson population that involved a loss in the number of alleles at the sex determining locus.

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The Hymenoptera are characterized by a haplo-diploid mechanism of sex determination; females are diploid and males are normally haploid. The mechanism involved is *arrhenotoky* (unfertilized eggs develop into males) that has arisen up to 12 times (Bull, 1981, 1983). Genic level mechanisms have been suggested for sex determination in haplo-diploid species (Crozier, 1977; Chuna and Kerr, 1957; Kerr, 1962, 1987). The data on *Apis mellifera* indicate that sex is most probably determined by major effects due to a single multi-allelic locus with 10 to 22 alleles, where homozygous and hemizygous individuals are males (Adams et al., 1977; Page and Metcalf, 1982; Woyke, 1976; and others; but see also Chaud-Netto and Kerr, 1980; Comargo, 1979). Data for *A. cerana* are also compatible with a single locus model (Woyke, 1979). A similar system occurs in the parasitoid wasp *Bracon hebetor* (Whiting, 1939); but in *Nasonia vitripennis*, also a parasitoid wasp species, carefully con-

trolled, long-term breeding experiments did not result in the production of diploid males (Skinner and Werren, 1980). In those species with a single locus sex determining mechanism, a large number of alleles is expected at the sex locus because high frequency alleles will be eliminated more often than low frequency alleles through occurring in diploid males (Yokoyama and Nei, 1979).

There are several consequences of the single locus mechanism of haplo-diploidy (see Crozier, 1985). Most importantly, a single locus mechanism imposes a genetic load, because any individual that is homozygous at the sex determining locus will be a diploid male with very low fitness (Comargo, 1982; Chaud-Netto, 1979, 1980; Chaud-Netto and Kerr, 1978; Petters and Mettus, 1980; Woyke, 1980, 1983). This phenomenon imposes a penalty for inbreeding. Brother-sister mating, or mating between relatives less closely related, will increase the likelihood that the offspring will be homozygous at the sex determining locus and therefore will be diploid males. In addition to individual level effects, in eusocial species the worker force, virtually always made up of females, will be substantially reduced if a considerable proportion of all diploid individuals are males thereby decreasing colony growth rates (Page

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and Laidlaw, 1982; Woyke, 1984). Social Hymenoptera might therefore be expected to be outbred even though inbreeding is thought to increase the likelihood of the evolution of eusociality in some situations (Craig, 1982; Michod, 1979, 1982; Wade and Breden, 1981).

The haplo-diploid system of sex determination also causes asymmetries in relatedness. The most notable asymmetries are that females are (1) more closely related to their sisters than to their own daughters, and (2) more closely related to their nieces and nephews than are diplo-diploid females. This may have been important in the multiple origins of altruism in the Hymenoptera when combined with sex ratio biasing in the case of evolution of eusociality (Pamilo, 1987a, 1987b) although this point is still open to debate (see Stubblefield and Charnov, 1986).

Diploid males have been reported in diverse taxa. In the social Hymenoptera they have been reported in ants (cf. Ross and Fletcher, 1985) and in the wasp species *Mischocyttarus immarginatus* (Strassmann and Queller, pers. comm.). They have also been reported in the Apidae; in the genera *Apis* (Hoshihara et al., 1981; Woyke, 1976), and *Bombus* (Garófalo, 1973), as well as in the stingless bees (Comargo, 1982). Diploid males have not been reported for any other family of bees. The occurrence of diploid males in primitively eusocial bees is of interest from several points of view because the evolution of sociality may be related to the haplo-diploid system of sex determination. First, the production of diploid males may indicate a subdivided population structure or inbreeding; and second, the production of diploid males may distort sex allocation ratios.

The Halictinae ("sweat bees") comprise a major component of the worldwide bee fauna (probably exceeding 2,000 species; Sakagami, 1980) and include a large proportion of the primitively social bee species. With rare exceptions, eusociality in the halictine bees is primitive (Plateaux-Quénu, 1962). All females are potential reproducers at emergence. In *Lasioglossum zephyrum*, the most intensely studied halictine, the reproductive division of labor is a result of dominance interactions among adult fe-

males (Brothers and Michener, 1974; Buckle, 1982a, 1982b, 1984, 1985; Greenberg and Buckle, 1981; Michener and Brothers, 1974; Michener et al., 1971a, 1971b). Halictines are an ideal group for the study of the evolution of worker altruism because all young females are physiologically and morphologically similar and behavioral interaction among adults is the primary agent of caste determination. The finding of diploid males in three populations of *L. zephyrum* is therefore of great interest.

#### METHODS

In the course of an initial survey for electrophoretic variation in *L. zephyrum* (Kukuk and May, 1985) two individuals thought to be males were scored as heterozygotes. Since the sex of *L. zephyrum* individuals is easily determined by inspection with the naked eye (males are smaller, more slender, and have much longer antennae), the sex of each individual in subsequent studies was noted three times: at the time of capture or emergence; when placing the individual in a storage vial before freezing; and when arranging the numbered vials in preparation for electrophoresis. No studies were carried out specifically to look for diploid males, but some were found in the course of other work. Consequently this report includes data from the five samples reported below.

Sample 1: The first sample was 125 morphologically normal males from the Monkey Run nest aggregation on Fall Creek near Ithaca, Tompkins County, New York, 1983. The males were netted as they flew over the nests searching for females. They were examined electrophoretically for 10 polymorphic loci (*Adh*, Alcohol dehydrogenase; *G3p-1*, Glycerol-3-phosphate dehydrogenase; *Gda*, Guanine deaminase; *Hbdh*, Hydroxybutyric dehydrogenase; *Idh*, Isocitric dehydrogenase; *Ldh*, Lactic dehydrogenase; *Mdh-2*, Malic dehydrogenase; *Me-2* and *Me-3*, Malic enzyme; and *Pep-LA-2*, Peptidase with leucyl-alanine) as described in Kukuk and May (1985).

Sample 2: The second sample (from the Robinson nest aggregation near Edinburg, New York, 1985) consisted of family groups, that is, the contents of 13 nests, consisting of adult females ( $N = 32$ ), female pupae ( $N = 74$ ) and male pupae ( $N = 60$ ). The spec-

imens were obtained by excavating the nests as described in Abrams and Eickwort (1980). Pupae were reared to adulthood in the laboratory. The region surrounding this aggregation was explored by automobile and any appropriate habitat seen was further investigated on foot. No other nest aggregations were found within five km of this site. The individuals in this sample were examined for protein variation at *Adh*; *Hbdh*; *Pep-PAP*, Peptidase with phenyl-alanyl-proline; and *Pep-LA-2*.

Sample 3: Three family groups were collected from the VanNatta Dam nest aggregation, in the township of Ithaca, New York, 1983. The sample consisted of 2 adult females, 12 female brood and a single male. These were examined electrophoretically for *Adh*, *Hbdh*, *Idh*, *Me-2*, *Pep-PAP*, *Pep-GL*, and *Pgm*, Phosphoglucumutase.

Sample 4: Seven families were collected from the Salmon Creek A nest aggregation, Tompkins County, New York, 1985. The sample consisted of adult females, female pupae or tenerals ( $N = 51$ ), and male pupae ( $N = 24$ ). Following emergence, these were examined electrophoretically at *Adh*, *Hbdh*, *Idh*, *Ldh*, and *Mdh-2*. Investigation of nearby suitable habitat on foot revealed several additional nest aggregations within 1 km.

Sample 5: This sample does not include any males. It consists of samples of females used in a separate study that provide useful background information. Samples of adult females from each of the four aggregations noted above were collected by removing a single female from each of the 40 colonies evenly spaced throughout each nest aggregation. The samples of 40 females from the aggregations noted above (and 34 others) were examined for 12 polymorphic loci (see Kukuk et al., 1987a) and provide data for comparing genetic heterozygosity and proportion of polymorphic loci for the 4 nest aggregations from which data on males were obtained.

To estimate the actual frequency of diploid males using the observed frequencies, it was necessary to calculate the frequency of undetected diploid males. This was done using the gene frequencies of females. The total number of diploid males expected ( $T_d$ ) is equal to the frequency of diploid males detected ( $D_d$ ), divided by the expected fre-

quency of being heterozygous in diploid individuals for at least one locus ( $R$ ).

$$T_d = \frac{D_d}{R}$$

where

$$R = 1 - \prod_{j=1}^L \left( \sum_{i=1}^A p^2_{ij} \right) \quad (1)$$

and  $i$  = the  $i$ th allele,  $j$  = the  $j$ th locus,  $L$  = the number of loci,  $A$  = the number of alleles at the  $j$ th locus, and  $p$  is the frequency of the  $i$ th allele at the  $j$ th locus.

Differences between the Robinson aggregation and the Salmon Creek A aggregation in the number of polymorphic loci and in the frequencies of diploid males were tested using a G-test for independence of two samples (Sokal and Rohlf, 1981).

The number of alleles present at the sex determining locus was estimated using Equation 15 of Adams et al. (1977) from the data in two fashions. First, the overall frequency of diploid males was calculated for each aggregation containing diploid males and the number of alleles at the sex determining locus was estimated directly. This calculation has two problems. First, no standard errors can be attached to these estimates; and second, colonies are not equally weighted by this method, and a greater weight is given to large colonies.

In the samples, diploid males were found primarily in large colonies and this may have introduced a bias. As most spring colonies are the progeny of a single female (Kukuk et al., 1987b) it was necessary to also estimate the number of alleles by weighing colonies equally. This was done by calculating the frequency of diploids that were males for each colony (= the inverse of the number of alleles at the sex locus; see Adam et al., 1977), finding the average of this frequency, and setting confidence limits for it using the jackknife method. The inverse of this calculation set confidence limits for the number of alleles at the sex locus for the Robinson nest aggregation.

## RESULTS

Sample 1: Two males from the Monkey Run aggregation were heterozygous; one at *Hbdh* and *Pep-LA-2*, and the other at *Adh*

TABLE 1. Number of males and females examined, aggregation size, number of nearby nest aggregations, proportion of loci polymorphic, estimated heterozygosity (Nei, 1978), observed heterozygosity and frequency of diploid males for three aggregations of *Lasioglossum (Dialictus) zephyrum*.

Aggregation	Monkey Run	Robinson	VanNatta Dam	Salmon Creek A
Number of males	125	60	1	24
Number of females	—	72	12	51
Size (# of nests)	1,000+	200	1,000+	1,000+
Aggregations within 1 km	2 or more	None	2 or more	2 or more
Proportion of loci polymorphic (FMCA* < 99%)**	0.58	0.58	0.67	1.00
Proportion of loci polymorphic (FMCA* < 95%)**	0.42	0.42	0.50	0.50
Expected heterozygosity**	0.160 (+0.059)	0.173 (+0.064)	0.180 (+0.061)	0.166 (+0.054)
Observed heterozygosity**	0.134 (+0.155)	0.185 (+0.070)	0.166 (+0.055)	0.164 (+0.055)
Observed frequency of males that are diploid	0.016	0.12	1.00	0.00
Estimated frequency males that are diploid (=Td)***	0.019 (+0.01)	0.135 (+0.04)	1.00	0.00
Estimated # of diploid males	2	8	1.00	0.00
Frequency of diploids that are male@	—	0.10	0.08	0.00

\* Frequency of the most common allele.

\*\* Estimated from the fifth data set of 40 females from each site by examination of 12 polymorphic loci only (Kukuk et al., 1987) and should be considered for comparison only.

\*\*\* Expected SD in frequency for a binomial distribution,  $SD = \sqrt{npq}$ .

@ Estimated # of diploid males/# of females + estimated # of diploid males.

and *Ldh* for an observed frequency of 0.016. Using the gene frequencies for females calculated from the sample of 40 females described under Sample 5,  $R = 0.82$  and the expected frequency of diploid males ( $T_d$ ) is 0.019. As these males were collected on the wing no data are available on the number of females associated with them.

Sample 2: Diploid males were found in 3 of 13 nests from the Robinson nest aggregation. The brood of nest 6 included five diploid males, nine females, and three haploid males. The diploid males were all heterozygous at *Pep-PAP*. Nest #J6 contained 1 diploid male (heterozygous at *Hbdh* and *Pep-PAP*), 14 females and 1 haploid male; and nest #J8 contained 1 diploid male (heterozygous at *Hbdh*), 12 females, and 8 haploid males. The overall observed frequency of males that are diploids is 0.12. Using the gene frequencies calculated from the 72 females included in this sample of 13 colonies, and Equation (1) the expected frequency of diploid males was calculated to be 0.135. The expected number of diploid males in this site is then eight.

Sample 3: The single male from the VanNatta Dam aggregation was electrophoretically heterozygous at *Idh* and *Pgm*.

Sample 4: No diploid males were found among the 24 males and 51 females from 7

family groups from the Salmon Creek A nest aggregation.

A summary of the results appears in Table 1 along with the number of polymorphic loci and genetic heterozygosity for the nest aggregations involved. The observed number of diploid males is significantly lower in the Salmon Creek A aggregation than in the Robinson aggregation ( $G = 7.08$ ,  $df = 1$ ,  $P < 0.01$ ). Further, since the Robinson aggregation is small and relatively isolated, the proportion of polymorphic loci or heterozygosity should be lower than that found at Salmon Creek A. If all loci in which the frequency of the most common allele is 95% are considered, there is no significant difference between the two aggregations. However, using loci in which the frequency of the most common allele is less than 99%, then the Robinson aggregation has significantly fewer polymorphic loci than does the Salmon Creek aggregation ( $G = 4.4$ ,  $df = 1$ ,  $P < 0.05$ ). There are no significant differences in levels of estimated or observed heterozygosity among the nest aggregations.

## DISCUSSION

The presence of more diploid males in the Robinson aggregation than in the Salmon Creek A aggregation is accompanied by a significantly lower proportion of poly-

morphic loci (loci in which the frequency of the most common allele is less than 99%) in the Robinson aggregation. Simultaneously, however, heterozygosity levels are the same between these aggregations and among all the aggregations studied (Table 1). If *L. zephyrum* has a single locus system of sex determination, the frequency of diploid males in random mating populations will depend on the number of alleles present at the sex determining locus. The number of alleles could be reduced by recent bottleneck effects or by the loss of alleles due to drift in a small population.

If the Robinson site has fewer polymorphic loci overall this result could be due to a loss of alleles through a bottleneck effect, or because it is a small, isolated population (see Table 1). The similar level of heterozygosity at this site relative to that found at other sites suggests that a bottleneck may have occurred in the past that was followed by rapid population growth. Such a result is expected since the number of alleles recovers slowly from reductions caused by a bottleneck event, whereas heterozygosity levels recover more quickly in populations that increase quickly following the bottleneck event (Nei et al., 1975). If alleles were lost due to a bottleneck effect, then the number of alleles at the sex determining locus would be lower than in large populations. One would expect, then, that the proportion of diploids that are males would be greater in the Robinson site as was confirmed by G-test.

Previous laboratory work has suggested that there is little or no inbreeding depression in *L. zephyrum* because brother/sister matings did not result in alterations of the sex ratio or any other noticeable differences (Michener, pers. comm.). The presence of diploid males in natural populations, however, does indicate that there is at least the potential for a penalty due to inbreeding. Since *L. zephyrum* males tend to stay near their natal nest when they search for females (Kukuk, 1989), it is likely that the learned, odor discrimination on the part of males (Greenberg, 1982; Smith, 1983; Smith and Ayasse, 1987) evolved to prevent extreme inbreeding.

If we assume that the populations within

which diploid males were found are panmictic and that the sex determining mechanism involves major effects due to a single locus, direct estimates of the number of alleles at the sex determining locus can be estimated using the method of Adams et al. (1977; formula 15). The estimates are 10, for the Robinson nest aggregation and 13 for the VanNatta Dam nest aggregation. Calculations for the number of alleles at the sex determining locus for the Robinson aggregation; that weight colonies equally estimate the average number of alleles to be 25; and the confidence limits suggest that a minimum of 10 loci are involved.

The presence of diploid males has several ramifications for empirical population genetic studies of social Hymenoptera. First, the effects of inbreeding may be obscured. Although the term inbreeding can be used in several ways (Jacquard, 1975), consider simply the case of sib mating. If there is brother/sister mating in a haplo-diploid then half the diploid progeny will be homozygous at virtually every locus (excluding the effects of crossingover), including the sex determining locus. The homozygous individuals will be diploid males. Normally, females are used in electrophoretic studies for estimation of inbreeding and other population genetic characteristics of a species. Therefore, the evidence indicating brother/sister mating or other less extreme forms of positive, assortative mating (i.e., excess homozygosity at protein coding loci) will not be recorded. Estimates of inbreeding should be adjusted for the frequency of diploid males as follows: Actual level of inbreeding = Measured level of inbreeding /  $1 - \text{frequency of diploid individuals that are males}$ .

Further, the presence of diploid males will bias observed sex allocation ratios in favor of males since individuals intended to be females (i.e., fertilized eggs) will become males. Given the importance of inbreeding and sex allocation ratios to theories concerning the evolution of eusociality in the Hymenoptera, it may be useful for empirical population genetic studies of haplo-diploid species to include screening an adequate number of males in order to detect the occurrence and frequency of diploid males.

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## LITERATURE CITED

- ABRAMS, J., AND G. C. EICKWORT. 1980. Biology of the communal sweat bee (*Agapostemon virescens* (Hymenoptera: Halictidae)). Search-Agriculture (Cornell University) 1:1-20.
- ADAMS, J., E. D. ROTHMAN, W. E. KERR, AND A. L. PAULINO. 1977. Estimation of the number of sex alleles and queen matings from diploid male frequencies in a population of *Apis mellifera*. Genetics 86:583-596.
- BROTHERS, D. J., AND C. D. MICHENER. 1974. Interactions in colonies of primitively social bees. III. Ethometry of division of labor in *Lasioglossum zephyrum* (Hymenoptera: Halictidae). J. Comp. Physiol. 90:129-168.
- BUCKLE, G. R. 1982a. Queen-worker behavior and nestmate interactions in young colonies of *Lasioglossum zephyrum*. Ins. Soc. 29:125-137.
- . 1982b. Differentiation of queens and nestmate interactions in newly established colonies of *Lasioglossum zephyrum* (Hymenoptera: Halictidae). Sociobiology 7:8-20.
- . 1984. A second look at queen-forager interactions in the primitively eusocial halictid, *Lasioglossum zephyrum*. J. Kansas Entomol. Soc. 57:1-6.
- . 1985. Increased queen-like behaviour of workers in large colonies of the sweat bee *Lasioglossum zephyrum*. Anim. Behav. 33:1275-1280.
- BULL, J. J. 1981. Coevolution of haplodiploidy and sex determination in the Hymenoptera. Evolution 35:568-580.
- . 1983. Evolution of Sex Determining Mechanisms. Benjamin Cummings, Menlo Park, CA.
- CHAUD-NETTO, J. 1979. Fertility of the diploid drones of *Apis mellifera* (Hymenoptera, Apidae). Cienc. Cult. 31:666-667.
- . 1980. Biological studies of triploid bees of *Apis mellifera* (Hymenoptera, Apidae). Cienc. Cult. 32:611-615.
- CHAUD-NETTO, J., AND W. E. KERR. 1978. Estimation of the adaptive value of adult diploid drones of *Apis mellifera* L. (Hymenoptera, Apidae). Cienc. Cult. 30:1457-1460.
- . 1980. Genetic mechanisms for the development of reproductive organs of *Apis mellifera* workers and diploid drones: A complementary hypothesis. Rev. Bras. Genet. 3:127-138.
- CHUNA, A. B. DA, AND W. E. KERR. 1957. A genetical theory to explain sex-determination by arrhenotokous parthenogenesis. Forma Functio 1:33-36.
- COMARGO, C. A. DA. 1979. Sex determination in bees. XI. Production of diploid males and sex determination in *Melipona quadrifasciata*. J. Agric. Res. 18:77-84.
- . 1982. Longevity of diploid males, haploid males, and workers of the social bee *Melipona quadrifasciata* (Hymenoptera, Apidae). J. Kansas Entomol. Soc. 55:8-12.
- CRAIG, R. 1982. Evolution of eusociality by kin selection: The effect of inbreeding between siblings. J. Theor. Biol. 94:119-128.
- CROZIER, R. H. 1977. Evolutionary genetics of the Hymenoptera. Annu. Rev. Entomol. 22:263-288.
- . 1985. Adaptive consequences of male-haplidity, pp. 201-221. In W. Helle and M. W. Sabelis (eds.), Spider Mites. Their Biology, Natural Enemies, and Control, Volume 1A. Elsevier Sci., Publishers, Amsterdam.
- GARÓFALO, C. A. 1973. Occurrence of diploid drones in a neotropical bumblebee. Experientia 29:726-727.
- GREENBERG, L. 1982. Persistent habituation to female odor by male sweat bees (*Lasioglossum zephyrum*). J. Kansas Entomol. Soc. 53:525-531.
- GREENBERG, L., AND G. R. BUCKLE. 1981. Inhibiting of worker mating by queens in a sweat bee (*Lasioglossum zephyrum*). Ins. Soc. 28:347-352.
- JACQUARD, A. 1975. Inbreeding: One word, several meanings. Theor. Pop. Biol. 7:338-363.
- HOSHIBA, H., I. OKADA, AND A. KUSANAGI. 1981. The diploid drone of *Apis cerana japonica* and its chromosomes. J. Apic. Res. 20:143-147.
- KERR, W. E. 1962. Genetics of sex determination. Annu. Rev. Entomol. 7:157-176.
- . 1987. Sex determination in bees. XXI. Number of XO heteroalleles in a natural population of *Melipona compressipes fasciculata* (Apidae). Ins. Soc. 34:274-279.
- KUKUK, P. F. 1989. Dispersal of males of the primitively eusocial sweat bee *Dialictus zephyrus* within a small nest aggregation. Sociobiology 15:1-10.
- KUKUK, P. F., AND B. MAY. 1985. A re-examination of genetic variability in *Dialictus zephyrus* (Hymenoptera: Halictidae). Evolution 39:226-228.
- KUKUK, P. F., R. H. CROZIER, G. C. EICKWORT, AND B. P. MAY. 1987a. Macrogeographic genetic variation in the sweat bee *Lasioglossum (Dialictus) zephyrum*. In J. Eder and H. Rembold (eds.), Chemistry and Biology of Social Insects. Verlag J. Pepernay, Munich.
- KUKUK, P. F., G. C. EICKWORT, AND B. P. MAY. 1987b. Multiple maternity and multiple paternity in first generation brood from single foundress colonies of the sweat bee *Dialictus zephyrus*. Ins. Soc. 34:131-135.
- MICHENER, C. D., AND D. J. BROTHERS. 1974. Were workers of eusocial Hymenoptera initially altruistic or oppressed? Proc. Nat. Acad. Sci. USA 71:671-674.
- MICHENER, C. D., D. J. BROTHERS, AND D. R. KAMM. 1971a. Interactions in colonies of primitively social bees I. Artificial colonies of *Lasioglossum zephyrum*. Proc. Nat. Acad. Sci. USA 68:1241-1245.
- . 1971b. Interactions in colonies of primitively social bees II. Queen-worker relations in *Lasioglossum zephyrum*. J. Kansas Entomol. Soc. 44:276-279.
- MICHOD, R. 1979. Genetical aspects of kin selection: Effects of inbreeding. J. Theor. Biol. 81:223-233.

- . 1982. The theory of kin selection. *Annu. Rev. Ecol. Syst.* 13:23–55.
- NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89:583–590.
- NEI, M., T. MARUYAMA, AND R. CHAKRABORTY. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29:1–10.
- PAGE, R. E., JR., AND H. H. LAIDLAW. 1982. Closed population honeybee (*Apis mellifera*) breeding. 1. Population genetics of sex determination. *J. Apic. Res.* 21:30–37.
- PAGE, R. E., JR., AND R. METCALF. 1982. Multiple mating, sperm utilization and social evolution. *Am. Nat.* 119:263–282.
- PAMILO, P. 1987a. Sex ratios and the evolution of eusociality in the Hymenoptera. *J. Genet.* 66:111–122.
- . 1987b. Sex ratios and the evolution of eusociality, p. 363. *In* J. Eder and H. Rembold (eds.), *Chemistry and Biology of Social Insects*. Verlag J. Pepernay, Munich.
- PETTERS, R. M., AND R. V. METTUS. 1980. Decreased diploid male viability in the parasitic wasp *Bracon hebetor*. *J. Hered.* 71:353–356.
- PLATEAUX-QUÉNU, C. 1962. Biology of *Halictus marginatus* Brulle. *J. Apic. Res.* 1:41–51.
- ROSS, K. G., AND D. J. FLETCHER. 1985. Genetic origin of male diploidy in the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae) and its evolutionary significance. *Evolution* 39:888–903.
- SAKAGAMI, S. 1980. Bionomics of the halictine bees in northern Japan I. *Halictus (Halictus) tsingouensis* (Hymenoptera, Halictidae) with notes on the number of origins of eusociality. *Kontyû* 48:526–536.
- SKINNER, S. W., AND J. H. WERREN. 1980. The genetics of sex determination in *Nasonia vitripennis*: (Hymenoptera, Pteromalidae). *Genetics* 94:s98.
- SMITH, B. H. 1983. Recognition of female kin by male bees through olfactory signals. *Proc. Nat. Acad. Sci. USA* 80:4551–4553.
- SMITH, B. H., AND M. AYASSE. 1987. Kin based male mating preferences in two species of halictine bee. *Behav. Ecol. Sociobiol.* 20:313–318.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman and Co., San Francisco, CA.
- STUBBLEFIELD, J. W., AND E. L. CHARNOV. 1986. Some conceptual issues in the origin of eusociality. *Heredity* 57:181–187.
- WADE, M. J., AND F. BREDEEN. 1981. Effect of inbreeding on the evolution of altruistic behavior by kin selection. *Evolution* 35:844–858.
- WHITING, P. W. 1939. Sex determination and reproductive economy in *Habrobracon*. *Genetics* 24:110–111.
- WOYKE, J. 1976. Population genetic studies on sex alleles on the honey bee using the example of Kangaroo Island bee sanctuary. *J. Apic. Res.* 15:105–123.
- . 1979. Sex determination in *Apis cerana indica*. *J. Apic. Res.* 18:122–127.
- . 1980. Evidence and action of cannibalism substance in *Apis cerana indica*. *J. Apic. Res.* 19:6–16.
- . 1983. Lengths of haploid and diploid spermatozoa of the honey bee and the question of the production of triploid workers. *J. Apic. Res.* 22:146–149.
- . 1984. Exploitation of comb cells for brood rearing in honeybee colonies with larvae of different survival rates. *Apidologie* 15:123–136.
- 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.

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