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## Mate Choice: Investigation of Mating Preference for Siblings Versus Nonsiblings in the Solitary Vespid Wasp *Euodynerus Foraminatus*

Omoury A. Chambegga

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**MATE CHOICE: INVESTIGATION OF MATING PREFERENCE  
FOR SIBLINGS VERSUS NONSIBLINGS IN THE SOLITARY  
VESPID WASP EUODYNERUS FORAMINATUS**

by

**Omoury A. Chambegga**

A Thesis  
Submitted to the  
Faculty of The Graduate College  
in partial fulfillment of the  
requirements for the  
Degree of Master of Science  
Department of Biological Sciences

**Western Michigan University  
Kalamazoo, Michigan  
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MATE CHOICE: INVESTIGATION OF MATING PREFERENCE  
FOR SIBLINGS VERSUS NONSIBLINGS IN THE SOLITARY  
VESPID WASP EUODYNERUS FORAMINATUS

Omoury A. Chambegga, M.S.

Western Michigan University, 1992

Caged wasps of Euodynerus foraminatus were given a choice of a sibling or a nonsibling for mates. Two types of experiments were conducted: female choice and male choice. For female choice experiments one female, a sibling male, and an unrelated male were introduced into an observation cage. For male choice experiments one male, a sibling female, and an unrelated female were introduced into an observation cage. Females preferred to mate with siblings, but males mated randomly with regard to family relationship.

## ACKNOWLEDGMENTS

I would like to dedicate this thesis in remembrance of my family, whose support and encouragement during the early stages of this study made this endeavor worth while.

Lastly, I would also like to express my deep appreciation to the family of the late Dr. John Rood for the initiation of this scholarship that enabled me to pursue a master's degree.

Omoury A. Chambegga

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foraminatus***

Chambegga, Omoury Amir, M.S.

Western Michigan University, 1992

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## INTRODUCTION

### Literature Review

When Hamilton (1964a,b) introduced the concept of inclusive fitness, he also showed that it could be advantageous for animals not only to distinguish self from non-self but in certain social situations to distinguish between relatives and nonrelatives and even between relatives of differing degrees. Consequently, in the study of social behavior much effort has been invested in assessing the abilities of animals to distinguish relatives (Gamboa, 1988; Gamboa, Reeve, & Pfenning, 1986; Keeping, 1990; Woyciechowski, 1990). Many studies involving insects, amphibians, birds, and mammals indicate that animals are capable of distinguishing relatives. Nest founding females of the wasp Belonogaster juncea discriminate kinship by accepting or rejecting females attempting to join nest associations (Keeping, 1990). Tadpoles preferentially associate with close relatives (Bufo americanus: Waldman, 1981, 1982, 1985; Bufo boreas, O'Hara & Blaustein, 1982; Rana sylvatica Cornell, Berven, & Gamboa, 1989). Primates recognize their kin (Gadagkar, 1985).

There are two basic functional aspects for kin-discrimination: first, adjustments of beneficial, cooperative, or antagonistic behavior among members of animal societies (Hamilton, 1964a,b); and second, mate selection to achieve optimal outbreeding (Bateson, 1980, 1983).

## Mechanisms of Kin Recognition

Mechanisms of kin recognition differ in different groups of animals. Sherman and Holmes (1985) discussed three possible ways in which animals recognize kin. These include spatial cues, social learning (association), and phenotype matching. Spatial cues, rely on the fact that individuals occurring in a particular nest may be an adequate indicator of sibling or offspring status. Thus, young adults might avoid close inbreeding by dispersing from the natal nest before selecting a mate; this is practiced by old world monkeys, baboons, chimpanzees and gorillas (Walter, 1981). If sibling mating is more advantageous, they would mate before dispersal as in the wasp Euodynerus foraminatus (Cowan, 1979).

Social learning (association) as a method of kin-recognition involves the association of an animal with circumstances that reliably indicate kinship and learning phenotypic traits of the individual that will permit later recognition. Parent offspring recognition in mammals relies heavily on this method (Michener, 1974; Michener & Sheppard, 1972). Mutual recognition between cows and their pups in the Galapagos seal Arctocephalus galapagoensis and the sea lion Zalophus californianus is based on the familiarity with each others vocalizations (Trillmich, 1981). Similarly, sibling recognition may be learned during association in the same nest. Gynes of the social wasps Polistes fuscatus (Ross & Gamboa, 1981), and Belonogaster junicea associate and learn phenotypic cues on their natal nest (Keeping, 1990). Later, when new nests are being founded elsewhere these cues are used to distinguish relatives.

Phenotype matching allows for the possibility that animals may be able to assess the genetic relatedness to individuals they have never previously encountered. This requires that one individual learn a set of phenotypic attributes (template) by self-observation or by learning the phenotypic attributes of a known relative. When

new individuals are encountered their phenotypic attributes are compared to the template. The amount of overlap between the phenotype of the new individual and the template provides an assessment of kinship. To be effective, this method requires a correlation between phenotypic similarity and genotypic similarity. However, the phenotypic traits themselves may be of either genetic or environmental origin. For example, if individual odors are employed, they may result from genetically determined chemicals that are secreted from the body, or they may be acquired from a nest site.

### Nepotism

Hamilton (1964a,b) pointed out that organisms may increase their genetic representation in subsequent generations not only by producing direct descendants but also by aiding the reproduction of individuals with which they share genetic material (nepotism). In nonhuman primates for example, kin-discrimination abilities are involved with cooperation such as alarm calling, alliance formation, paternal infanticides, and improved foraging efficiency (Cheney & Seyfarth, 1982). Walter (1987) reported individual African hunting dogs sometimes give up their own reproduction to aid another individual in raising its young. Similar situations have been reported for jackals (Moehlman, 1979), and naked-mole rats (Reeve, Westneat, Noon, Sherman, & Aquadro, 1990).

In social wasps, discrimination has "search" and guard contexts (Gamboa et al. 1986). In search context, the discriminating individual chooses which individuals or colonies to usurp, rob, or join. In guard context the discriminating individual decides whether to admit or reject an approaching individual (Gamboa et al., 1986). Usurpation or nest takeover is common among foundresses of temperate species of social wasps. In general, usurpers are not closely related to foundresses of the

usurped colony (Gamboa, 1978). Although usurpers may minimize attacks on a relative's nest by long-distance dispersal, it is possible that they also use odor cues to guide their choice of a target colony. By preferentially targeting unrelated individuals or colonies, usurping females may avoid losses in the kin component of their inclusive fitness. In species where females seek to join and subsequently aid other colonies, individuals may preferentially join relatives (Bornais, Larch, & Gamboa, 1983). These search behaviors can give rise to natural selection for guard context kin discrimination; colony residents decide whether to accept or reject visiting conspecifics. Colony residents clearly would benefit in one or both components of inclusive fitness from an ability to discriminate between potential helpers and usurpers.

### Optimal Outbreeding

The concept of optimal outbreeding is based on the likelihood that both close inbreeding and extreme outbreeding impose costs. An optimal mate is the one that minimizes the combined costs of mating (Bateson, 1983). Inbreeding occurs when organisms mate with relatives and outbreeding is the mating of unrelated individuals. Thus, there will be an optimal compromise that minimizes the damage of the extremes and results in selecting mates of intermediate relatedness.

Inbreeding can result in the expression of deleterious recessive genes, lack of variable offspring that could cope with a varying environment, loss of heterozygote advantage (overdominance) due to beneficial interaction between different alleles at the same locus, and genetically more similar individual offspring that compete more intensely among themselves (Bateson, 1983; Parker, 1979; Smith, 1979). The costs of outbreeding may include the loss or suppression of genes required for adaptations to a particular environment, and co-adapted gene complexes broken up by



recombination, traveling into other populations to seek mates is costly and dangerous, and lastly a mismatch of habits acquired by mates in different environments disrupts parenting (Bateson, 1983).

Most reports of "outbreeding mechanisms" focus on preventing close inbreeding such as parent offspring or sibling mating and ignore the possibility that distant outcrossing may also be disadvantageous. There are however examples that indicate that mating with relatives may be optimal. Females of some solitary wasps readily mate with brothers when finding an unrelated mate would be easy (Cowan, 1979); and Bateson (1983) found that Japanese quail prefer to associate and potentially mate with first cousins.

Cowan (1979) argued that inbreeding combined with sex ratio control would allow females to reduce the costs of sexual reproduction without becoming strictly asexual. A female that mates with her brother increases her relatedness to her offspring, and thus may increase her genetic representation in subsequent generations relative to outcrossing females. Once inbreeding has begun, females may be able to gain further by diverting resources to genetically more similar daughters and away from "excess" sons.

There is controversy about whether animals actually do choose mates so as to achieve optimal outbreeding. However mate discrimination and selection does occur because females mate with some males and reject others (Cowan, 1991). Optimal outbreeding may be achieved by any of the three mechanisms of kin recognition: Spatial cues, association, or phenotype matching. Spatial cues may involve dispersal of one sex away from the natal area. Providing they do not move too far, their mates are likely to be moderately related so optimal outbreeding could be achieved. Animals may associate when immature (as sibling nest mates), learn to recognize one another, and later when mature seek out each other or discriminate against each other.

Or, animals may be able select mates based on phenotype matching. Choice of a mate that looks, sounds, or smells a bit different, but not too different from close kin, could also result in optimal outbreeding (Bateson, 1983). For example, among apes if males remain in the same social unit with their mother they interact sexually with her at much lower rates than with other females (Walter, 1981). This probably involves both social learning by associating and/or phenotype matching.

In the social wasp Polistes fuscatus, males appear to lack ability to discriminate between nest mate (sibling) and non-nest mate unrelated females, and choose their mates without regard to relatedness (Larch & Gamboa, 1981; Post & Jeanne, 1982). Unlike males, females do appear to have the ability to discriminate nest mates from non nest mates for mating. Shellman-Reeve and Gamboa (1985) reported that females of P. fuscatus discriminate against their male nest mates when mating.

The objective of this study is to determine whether individuals of the solitary vespid wasp Euodynerus foraminatus discriminate between potential mates that are either (siblings) or unrelated. Cowan (1979) reported that E. foraminatus exhibits sibling mating as virgin females emerge from their natal nest. These observations suggest that sibling mating may be preferred by this wasp and that discrimination is at least partly based on spatial cues. However, spatial cues may not be the only mechanisms involved. The hypotheses tested in this study are that in the absence of spatial cues: (1) females of E. Foraminatus discriminate between sibling and unrelated males, and (2) males of E. foraminatus discriminate when given a choice between sibling and unrelated females.

## NATURAL HISTORY OF Euodynerus foraminatus

### Nesting and Oviposition Behavior

Solitary vespid females nest individually and show considerable parental care, but there is no contact between parents and their developing young (Cowan, 1991). E. foraminatus like most other solitary vespids is a mass provisioning species. Females nest in vacant insect tunnels in wood. Within the tubular hole, a female sequentially constructs and provisions a series of linearly arranged cells separated by mud partitions (Figure 1). She lays an egg at the end of the cavity and then rapidly makes several foraging trips for prey caterpillars and stores them with her egg. When enough food has been placed in the cell for the complete growth of the larva, she seals the cell and begins work on another. Eggs hatch in two to four days (Iwata, 1953). The first instar larva may either slip out of the egg shell immediately or remain suspended within it for a day while feeding on the nearest prey (Jorgensen, 1942). Duration of the larval stages ranges from five to twelve days. When feeding is completed, the larva spins a cocoon and pupates. After a wasp has transformed into the adult stage, it chews an exit hole and escapes from the cell.

### Construction Materials

Females of E. foraminatus obtain their mortar for nest construction by drinking water at one place and then flying to a site of dry clay soil where they bite at the ground, regurgitate water, and mix the resulting mud to proper consistency (Cowan, 1981). The female then flies to the nest with the globule of mud and incorporates it into the nest structure. Nests are often located near a source of water

(Isely, 1983; Markin & Gittins, 1967). Females of *E. foraminatus* nest in a variety of preexisting cavities. Almost any type of nook or cranny may be used, but the most common are tubular cavities in the hollowed pith of twigs or vacant insect tunnels in dead wood. They also accept artificial nest sites that are made by drilling holes in blocks of wood (trap-nests) (Krombein, 1967). Through the use of such nests, wasps can be manipulated, and trap-nests can be opened for study.

Female wasps usually rear both sexes in the same nest hole: females in the innermost and males in the outer cells. The sexes are not intermixed (Figure 1) (Cowan, 1981; Krombein, 1967). Controlled arrangement of the sexes is possible because of the haplodiploid genetic system found in the Hymenoptera. Diploid females are produced when eggs are fertilized at the time of oviposition by sperm stored in the females spermatheca. Haploid males are produced when sperm are withheld so that unfertilized eggs are deposited (Cowan, 1979).

### Mating Behavior

Males develop more rapidly than females, and emerge from their nest several days ahead of their sisters. Emergence occurs in the morning, and it is usually synchronized so that all individuals of the same sex exit on the same morning within a fairly short period. When a single nest produces two or more males, they interact aggressively and compete for control of the entrance to their natal nest. The winning brother remains at the nest and awaits emergence of the females several days later (Cowan, 1979, 1981).

The females' emergence from the nest is heralded by vibrations they make as they chew through the mud partitions between the cells. At this time the resident male remains standing over the nest hole. As a female exits, the male mounts and copulates with her for 1 to 2 minutes (Figure 2). After mating, the male returns

directly to the nest hole and waits for the next female. If another female is already out of the nest, the male initiates copulation directly. Females not inseminated as they emerge from their natal nest mate later at flowers or foliage perhaps with unrelated males (Cowan, 1979). Once inseminated, females do not mate again.

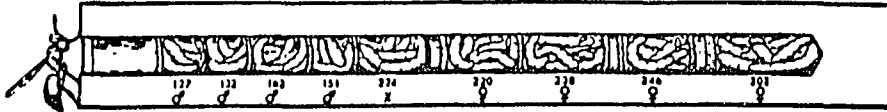


Figure 1. Nest Structure for *Euodynerus foraminatus*. Numbers below cells indicate weight in mg of cell contents. Symbols indicate the sex of the wasp reared from each cell. X indicates wasp died prematurely. Source: Cowan (1978), p. 2. Used with permission.

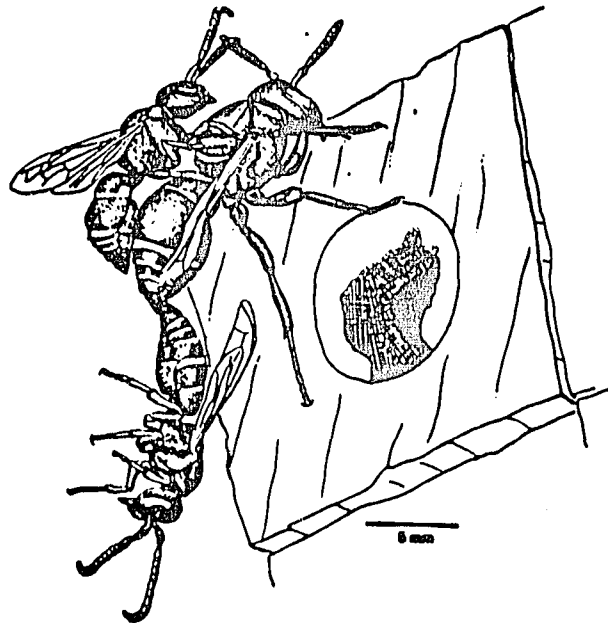


Figure 2. A Disturbed Copulation of *Euodynerus foraminatus*. The wasp standing on the front of the trap nest is a female. The others are males. The male hanging from the female initiated copulation as she emerged from the nest. The male grasping the female is an intruder. Source: Cowan (1986), p. 538.

## MATERIALS AND METHODS

In the summer of 1991 and spring of 1992, I studied mate choice by Euodynerus foraminatus using caged wasps. I obtained wasps for mating experiments using the technique of trap nesting (Krombein, 1967). Immature wasps were collected from the field and reared to adulthood in laboratory using trap-nests made from 19mm x 19mm x 152mm pine sticks with a hole drilled longitudinally to a depth of about 140mm. Trap-nests were placed out at two sites about 10km apart. At each site 50 bundles of six traps each were wired to tree limbs at about 5 meter intervals.

Nests were examined weekly, and when the nest within a stick was finished as determined by a final mud closure, the nest was collected and replaced with an empty trap-nest. A diagram of the structure and dimensions of each nest was made. All developmental stages were noted. The development of larval stages was monitored until they approached adulthood. Because nest odors have been implicated in kin recognition among social wasps (Gamboa et al., 1986), adults were allowed to chew their way through the nests' mud partitions and exit the nest as they would in nature. Emerging adults were captured in vials taped over the nest opening. The newly emerged adults were isolated in 500mm (one pint mason) jars covered with insect netting. I kept males in the laboratory for two or three days to wait for emergence of the females. Wasps were provided sugar and water and maintained at 22-24°C temperature with natural photoperiods. To keep track of individuals during experiments, I marked wasps with dots of colored paint on the dorsum of the thorax. Wasp sizes were determined by measuring the wing length with dial calipers. Wasp ages were determined by counting from the day a wasp exited its nest to the day it was used in a trial.

Two types of experiments were conducted: female choice and male choice. For female choice experiments, one female and two males (one a sibling of the female and the other unrelated) were introduced into the observation cage. The two males were introduced into the cage first and the female was introduced last. A total of 62 separate trials were conducted. For male choice experiments, one male and two females (one a sibling of the male and the other unrelated) were introduced into the observation cage. The females were introduced before the male. A total of 41 separate trials were conducted. Wasps emerging from the same trap-nest were assumed to be siblings. Wasps obtained from the other field site 10km distant were assumed to be non-siblings. The time intervals of the following male-female interactions were recorded. "Contact time" is the time between when the last wasp was introduced to the observation cage to the time a male first touched a female. "Duration of courtship" refers to the activities between a male's mounting and intromitting a female (behaviors that seemed to function in stimulating females to receptivity). "Quiet" refers to the early period of intromission when the wasps appear calm, and "struggle" refers to the later period of intromission when females apparently struggle to be released. The data were analyzed by means of chi square tests and t tests (Zar, 1984).

## RESULTS

### Female Choice Experiment

In 62 trials of the female choice experiment 41 females mated with siblings , 17 mated with non-siblings, and in four trials the female did not mate (Appendix A). Females mated significantly more often with brothers than with unrelated males (chi square=9.95,  $P < 0.005$ ). There was no tendency for siblings or nonsiblings to be the first male to approach the female. In trials where one male clearly approached and contacted the female first, siblings were first in 21 trials and nonsiblings were first in 22 trials (chi square=0.023,  $P > 0.5$ ). However, in 16 trials when nonsiblings approached first, they were rejected and the female later mated with a sibling. This occurred when a female that was being courted curled her antennae and abdomen downward and prevented intromission. Thus, nonsibling males tended to be rejected by females that later mated with a brother.

Table 1 presents data on male age, size, and the durations of the stages of matings for sibling versus nonsibling copulations. There were no significant differences between matings involving sibling versus nonsibling males with regard to male age, male size, time to contact, or the durations of the two phases of intromission. However, courtship by sibling males led to intromission more rapidly than with nonsibling males.



Table 1  
Results of Female Choice Experiment.

	sibling matings	non-sibling matings	t statistic	significance value
Age	3.8 (1.14)	4.2 (1.69)	1.38	$\underline{P}>0.1$
Size	8.2 (0.41)	8.1 (0.48)	0.41	$\underline{P}>0.5$
Time to contact	15 (8.75)	19 (11.4)	1.45	$\underline{P}>0.2$
Duration of courtship	10 (3.77)	26 (8.91)	9.58	$\underline{P}<0.001$
Duration of quiet phase	18 (5.41)	17 (6.19)	1.03	$\underline{P}>0.1$
Duration of struggle phase	19 (8.15)	20 (6.64)	1.57	$\underline{P}>0.1$

Mean male age, male size, time to contact, duration of courtship, duration of quiet phase, and duration of struggle phase. Age in days, size mm, and time in seconds. Standard errors are in parentheses.

#### Male Choice Experiment

In 41 trials of the male choice experiment 21 males mated first with the sibling female, 16 mated first with the nonsibling female, and four trials produced no mating. The tendency for sibling mating to prevail is not statistically significant (chi square=0.70,  $\underline{P}>0.25$ ).

Table 2 presents data on female age, size, and the duration of the stages of matings for sibling versus nonsibling copulations. There were no significant differences between matings involving sibling versus nonsibling females with regard to female age, female size, time to first contact, or the durations of the two phases of

intromission. However, as with the female choice experiment, the period of courtship before intromission is shorter for sibling pairs than nonsibling pairs.

Table 2  
Results of Male Choice Experiment.

	sibling matings	nonsibling matings	t statistic	significance value
Age	3.0 (1.52)	3.5 (1.92)	1.17	$\underline{P}>0.1$
Size	10 (0.48)	10 (0.51)	0.70	$\underline{P}>0.2$
Time to contact	18 (14.9)	20 (18.5)	0.29	$\underline{P}>0.5$
Duration of courtship	9.6 (3.21)	19 (6.88)	5.63	$\underline{P}<0.001$
Duration of quiet phase	19 (5.22)	16 (4.34)	1.69	$\underline{P}>0.1$
Duration struggle phase	22 (9.59)	23 (11.6)	0.40	$\underline{P}>0.5$

Mean female age, female size, time to contact, duration of courtship, duration of quiet phase, and duration of struggle phase. Age in days, size mm, and time seconds. Standard errors are in parentheses.

## DISCUSSION

Based on observational data, Cowan (1979) argued that E. foraminatus preferred mating with relatives. Males recognized their sisters by remaining near the natal nest hole and waiting for the emergence of females. By mating before dispersal from the natal nest, females are more likely to mate with a brother than if they mate after leaving the area. Thus in nature, site location provides a cue for kin recognition and mate selection. In this study, I found that females prefer to mate with their siblings rather than unrelated males. This preference is manifest by rejecting unrelated males and mating later with siblings, and by the longer courtship required of nonsiblings before females will mate. However males mate randomly with regard to kinship. Thus, the male behavior of waiting at the nest has no relevance with regard to preferring sisters as mates and can be interpreted entirely on the basis of maximizing the number of encounters with receptive females (Cowan, 1979) whether they are related or not. Since E. foraminatus were removed from their natal nest upon emerging and placed in cages for mating, site location (spatial cue) is not the only mechanism used by females for kin recognition and mate selection in this wasp. This indicates that additional mechanisms are also involved with and reinforce kin recognition and mate selection. Social learning (association) could occur as females detect chemical cues while exiting the nest through the cells where their brothers developed, or phenotypic matching could occur if females compare potential mates to a template based on self examination.

Social learning as a mechanism for kin recognition has been implicated in the behavior of other vespid wasps. Shellman-Reeve and Gamboa (1985) reported that females of Polistes fuscatus use social learning to recognize their male nest-mates, but

in this case brothers were discriminated against as potential mates rather than being favored. However, males of P. fuscatus are similar to E. foraminatus in their failure to discriminate nest-mates from non-nest mates when choosing mates (Larch & Gamboa, 1981; Post & Jeanne, 1982; Ryan, Cornell, & Gamboa, 1984).

An optimal mate is the one that minimizes combined costs of inbreeding and outbreeding (Bateson, 1983; Parker, 1979; Smith, 1979). Outbreeding costs include the loss or suppression of genes required for adaptations to particular environments, loss of co-adapted gene complexes broken up by recombination, and costly and dangerous travel to other populations in search of mates. E. foraminatus by favoring sibling mating reduces these costs. Inbreeding results in the expression of deleterious recessive genes, loss of heterozygote advantage overdominance due to beneficial interactions between different alleles at the same locus, and genetically more similar individual offspring that compete more intensely among themselves. These costs may not be severe for wasps because deleterious recessive alleles do not accumulate because they are regularly expressed in the haploid males where selection can eliminate them. For animals that move about freely, local competition among genetically similar offspring from a single inbred brood is probably not as severe as it would be for some plants. For E. foraminatus, however, some females are not inseminated by a sibling as they emerge from their natal nest. These individuals disperse to vegetation or flowers where the chance of mating with a brother is reduced (Cowan, 1979). This prevents the population from becoming purely inbred.

Smith (1979) and Cowan (1979) argued that inbreeding combined with sex ratio control would allow females to reduce the costs of sexual reproduction without becoming strictly asexual. A female that mates with her brother increases her relatedness to her offspring relative to outcrossing females. In addition, the sex ratio control afforded by the haplodiploid genetic system of the Hymenoptera allows

females to gain further by diverting resources toward genetically more similar daughters and away from excess sons once inbreeding has begun. This results in a faster increase of the genetic line than would occur with outbreeding, but this occurs at the expense of genetic variability. It seems that for E. foraminatus, the costs of reduced genetic variability, resulting from partial inbreeding, are outweighed by the benefits of large numbers of daughters with higher genetic relatedness to the parents (Cowan, 1981).

Mate choice favoring inbreeding seems not to be particularly common. Most discussions of optimal outbreeding mechanisms focus on behaviors that apparently function to prevent close inbreeding. There are, however, several examples in which mating with relatives may be optimal. Bateson (1983, 1988) found that Japanese quail prefer to associate and potentially mate with first cousins or siblings, and Barnard and Aldhous (1991) review mate selection in mice. It is increasingly apparent that animals exercise subtle distinctions about kinship when selecting mates.

**Appendix A**  
**Data from Female Choice Experiment**

## APPENDIX A

## Data from Female Choice Experiment

Trial No.	Mat sib/non	Sib age/size	Nonsib age/size	Time to Contact	Court-ship Duration	Quiet Phase.	Struggle Phase	1st Male to touch Female
1	sib	-	-	10	10	11	39	sib
2	sib	-	-	24	10	25	15	nonsib
3	sib	-	-	8	10	14	16	sib
4	sib	1/8.5	2/8.3	10	8	14	16	nonsib
5	nonsib	2/8.6	2/8.8	10	20	11	30	nonsib
6	nonsib	3/8.7	5/7.6	30	15	14	17	nonsib
7	sib	7/8.9	7/8.9	40	15	31	19	sib
8	sib	2/8.6	2/9.6	25	10	13	46	nonsib
9	sib	2/8.3	2/8.5	38	6	12	38	nonsib
10	sib	1/8.6	1/8.4	15	10	21	15	sib
11	no mat	-	-	-	-	-	-	sib
12	nonsib	4/7.8	8/8.8	40	25	15	15	nonsib
13	sib	3/7.9	4/7.6	9	11	15	20	sib
14	no mat	-	-	-	-	-	-	sib
15	sib	3/7.6	3/7.4	30	16	14	30	sib
16	nonsib	3/8.0	2/8.5	14	20	15	25	nonsib
17	sib	2/8.0	2/8.2	14	10	10	15	nonsib
18	nonsib	3/7.7	1/7.7	8	24	18	32	nonsib
19	nonsib	3/7.5	4/7.0	40	13	11	30	nonsib
20	sib	5/7.0	10/7.8	5	9	21	20	sib
21	sib	3/8.0	1/8.4	9	10	13	12	sib
22	nonsib	4/7.5	3/8.0	2	12	7	11	sib
23	sib	2/8.0	6/7.0	20	14	11	13	sib
24	sib	4/8.0	6/7.8	7	8	12	20	sib
25	sib	4/8.0	6/7.8	10	16	13	20	sib
26	sib	7/7.5	6.7.6	26	11	10	14	sib
27	nonsib	4/7.5	7/8.0	10	25	12	10	nonsib
28	sib	4/8.0	7/8.0	19	18	15	18	sib
29	no mat	-	-	-	-	-	-	sib
30	no mat	-	-	-	-	-	-	-
31	sib	4/8.5	4/8.0	8	12	15	25	sib
32	silbing	4/8.5	4/8.5	20	5	15	25	nonsib
33	nonsib	4/8.0	4/8.5	19	40	20	20	nonsib
34	sib	4/8.5	4/8.0	5	7	17	15	sib
35	sib	4/8.0	4.8.0	20	10	15	10	sib
36	nonsib	4/8.0	4/8.5	27	26	34	15	nonsib
37	silbing	4/8.5	4/8.5	20	20	20	20	sib
38	sib	4/8.5	4/8.5	30	10	15	25	sib
39	sib	4/8.5	4/8.5	15	5	25	20	sib
40	nonsib	4/8.0	4/8.0	10	35	12	23	nonsib

## Appendix A--Continued

Trial No.	Mat sib/non	Sib age/size	Nonsib age/size	Time to Contact	Courtship Duration	Quiet Phase.	Struggle Phase	1st Male to touch Female
41	sib	4/8.5	4/8.5	10	10	25	20	nonsib
42	sib	4/8.5	4/8.5	10	15	20	15	-
43	nonsib	4/8.0	4/8.5	25	25	20	15	nonsib
44	sib	4/7.5	4/8.0	10	8	20	20	nonsib
45	sib	4/8.0	5/8.0	10	5	20	25	sib
46	nonsib	4/8.5	4/8.5	20	26	10	20	-
47	nonsib	4/8.5	4/8.5	15	25	20	20	-
48	sib	3/8.5	3/8.5	10	5	10	26	-
49	sib	4/8.5	4/8.5	15	10	20	18	-
50	nonsib	4/8.5	4/8.5	10	40	16	24	nonsib
51	sib	4/8.5	4/8.0	10	10	28	10	nonsib
52	sib	4/8.0	4/8.5	10	15	15	20	-
53	sib	4/8.5	4/8.0	10	5	25	15	-
54	sib	4/7.5	4/8.0	5	5	20	10	-
55	sib	4/8.5	4/7.5	10	10	20	10	-
56	silbing	5/8.5	4/8.0	15	15	25	15	-
57	nonsib	5/8.0	5/8.0	30	40	20	15	-
58	sib	5/8.4	5/7.5	15	10	15	5	-
59	sib	5/8.5	5/7.5	2	5	20	20	-
60	nonsib	5/8.5	5/8.5	10	32	20	25	-
61	sib	5/8.0	5/8.0	20	10	25	10	-
62	sib	5/8.5	5/8.0	12	10	20	20	-



**Appendix B**  
**Data from Male Choice Experiment**

## APPENDIX B

## Data from Male Choice Experiment

Trial No.	Mating sib/non	Sib age/size	Nonsib age/size	Time to Contact	Duration of Courtship	Quiet Phase	Struggle Phase
1	nonsib	-	-	7	11	9	51
2	nonsib	-	-	10	15	15	45
3	nonsib	3/10.8	4/10.2	65	20	20	25
4	sib	3/10.4	3/10.4	60	10	18	15
5	sib	2/10.5	3/10.2	15	10	23	26
6	silbing	3/10.4	3/10.5	36	15	21	37
7	sib	4/9.5	1/9.3	30	10	16	12
8	nonsib	2/9.3	2/10.2	30	29	23	17
9	silbling	5/9.8	3/9.9	50	12	18	6
10	sib	6/10.0	7/9.6	8	15	25	20
11	nonsib	2/10.0	2/9.4	10	10	11	25
12	sib	1/10.5	3/10.5	20	10	34	43
13	nonsib	1/10.0	5/9.9	52	11	21	14
14	nonsib	1/9.9	8/9.9	15	15	15	20
15	sib	2/10.0	3/10.2	8	15	17	20
16	sib	1/11.0	4/9.0	20	13	15	22
17	sib	1/10.0	1/9.5	28	7	15	45
18	nonsib	8/10.4	10/10.5	47	29	12	10
19	no mating	-	-	-	-	-	-
20	no mating	-	-	-	-	-	-
21	nonsib	5/9.8	5/10.0	5	11	9	15
22	nonsib	6/8.5	7/8.4	20	30	20	38
23	sib	2/11.0	1/10.6	7	8	12	20
24	no mating	-	-	-	-	-	-
25	no mating	-	-	-	-	-	-
26	sib	2/10.5	2/10.5	5	10	15	15
27	sib	3/10.2	3/10.5	10	5	20	20
28	nonsib	2/10.5	2/10.4	10	25	15	20
29	nonsib	3/10.5	3/10.5	10	20	20	15
30	nonsib	3/10.2	3/10.5	10	18	15	20
31	sib	3/10.5	3/10.5	10	8	15	15
32	nonsib	3/10.5	3/10.5	10	25	15	15
33	sib	3/10.5	3/10.5	10	5	15	20
34	sib	3/10.5	3/10.5	10	5	10	15
35	nonsib	3/10.5	3/10.5	12	22	15	15
36	sib	3/10.2	3/10.4	12	8	18	20
37	sib	3/10.6	3/10.4	10	5	20	25
38	sib	3/10.2	3/10.4	12	12	15	20
39	nonsib	3/10.4	3/10.4	10	15	20	25
40	sib	3/10.5	3/10.5	10	10	25	25
41	sib	3/10.5	3/10.5	15	10	20	25

## BIBLIOGRAPHY

- Barnard, C.J., & Aldhous, P. (1991). Kinship, kin discrimination and mate choice. In P. G. Hepper (Ed.), Kin recognition (pp. 125-147. ) Cambridge, U.K.: University Press.
- Bateman, A.J. (1948). Intra-sexual selection in Drosophila. Heredity, 2, 249-368.
- Bateson, P. (1980). Preferences for cousins in Japanese quail. Nature, 295, 236-237.
- Bateson, P. (1983). Optimal outbreeding. In P. Bateson, (Ed.), Mate choice (pp. 256-257). Cambridge, U.K.: Cambridge University Press.
- Bateson, P. (1988). Preferences for close relations in Japanese quail. Congress International Ornithology, 1, 961-972.
- Bornais, K.M., Larch, C.M., & Gamboa G.J. (1983). Nestmate discrimination among laboratory overwintered foundress of the paper wasp, Polistes fuscatus (Hymenoptera: vespidae). Canadian Entomologist, 115, 655-658.
- Cheney, D.L., & Seyfarth, R.M. (1982). Recognition of individuals within and between groups of free-ranging vervet monkeys. American Zoologist, 22, 519-530.
- Cornell, T.J., Berven, K.A., & Gamboa, G.C. (1989). Kin recognition by tadpoles and froglets of the wood frog Rana sylvatica. Oecologia, 78, 312-316.
- Cowan, D. P. (1978). Behavior, inbreeding, and parental investment in solitary Eumenid wasps (Hymenoptera: Vespidae) (Doctoral dissertation, University of Michigan, 1978). Dissertation Abstracts International, 39/10, 4766-B.
- Cowan, D.P. (1979). Sibling mating in a hunting wasp: Adaptive inbreeding? Science, 205, 1403-1405.
- Cowan, D.P. (1981). Parental investment in two solitary wasps, Ancistrocerus adiabus and Euodynerus foraminatus (Eumenidae: Hymenoptera). Behavioral Ecology and Sociobiology, 9, 95-102.
- Cowan, D.P. (1986). Sexual behavior of eumenid wasps (Hymenoptera: Eumenidae). Proceedings of the Entomological Society of Washington, 88, 531-541.
- Cowan, D.P. (1991). The solitary and presocial Vespidae. In K. Ross & T. Mathews (Eds.), Social behavior of wasps (pp. 55-70). Ithaca, NY: Cornell University Press.

- Cowan, D.P., & Waldbauer, G.P. (1984). Seasonal occurrence and mating at flowers by; Ancistrocerus antilope (Hymenoptera: Eumenidae). Proceedings of the Entomological Society of Washington, 86, 930-934.
- Freeman, B.E., & Jayasingh, D.B. (1975). Population dynamics of Pathodynerus nasidens (Hymenoptera) in Jamaica. Oikos, 26, 86-91.
- Gadagkar, R. (1985). Kin recognition in social insects and other animals: A review of recent findings and a consideration of their relevance for theory of kin selection. Proceedings of the Indian Academy of Science, 94, 587-612.
- Gamboa, G.J. (1978). Intraspecific defense: Advantage of social cooperation among paper wasp foundress. Science, 99, 1436-1465.
- Gamboa, G.J. (1988). Sister, aunt-niece, and cousin recognition by social wasps. Behavior Genetics, 18, 409-423.
- Gamboa, G.J., Reeve, H.K., & Pfenning, D.W. (1986). The evolution and ontogeny of nestmate recognition in social wasps. Annual Review of Entomology, 31, 431-454.
- Gess, F.W. (1981). Some aspects of an ethological study of the aculeate wasps and bees of a karroid are in the vicinity of Grahamstown, South Africa. Annals of the Cape Provincial Museum of Natural History, 14, 1-80.
- Hamilton, W.D. (1964a). The genetical evolution of social behavior I. Journal of Theoretical Biology, 7, 1-16.
- Hamilton, W.D. (1964b). The genetical evolution of social behavior II. Journal of Theoretical Biology, 7, 17-52.
- Isley, D. (1913). The biology of some Kansas Eumenidae. Kansas University Science Bulletin, 8, 233-309.
- Iwata, K. (1953). Biology of eumenes in Japan. Mushi, 12, 83-85.
- Jorgensen, P. (1942). Biological observations on some solitary vespidae. Entomologiske Meddelelser, 22, 299-335.
- Keeping, M.G. (1990). Colony foundation and nestmate recognition in the social wasp Belonogaster petiolata. Ethology, 85, 1-12.
- Krombein, K.V. (1967). Trap nesting wasps and bees: Life histories, nests and associates. Washington, DC: Smithsonian Press.
- Larch, C.M., & Gamboa, G.J. (1981). Investigation of mating preference for nestmates in the Paper Wasp, Polistes fuscatus (Hymenoptera: vespidae). Journal of the Kansas Entomological Society, 54, 811-814.

- Markin, G.P., & Gittins, A.R. (1967). Biology of Stenodynerus claremontensis (Cameron) (Hymenoptera: Vespidae). University of Idaho, College of Agriculture, Research Bulletin, 74, 1-25.
- Michener, G.R. (1974). Development of adult-young identification in Richardson's ground squirrels. Psychobiology, 7, 375-384.
- Michener, G.R., & Sheppard, D.H. (1972). Social behavior between adult female Richardson's ground squirrels (Spermophilus richardsonii) and their own and alien young. Canadian Journal of Zoology, 50, 1343-1349.
- Moehlman, P.D. (1979). Jackal helpers and pup survival. Nature, 277, 382-383.
- O'Hara, R.K., & Blaustein, A.R. (1982). Kin preference behavior in Bufo boreas tadpoles. Behavioral Ecology, 11, 43-49.
- Parker, G.A. (1979). Sexual selection and sexual conflict. In M.S. Blum & N.A. Blum (Eds.), Sexual selection and reproductive competition in insects (pp.123-166). New York: Academic Press.
- Post, D.C., & Jeanne, R.L. (1982). Recognition of former nestmates during colony founding by the social wasp Polistes fuscatus (Hymenoptera, Vespidae). Behavioral Ecology and Sociobiology, 11, 283-285.
- Post, D.C., & Jeanne, R.L. (1983). Relatedness and mate selection in Polistes fuscatus (Hymenoptera, Vespidae). Animal Behavior, 31, 1260-1261.
- Reeve, H.K., Westneat, D.F., Noon, W.A., Sherman, P.W., & Aquadro, C.F. (1990). DNA fingerprinting reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. Proceedings of the National Academy Science, 87, 2496-2500.
- Ross, N.M., & Gamboa, G.J. (1981). Nestmate discrimination in social wasps, Polistes metricus (Hymenoptera, vespidae). Behavioral Ecology and Sociobiology, 9, 163-165.
- Ryan, R.E., Cornell, T.J., & Gamboa, G.J. (1985). Nestmate recognition in the bald faced hornet, Dolichovespula maculata (Hymenoptera, Vespidae). Zeitschrift fuer Tierpsychologie, 69, 19-26.
- Shellman, J.S., & Gamboa, G.J. (1982). Nestmate discrimination in social wasps: The role of exposure to nest and nestmates (Polistes fuscatus; Hymenoptera: Vespidae). Behavioral Ecology and Sociobiology, 11, 51-53.
- Shellman-Reeve, J.S., & Gamboa, G.J. (1985). Male social wasps (Polistes fuscatus, Hymenoptera: Vespidae) recognize their male nestmates. Animal Behavior, 33, 331-333.
- Sherman, P.W., & Holmes, W.G. (1985). Kin recognition issues and evidence. In B. Holldobler & M. Lindaure (Eds), Experimental behavioral ecology and sociobiology (pp. 437-460). Sunderland, MA: Sinauer.

- Smith, R.H. (1979). On selection for inbreeding in polygynous animals. Heredity, 43, 205-211.
- Sutherland, W.J. (1985). Chance can produce a sex difference in variance in mating success and explain Bateman's data. Animal Behavior, 33, 1349-1352.
- Trillmich, F. (1981). Mutual mother-pup recognition in Galapagos fur seals and sea lions: Cues used and functional significance. Behavior, 78, 21-42.
- Waldman, B. (1981). Sibling recognition in tadpoles: The role of experience. Zeitschrift fuer Tierpsychologie, 56, 341-358.
- Waldman, B. (1982). Sibling association among school tadpoles: Field evidence and implications. Animal Behavior, 30, 700-713.
- Waldman, B. (1985). Olfactory basis of kin recognition in toad tadpoles. Journal of Comparative Physiology, 156, 565-577.
- Walter, J.R. (1981). Inferring kinship from behavior maternity determinations in yellow baboons. Animal Behavior, 29, 126-136.
- Woyciechowski, M. (1990). Do honey bee, Apis mellifera L., workers favor sibling eggs and larvae in queen rearing? Animal Behavior, 39, 1220-1222.
- Zar, J.H. (1984). Biostatistical analysis. Englewood Cliffs, NJ: Prentice-Hall.