

Natural History, Learning, And
Social Behavior in Solitary Sweat
Bees (Hymenoptera, Halictidae)

by William T. Weislo

B.S., University of Michigan, Ann Arbor, 1982

Professor in Charge

Charles D. Michener

Committee Members

Rachel Jander

William Bell

NATURAL HISTORY, LEARNING, AND
SOCIAL BEHAVIOR IN SOLITARY SWEAT
BEES (HYMENOPTERA, HALICTIDAE)

BY W. WCISLO

NATURAL HISTORY, LEARNING, AND SOCIAL BEHAVIOR
IN SOLITARY SWEAT BEES (HYMENOPTERA, HALICTIDAE)

by

William T. Wcislo
B.S., University of Michigan- Ann Arbor, 1982

Submitted to the Department of
Entomology and the Faculty of the
Graduate School of the University
of Kansas in partial fulfillment
of the requirements for the degree
of Doctor of Philosophy



Professor in Charge





Committee Members

Date Defended: 2 April 1991

R00225 22696

MAY 19 1991

DISSERTATION ABSTRACT

Natural History, Learning, and Social Behavior
in Solitary Sweat Bees (Hymenoptera, Halictidae)

William Thomas Wcislo
Department of Entomology
University of Kansas

The natural history of two Costa Rican species of sweat bees was studied to better understand the advantages and disadvantages associated with group-living and cooperative behavior in bees. One of the bees was a new species, and was described and named after José Figueres Ferrar, a famous Costa Rican patriot. Studies of the behavior of these bees, in turn, are used as general models for studying social behavior.

Experimental studies on one of the species (Lasioglossum figueresi) showed that females recognize their homes (nests) in part by means of individual "chemical signatures" deposited at the entrance-way. The use of chemical signatures by solitary bees to recognize their nests is useful because the same perceptual systems can be used by the bees to recognize other bees, and so form stable social groups.

Experiments on mate recognition by male bees also showed that males can recognize individual females by their odors. Details of the courtship behavior of a solitary bee (Nomia triangulifera) show it to have the most complex courtship behavior known to date in bees.

Together these studies show the importance of behavior as both products, and producers, of evolution.

The most vital task of the present age is to formulate a social basis for civilization, to dethrone economic ideals and replace them by human ones...It requires a new world-picture as its basis, a new framework of ideas. And biology is needed to give that picture its proper background.

- Julian Huxley, Man Stands Alone

If I were now to rewrite the book (1932), I would offer the Savage a third alternative. Between the utopian and the primitive horns of his dilemma would lie the path of sanity...

- Aldous Huxley, preface to a 1969 reprint of
Brave New World

TABLE OF CONTENTS

Table of Contents.....	iii
List of Figures and Tables.....	vi
Acknowledgements.....	x
Chapter 1. Introduction.....	1
Chapter 2. Comparative Biology of the Social and Solitary Sweat bees, <u>Lasioglossum aeneiventre</u> and <u>L. figueresi</u>	4
Materials and Methods.....	6
Results.....	9
Habitat.....	9
<u>Lasioglossum figueresi</u>	10
Nest sites.....	10
Nests.....	12
Seasonal cycle.....	15
Larval development.....	17
Diel activity.....	18
Social behavior.....	19
Natural enemies or associates.....	20
<u>Lasioglossum aeneiventre</u>	21
Nest sites.....	21
Nests.....	22
Seasonal cycle.....	24
Larval and colony development.....	25
Males.....	26
Diel activity.....	26
Social behavior.....	27
Natural enemies.....	30
Discussion.....	30
Ethological comparisons.....	31
Nest architecture.....	31
Social organization.....	32
Costs and benefits of social behavior.....	32
The evolution of solitary behavior?.....	34
Acknowledgements.....	36
Figures.....	39
Tables.....	75
Chapter 3. Nest recognition in a solitary bee, <u>Lasioglossum figueresi</u>	82
Synopsis of nesting biology and study site.....	83
Experimental studies.....	84
Experiment 1. Visual cues.....	85
Experiment 2. Turrets.....	87
Experiment 3. Olfactory cues.....	87
Results.....	89

Exploratory behavior.....	89
Experiment 1. Visual cues.....	89
Experiment 2. Turrets.....	90
Experiment 3. Olfactory cues.....	91
Discussion.....	93
Mechanisms of nest recognition.....	93
Recognition, contextual changes, and social evolution.....	98
Acknowledgements.....	101
Figures.....	102
Tables.....	108
Chapter 4. Mate attraction and Mating Biology of Solitary Halictid Bees..	115
Natural History and Background Information.....	117
<u>Lasioglossum figueresi</u> (Halictinae).....	117
<u>Nomia triangulifera</u> (Nomiinae).....	118
Voucher specimens.....	120
Methods.....	120
<u>Lasioglossum figueresi</u>	120
Olfaction and mate location (cage experiments).....	120
Olfaction and mate location (field experiments).....	121
Male patrolling.....	122
Male learning.....	122
<u>Nomia triangulifera</u>	123
Emergence phenologies and sex ratio.....	123
Male patrolling.....	124
Male learning of female odors.....	126
Social facilitation.....	126
Flight paths.....	126
Courtship and mating behavior.....	127
Results.....	129
<u>Lasioglossum figueresi</u>	129
Olfaction and mate location (cage experiments).....	129
Olfaction and mate location (field experiments).....	129
Male patrolling range.....	130
Male learning.....	130
<u>Nomia triangulifera</u>	132
Emergence phenologies and sex ratio.....	132
Male patrolling.....	133
Courtship and mating behavior.....	133
Male learning of female odors.....	138
Social facilitation.....	140
Discussion.....	141
Courtship behavior and sexual selection.....	141
Mate localization and identification.....	146
Male learning.....	148

Mating, learned recognition, and social evolution.....	150
Acknowledgements.....	151
Figures.....	152
Tables.....	180
Chapter 5. Epilogue.....	183
Bibliography.....	186

LIST OF FIGURES AND TABLES

FIGURES:

- Figure 2.1. Mandible of female Lasioglossum aeneiventre.
- Figure 2.2. Nest-site of Lasioglossum figueresi (San Antonio de Escazú, Costa Rica).
- Figure 2.3. Fused nest turrets of Lasioglossum figueresi (ruler is in mm).
- Figure 2.4. A cell with pollen ball from a nest of Lasioglossum figueresi.
- Figure 2.5. Schematic top-view sections of nests of Lasioglossum figueresi.
- Figure 2.6. Diagrammatic representation of the nesting phenologies and social organizations of Lasioglossum figueresi and L. aeneiventre.
- Figure 2.7. Population-level summary of developmental stages of brood of Lasioglossum figueresi.
- Figure 2.8. Scatter plot of the number of male pupae versus the number of female pupae in a nest of Lasioglossum figueresi.
- Figure 2.9. Diel provisioning activity of Lasioglossum figueresi and L. aeneiventre.
- Figure 2.10. Distribution of the durations of pollen-gathering foraging trips by female Lasioglossum figueresi.
- Figure 2.11. Head-width of female Lasioglossum figueresi as a function of the date the bee was collected.
- Figure 2.12. The number of cells per nest of Lasioglossum figueresi.
- Figure 2.13. Schematic representations of nests of Lasioglossum aeneiventre.
- Figure 2.14. Histogram of an estimate of pollen ball size (L x W x H, mm) for Lasioglossum aeneiventre.
- Figure 2.15. Population-level summary of seasonal changes in developmental stages of brood of Lasioglossum aeneiventre.

Figure 2.16. Seasonal variation in the proportion of fertilized females per nest of Lasioglossum aeneiventre.

Figure 2.17. Seasonal variation in the total number of nests (circles) of Lasioglossum aeneiventre

Figure 2.18. Distributions of head-widths for female Lasioglossum aeneiventre, according to whether she was a solitary female, mated and living in a group, or unmated and living in groups.

Figure 2.19. Seasonal variation in mean head-width of female Lasioglossum aeneiventre.

Figure 2.20. Distributions of lengths of longest oocyte in female Lasioglossum aeneiventre.

Figure 3.1. Diagram showing six painted discs placed in a ring centered on the nest turret of Lasioglossum figueresi.

Figure 3.2. Schematic illustration showing the flight paths of three approach flights of a Lasioglossum figueresi female.

Figure 3.3. Diagram showing a nest turret in situ, as well as the method for supporting the turret during experiments.

Figure 3.4. Responses of female Lasioglossum figueresi returning to their nests after turrets were removed, and the entrances were covered with a mud paste. The bee's turret and an alien turret were placed to the right and left of the true entrance (as in Fig. 3.3).

Figure 4.1. A male Lasioglossum (Dialictus) figueresi approaching a pinned, frozen female (cropped from photograph).

Figure 4.2. A male Lasioglossum (Dialictus) figueresi attempting copulation with an unextracted frozen female.

Figure 4.3. Several male Lasioglossum (Dialictus) figueresi crawling over a male that is trying to mate with a frozen female (as in Fig. 4.2).

Figure 4.4. Digitized flight paths of male Nomia triangulifera in response to a frozen unextracted female (black circles).

- Figure 4.5. Means of male Lasioglossum (Dialictus) figueresi response to odors of frozen unextracted females.
- Figure 4.6. Line graphs showing the contacts/approaches by males towards individual unextracted females Lasioglossum figueresi.
- Figure 4.7. Histogram of the numbers of male (black) and female (hatched) Nomia triangulifera captured in emergence traps.
- Figure 4.8. Daily operational sex ratio for Nomia triangulifera for 1989 and 1990.
- Figure 4.9. Histograms of the inter-tegular distance (mm) for males and females of Nomia triangulifera.
- Figure 4.10. Histograms of the inter-tegular distance (mm) for males of Nomia triangulifera patrolling at sunflowers, patrolling at the emergence site, or mating.
- Figure 4.11. Schematic diagram of the pre-copulatory behavior of male Nomia triangulifera.
- Figure 4.12. Representative sonagram of the pre-copulatory vibrations of male Nomia triangulifera.
- Figure 4.13. Representative sonagram of the copulatory vibrations of male Nomia triangulifera.
- Figure 4.14. The mean response of male Nomia triangulifera presented with the unextracted females.
- Figure 4.15. The mean number of contacts per approach for male Nomia triangulifera in response to the odors of frozen unextracted females at different sites and times.
- Figure 4.16. Line graphs showing the contacts/approaches by males towards individual frozen unextracted female Nomia triangulifera.
- Figure 4.17. Summary of social facilitation studies in Nomia triangulifera.

TABLES:

Table 2.1. Egg to adult development rates in halictid bees.

Table 2.2. Summary of multi-female nests in Lasioglossum figueresi.

Table 2.3. Summary of nest characteristics of Lasioglossum aeneiventre.

Table 2.4. Durations of life-history stadia for Lasioglossum aeneiventre.

Table 2.5. Summary of mating status and estimates of labor.

Table 2.6. Comparison of behavioral and nest architectural attributes of Lasioglossum figueresi and L. aeneiventre.

Table 3.1. Responses of female Lasioglossum figueresi to visual objects near the nest.

Table 3.2. Responses of female Lasioglossum figueresi to manipulations involving nest turrets.

Table 3.3 Responses of female Lasioglossum figueresi to manipulations involving the application of hexane.

Table 3.4. Responses of female Lasioglossum figueresi to manipulations involving the application of hexane and turrets.

Table 3.5. Summary of mechanisms of nest localization and identification in Apoidea.

Table 4.1. Responses of caged male Lasioglossum figueresi to female odors.

Table 4.2. Summary of mark-recapture data for Nomia triangulifera.

Table 4.3. Summary of data on sexual receptivity of female Nomia triangulifera.

ACKNOWLEDGEMENTS

Lasioglossum (Dialictus) figueresi was named for José Figueres Ferrar (1903 - 1990; a reference to his biography is given in Wcislo, 1990a). "Don Pepe" was a famous Costa Rican patriot who helped overthrow a military government in the middle of the twentieth century, and helped establish a neutral democracy; these actions undoubtedly helped make Costa Rica such a peaceful place to live and study .

I am deeply grateful to all the members of the Department of Entomology (1983- present) for creating such a nice social environment in which to learn. Among current or past faculty (including those from other Departments), the following have been particularly helpful with ideas, criticisms, suggestions, use of equipment, or encouragement and friendship: Byron Alexander, William Gordon, Phillip Hedrick, Robert Holt, and especially William Bell and Rudolf Jander; my advisor, Charles Michener, gets special mention because he helped more than anybody. Hopefully, their influence will be evident throughout. Some other people are acknowledged at the ends of Chapters 2 through 4.

During studies in Costa Rica I adopted William Eberhard and Mary Jane West-Eberhard as surrogate advisors, which was one of my smartest moves. They helped enormously. Additionally, I am grateful to Anna, Jessica, and especially Andrés Eberhard for their hospitality. Alvaro Wille and Enrique Orozco also generously provided assistance while I was in

Costa Rica.

A number of friends also deserve special thanks for either doing some of my work for me, or for ideas, suggestions, and assistance, but mostly for their friendship: among former students, I am grateful to Cole Gilbert, Thor Holmes, Marilyn Teeter, John Wenzel and Marla Spivak-- she and Bryan Alvarez Spivak helped greatly in Costa Rica; among current students and friends, the same to Nancy Ares, Bryan Danforth, Elaine Holmes, Stephen Reyes, Michael Tourtellot, Douglas Yanega, and especially Robert Minckley and Donna Conlon. I also thank my parents, brothers and sisters, because without their help I likely would have done something different.

I am also thankful to the following agencies for supporting this research: the H.B. Hungerford Fund, Department of Entomology, University of Kansas; the Piere L. Stouse Memorial Fund, Department of Geography, University of Kansas; Dissertation and Summer Honors Fellowships from the Graduate College of the University of Kansas; a Smithsonian Tropical Research Institute Short-term Fellowship; National Science Foundation (U.S.A.) Doctoral Dissertation Improvement Grant BNS 87- 01046; a National Science Foundation (U.S.A.) grant BNS 82- 00651 (C.D. Michener, principle investigator); the Theodore Roosevelt Fund of the American Museum of Natural History; and a Sigma Xi Grant-in-Aid of Graduate Research.

CHAPTER 1

INTRODUCTION

In his notebooks Darwin wrote that "the Citadel had fallen," referring to his belief that the study of mind could be approached from an evolutionary point of view. Despite this bold assertion, the relationships among mind, behavior, and evolution remain obscure and even sometimes denied as a worthwhile area of investigation. Indeed, we know little about the relationships between mind and behavior, or between behavior and evolution. I consider this "Dissertation" to be a synopsis of part of my plan to explore Darwin's Citadel and an outline of a future longer work, since studies as brief as those that follow cannot possibly aim to be like a set of architect's blueprints.

I studied the natural history of sweat bees in two of the three subfamilies of Halictidae (Nomiinae and Halictinae), with emphasis on how simple learning abilities relate to the evolutionary development of social behavior. The research involves organisms whose behavior creates some significant features of their environment; this behavioral attribute occurs independently in numerous organisms, including humans (Wcislo, 1989). One pattern I am trying to understand concerns the fact that social and parasitic behavior have evolved repeatedly among many different lineages of >20,000 species of bees, yet the vast majority of the

>7,000 species of related sphecid wasps are solitary and free-living.*

Although studying natural history is presently not very fashionable, the first third of this Dissertation (Chapter 2) concerns descriptive behavioral studies of two species of sweat bees. This behavioral "alpha-taxonomy" complements a morphological species description given elsewhere (Wcislo, 1990 a); natural history studies of the other solitary bee, *N. triangulifera*, are reported by Minckley, Wcislo, Buchmann, and Yanega (in prep.). These descriptive studies are needed as bases for other studies (Chapters 3 and 4).

Societies of insects do not become very complex unless the interactants are kin, and kin associations are established and maintained by learning. I decided, therefore, to study behaviors associated with the role of learning for recognition of individuals in different contexts for solitary and social bees. These other contexts included behaviors associated with mating, and the localization and identification of nests. Experimental studies of nest recognition by solitary females (Chapter 3), and of mate localization and simple learning by males of two solitary bees (Chapter 4) showed that olfactory information is important in non-social contexts. Similar experiments on males of a eusocial sweat bee showed they also learn information for use in non-social contexts (Wcislo, 1987a). These studies considered together

* The early stages of cooperative evolution blur with parasitism, and it is probably impossible to understand the evolution of one without the other (see Wcislo, 1987a and Wcislo et al., 1988).

suggest a simple hypothesis which may help account for the observation mentioned above that sociality has evolved repeatedly in bees, yet rarely in wasps within Apoidea (Chapters 3 and 4).

CHAPTER 2

COMPARATIVE BIOLOGY OF THE SOCIAL AND SOLITARY SWEAT BEES, LASIOGLOSSUM (DIALICTUS) AENEIVENTRE AND L. (D.) FIGUERESI (HYMENOPTERA: HALICTIDAE)

The life-histories of two closely related Dialictus sweat bees in central Costa Rica are described as the basis for experimental studies (see Chapters 3 and 4), and as a contribution to the comparative biology of Halictidae. Sweat bees (Halictidae) are a socially complex group of mainly ground-nesting bees, and are abundant world-wide. Intra-specific geographic variation in social behavior is prevalent in Halictidae, and is a presumed indicator of environmentally controlled modifications in social behavior. High altitude populations of Lasioglossum (Evyllaesus) calceatum (Scopoli), for example, are solitary while lower ones are eusocial* (Sakagami and Munukata, 1972). Temperate populations of Halictus ligatus Say tend to be eusocial, while subtropical (Packer and Knerer, 1986) and tropical populations (Michener and Bennett, 1977) have less differentiated societies. Within populations, individuals develop diverse

*Terms such as "eusocial," "semisocial," "solitary," etc. are shorthand, and describe the usual level of social organization observed among individuals; nothing is implied about whether the behavior is obligatory or facultative.

social behaviors, depending on local environmental cues, including social ones (e.g., Yanega, 1988, 1989; Packer et al., 1989; Packer, 1990). A weakly-differentiated social organization characterizes many tropical halictines (Eickwort, 1989; Michener et al., 1979), and those at the margins of their ranges in temperate zones (Packer et al., 1989); this organization is similar to the egalitarian colonies of social spiders (Darchen and Delage-Darchen, 1986). The preceding generalizations are often taken loosely as "halictine biogeographic rules," yet are based on studies of remarkably few species.

The subgenus Dialictus of Lasioglossum is a primarily Western Hemispheric group of several hundred species (see Moure and Hurd, 1987), monotonously similar in structure and appearance yet diverse in social behavior. Lasioglossum (Dialictus) figueresi Wcislo is mostly solitary and is structurally very similar to the social L. (D.) aeneiventre (Friese) (Wcislo, 1990 b). The systematic placement of these species relative to other Dialictus is uncertain, but they are not obviously related to recognized species-groups (G.C. Eickwort, pers. comm.). Most nests of L. (D.) figueresi contain a solitary female, and a minority of nests contains 2 or 3 females each; L. (D.) aeneiventre nests usually begin as solitary foundress nests, and most nests develop to eventually contain social groups. Morphological features such as its large size, yellowish wings and pubescence suggest that L. (D.) figueresi is the more derived of the two relative to other Dialictus, and thus may be secondarily solitary; several

behavioral attributes also support this contention. Comparative questions are unresolved until the phylogenetic relationship between these species is better understood. The life-histories and social organizations of these tropical species are compared with those of other Apoidea, and a review suggests a hypothesis concerning rates of development and regressive social evolution in Halictidae.

Unpublished data from nest excavations and dissections of L. (D.) aeneiventre were generously given to me by Dr. Alvaro Wille, professor emeritus, Universidad de Costa Rica, for comparisons with the biology of the L. (D.) figueresi (Wcislo et al., in prep.). W. Wcislo was responsible for the work on L. (D.) figueresi, analyses of data on D. aeneiventre, some brief observations at a small L. (D.) aeneiventre nest aggregation, and preparation of this manuscript.

MATERIALS AND METHODS

Methods were those commonly used in investigations of bee nesting biology (e.g., Michener et al., 1958). Information was collected that provided summaries of individuals' social and sexual behavior, which can be used to infer group-level social behavior (for the rationale and supporting evidence, see Michener, 1974).

Prior to being excavated, nests in horizontal ground were filled with liquid plaster-of-Paris which was allowed to harden; nests in vertical banks were filled with a fine powder such as flour or dry plaster-of-Paris blown

into the tunnel. These methods were used to follow the tunnels through the soil, and thus collect cell contents with their adult and larval populations at various times of the year. Cell contents were placed either in preservatives or in individual chambers of wax or plastic tissue-culture trays covered with moistened filter paper. Data on nest architecture were taken following Sakagami and Michener (1962), and Sakagami and Eickwort (1979); sometimes features were observed with a 10X hand-lens. Nearest-neighbor distances (Clark and Evans, 1954; Simberloff, 1979) between nest entrances were recorded in the field (D. figueresi) or determined from maps in the case of D. aeneiventre for the "Area cafetal".

Adult body size (head width, and for some specimens, length of right forewing from the tegula to the extended wing tip) was measured with an ocular micrometer in a dissecting microscope. Females were dissected to examine and measure ovarian development (length and width of the largest developing oocyte); spermathecae were dissected out, squashed between a clean glass slide and coverslip, and examined under a compound microscope for the presence of a clump of spermatozoa. Dry weights of males and females were obtained as described for Nomia (Chapter 4). An estimate of the amount of work done by individuals was obtained by determining the degree of mandibular wear (see Figure 2.4), because the bees excavate soil with their mandibles. Wing wear was estimated by counting the number of nicks on the edges of the forewings.

Data on provisioning behavior were obtained by observing bees individually marked with paints placed on the thorax (sample sizes given in Tables or Figures). Durations of activities were timed to the nearest second with a watch.

Statistical methods are indicated in the text, and were taken from Sokal and Rohlf (1981), or from Statworks® or Statview® on a Macintosh SE® computer.

Biological observations accompanied by nest excavations of L. aeneiventre were made by Alvaro Wille and Enrique Orozco in March, April, June, and October 1970, October 1982, and February, April, and May 1983, with brief visits at various other times. In December, 1985, with Sr. Orozco, I visited the sites where they studied L. aeneiventre, without finding any bees. I made some brief observations (< 10 hours total over 5 - 10 days) at a small aggregation of this species in December, 1985, before it went extinct.

Observations on L. figueresi were made 2-3 times each week while bees were flying, and weekly or bi-weekly when they were not actively provisioning, for most weeks from 15 January to 20 April 1986 (23 visits); 14 December 1986 to 28 May 1987 (40 visits); 10 December 1987 to 16 January 1988 (22 visits); and 30 May to 2 August 1988 (20 visits). Some of these periods were devoted to experimental studies (see Chapters 3 and 4). At irregular intervals during May - November 1986, Marla Spivak (CIS,

University of Arizona) and Bryan Alvarez Spivak briefly observed the bees and excavated several nests.

Voucher specimens of L. figueresi, associated parasites, cells, turrets, soil and pollen samples are in the Snow Entomological Museum, University of Kansas; specimens of L. aeneiventre with "Coronado" locality data (collected: A. Wille) are also in the same collection.

RESULTS

HABITAT: The study site was in a highly disturbed, heavily populated and intensely cultivated area near San José, San José Province, Costa Rica. Many halictine bees are "weedy," and live in disturbed habitat. The sprawling urban areas of the Meseta Central region were once "Tropical Premontane Moist Forest" (Holdridgian life zones), but today only remnants of that forest are extant in otherwise agricultural areas on the slopes of the surrounding mountains. In these rural areas there are many trails and earthen roads cut through hillsides, creating endless stretches of substrate for ground-nesting bees and wasps.

The cantons of Coronado and Escazú (~1100 m elevation each) overlook the capital city of San José, facing each other from opposite slopes of the Cordillera Central, northeast and southwest, respectively, nearly 20 km apart. The climate and seasonal phenology of plants seemed similar on both slopes, although I did not make a detailed study; in general, Coronado is slightly cooler and wetter than Escazú (W.G. Eberhard, pers.

comm.). The dry season begins in late November or December, and lasts through April or May when the rains begin. The rainy season continues through November, with a brief period (veranillo) of reduced rainfall in August (see Figure 2.6; also Coen, 1983).

Lasioglossum (Dialictus) figueresi

NEST SITES: Lasioglossum figueresi usually nested within aggregations, which are abundant at higher elevations (>1100 m) in mixed residential-agricultural areas southwest of San José. Nest sites can be found by searching the banks (Figure 2.1) for conspicuous turrets (Figure 2.2) while walking trails or earthen roads, in various compass directions, in the Cerros de Escazú. One small aggregation was observed near Puriscal. Another small aggregation of what appeared to be this bee was found near Cartago (Cartago Province) (W.G. Eberhard, pers. comm.). Turrets and old nests which were very similar to those of L. figueresi were found at ~1400 m on the road to Volcán Poas, and near Coronado. Among 17 drawers (> 5,000 specimens) of undetermined Mexican, Central and South American Dialictus in the Snow Entomological Museum there was a single specimen of L. (D.) figueresi [label data: Costa Rica, San Antonio de Escazú, 3 Dic. 1959, A. Wille].

I visited the following sites briefly, specifically looking for nests of ground-nesting bees, and collecting adult bees on flowers (deposited in the Snow Entomological Museum). These locality data are intended only to

indicate that the bee is not abundant and widespread. I never collected L. figueresi at various sites in both preserved or disturbed habitats at lower elevations (< 1000 m) in San José Province or on any of the surrounding volcanoes (except as above), various sites in Alajuela Province, near Turrialba (CATIE and vicinity), Tapantí and Orosí areas, agricultural areas near San Isidro de El General or at higher elevations toward Cerro del Muerte; on the Pacific Coast, Carrera Reserva Biológica through the Quepos and Damitas areas; northern Punteranas and various sites in Guanacaste; mid-elevations near Monte Verde; Parque Nacional Braulio Carrillo, including an elevational transect ("La Zona") from near the summit of Volcán Barva (~2600 m) to the Atlantic lowlands near Puerto Viejo; and areas near Limón, and Cahuita.

At all sites where bees nested there were fence posts, shrubs, and trees along the tops of the banks where they bordered fields. The majority of the observations on natural history were made at the following sites:

Near site (Figure 2.1): Several hundred bees nested in a west-facing vertical bank of an earthen road passing through cultivated land (coffee, corn, sugar cane, beans, etc.) at about 1450 m elevation, approximately 2 km southeast of San Antonio de Escazú, San José Province (9° 56'N, 84°21'W). A very old local farmer told me these bees had been nesting at this site for many years.

Station 9: Bees nested in a north-facing vertical earthen bank on the

first side trail about 300 m south of the religious shrine «IX ESTACION Jesús Cae por Tercera Vez» on the way to «La CRUZ», which is on the summit of Cerro San Miguel. This aggregation (elevation = ~1600 m) is approximately 1.5 km southeast of Near site, and is surrounded by coffee trees and open pasture. This site is heavily shaded by cypress evergreens (Cupressaceae). In 1985 this aggregation was thriving (> 300 active nests), and by 1988 it was nearly extinct (2 active nests out of ~35 rapidly excavated nests; the remainder were obviously old, abandoned nests). The vegetation had become much thicker, and it seems likely that the site had become less suitable due to the increased shade.

Nice view: Bees nested in both east- and west-facing banks (elevation: 1700 m) on a trail approximately 3 km due south (uphill) of a school-house, Escuela Carmen, which is several km southwest of San Antonio de Escazú. The area surrounding this nest site is open pasture, with pockets of woods on the steep slopes and bordering trails.

NESTS: Females usually nested within aggregations, although rarely isolated nests can be found from 50 m to several km from the nearest aggregation. Nests are clustered within aggregations, such that sometimes two or three turrets actually fused one to another (Figure 2.2). The distribution of nests within aggregations suggests some gregarious tendencies since nests are, on average, separated from their neighbors by about half the distance expected under randomness ($R = 0.5$, $r_A = 6.9$, $c = 2$, n

= 58) ($0.01 < p < 0.05$) [Clark and Evans (1954); Simberloff's (1979) correction is not necessary since the nest entrance diameter (0.3 to 0.4 cm) is much less than $\{1/2 \cdot (\text{expected mean NND})\}$].

Nests were conspicuous due to the 4 - 28 mm ($\bar{x} = 6.4 \pm 4.1$ mm) earthen turrets usually projecting from the entrances on the vertical bank (Figure 2.2). Nest architectural features otherwise did not differ in qualitative ways from those of other Dialictus, and were of the type O(Ch-ⁿB (subtype IIIB of Sakagami and Michener, 1962); for values of n, see below^{**}. Turrets were constricted at the entrances, having inner diameters from 2.7 to 3.4 mm ($\bar{x} = 3.0 \pm 0.3$ mm, $n = 42$); the outer diameter ranges from 4.1 - 6.0 mm ($\bar{x} = 5.2 \pm 0.5$, $n = 42$). Turrets were more or less parallel sided, with the walls gradually thickening at the bases^{***}. Each turret consisted of numerous small balls of mud, visible as rough bumps on the exterior surface, while the interior surface is smoother and the outlines of the bumps are obscured. The inner surface, however, was neither totally

^{**}Letters represent structures which are produced by complex behaviors: O=main burrow; Ch=horizontal cell; Ci= slightly inclined cell; and B= blind burrow. The superscripts give the number of iterations (see Sakagami and Michener, 1962).

^{***}An unusual turret incorporated an entire leaf into its structure. A leaf had blocked the entrance to a short turret, and the bee made a hole in the blade, and then extended the turret several mm; this specimen is in the Snow Entomological Museum.

smoothed nor polished, and there were no obvious signs of secretions such as can be seen in the cell-linings, or turret linings of some other halictids. Turrets were constructed at night during the beginning of the active season. Females carried soil from within the nest, and then tamped it into place with the apices of their abdomens. Turrets were sometimes replaced or repaired if damaged, but only when the soil was still moist and malleable [see Hicks (1931) for similar behavior in Augochlorella striata]. L. figueresi females did not add a constriction to the burrow entrance after a turret had been removed, or when it was damaged, unlike other halictine bees (Sakagami and Michener, 1962).

The inner diameter of the turret gradually increased until it joined the bank. Beyond the surface of the bank the tunnel diameter ranged from 4.1 to 6.0 mm ($\bar{x} = 5.2 \text{ cm} \pm 0.05$, $n = 42$), and did not change as the burrow went deeper into the bank. The first cells were 2 to 11 cm beyond the surface at three sites, based on nests excavated in February, 1986 [Near: $\bar{x} = 5.1 \text{ cm} \pm 2.35$ (s.d.), $n = 12$; Station 9: $\bar{x} = 5.9 \text{ cm} \pm 2.9$ (s.d.), $n = 12$; Nice: $\bar{x} = 5.5 \text{ cm} \pm 2.37$ (s.d.), $n = 12$]. Nest burrows were nearly perpendicular or slightly sloped downward with respect to the surface with some slight meanderings, and extended up to 24 cm into the bank. Mean maximum burrow depth at Near was $11.9 \text{ cm} \pm 5.28$ (s.d.) ($n = 12$); Station 9, $\bar{x} = 15.4 \text{ cm} \pm 4.6$ (s.d.) ($n = 12$); Nice, $\bar{x} = 16.4 \text{ cm} \pm 5.2$ ($n = 12$).

Cells had the usual shape for those of Halictini (Figure 2.3), and

were ~10 to 11 mm long, 4 to 5.5 mm in diameter at the widest part, tapering to 2 to 3 mm at the collar, and were lined with a thin wax-like layer. Plugs consisted of ~2 to 4 mm of packed soil (arrow, Figure 2.3; also Figure 2.5). Usually cells were joined to the main tunnel without lateral tunnels, although rarely there were laterals up to 10 mm long, which were filled in with packed soil. The long axes of cells sloped slightly ($< 10^\circ$) downward from the entrances. Old cells with feces usually were not re-used, and were sometimes partially filled with soil. Feces were deposited by the larva on the upper rear wall of the cell. In one case (partially shaded cell in Figure 2.5 G) a cell contained both old dried feces, and a fresh partially eaten pollen ball with a third-instar larva, showing that it was re-used. Several to many cells were built early in a nest's ontogeny, unlike some other halictines, so that very young nests might have up to several open, empty cells; older mature nests likewise contained open, empty cells (e.g., Figure 2.5 M).

SEASONAL CYCLE: In Lasioglossum figueresi the majority of nests were occupied by a single female and her immature offspring (below). A schematic representation of the life-cycle is given in Figure 2.6. During a brief dry period from late June to July females emerged from the nests, mated, and then established a nest. Most females established new nests, while the others ($<10\%$) re-used old nests. Some females provisioned a few cells during brief periods of favorable weather in July through

September, but during October and most of November the heavy rains resulted in the cessation of activity. At the start of the dry season in late November to early December, females began to extend burrows and construct cells. Most of these nests were re-activated from the previous July - September, as shown by the occurrence of up to several old cells containing dried feces. Bees provisioned cells with pollen until mid-February when provisioning ceased. After this time adult females usually did not leave nests to forage. This behavior is reported for many spring foundresses of seasonal social halictids (see Discussion). L. figueresi adult females, however, became senescent and died. No marked bees (n = 143) were ever recovered in a second year. Nests excavated through late February typically contained worn adult females, while those excavated after this time were increasingly likely to contain dead, dried females.

The brood develop continuously throughout the provisioning phase. Development continues until the end of April when young eclose in the nest as callow adults (Figure 2.7). At this time the soil is hard and dry, and it is probably difficult for bees to establish nests (although nearby several newly established nests of a small Dialictus were discovered). Young adults of L. figueresi remain in their nests until mid-June (pre-reproductive assemblages), when both males and females emerge and mate (see Chapter 4). Callow females taken from different nests in April did not have sperm in their spermathecae (N = 10).

Data on nest survivorship unfortunately were not collected. A crude indirect estimate comes from considering the percentages of excavated nests that contained adult females. Considering only nests that were excavated after daily bee activity had ceased, the percentages of nests with living females were 83%, 69%, 25%, 35%, and 25%, respectively, for December (1987), January (1986, 1987), February (1986, 1987), March (1986, 1987), and April (1986).

LARVAL DEVELOPMENT: The durations of developmental stages for L. figueresi are given in Figure 2.7. Partly due to their long developmental time, immature stages were not successfully reared in the laboratory.

Extrapolating from these data, given the phenology of nests in Figure 2.6, the estimated total duration of the egg to adult developmental rate is ~80 days. This span is larger than in other halictine bees (Table 2.1)^{****}, although the causal reasons are unclear (see Discussion). Of special interest is the seasonal synchrony among aggregations: nests at various aggregations were at comparable developmental stages, with a slight lag time at higher elevations. Eggs were found only at the very beginning of the nesting season, and by mid-April nearly all of the brood were callow

^{****}Doug Yanega independently had been compiling data on developmental rates in halictine bees. The table given here has been incorporated into Yanega's table (ms.), and so will not be re-produced in Wcislo et al. (in prep.).

adults in their cells.

Data on pupal sex ratio are given in Figure 2.8. The number of female pupae per nest ranged from 0 - 8 [$\bar{x} = 2.76 \pm 2.39$ (S.D.), $N = 25$], and the number of male pupae ranged from 0 - 6 [$\bar{x} = 2.24 \pm 1.67$, $N = 25$] ($p > 0.4$, Mann Whitney U-test). The average sex ratio (number males/total) was 0.48 (S.D. = 0.29). The mean dry weight of females ($\bar{x} = 7.25$ mg, SD = 2.38, $N = 8$) was slightly greater than that of males ($\bar{x} = 5.41$ mg, SD = 1.73, $N = 12$) ($p = 0.06$, $t_s = -2.00$).

DIEL ACTIVITY: L. figueresi has a diel activity pattern similar to that of L. aeneiventre, although females tended to begin foraging later in the day, between 8:00 and 9:00. Moreover, bees were skittish and easily disturbed. A histogram of the number of bees returning with pollen throughout the day, along with data for L. aeneiventre, is given in Figure 2.9 (pollen trip durations pooled over January and February, 1986). Foraging trip durations were 7 to 46 minutes [$\bar{x} = 28.4 \pm 7.1$ (s.d.), $n = 62$]; they were usually making 1 to 5 trips per day when weather was favorable (data from January, 1987) (Figure 2.10). Bees generally began flying when the air temperature exceeded 20 to 21°C, and often required long periods of time at the nest entrance (up to 14 minutes) before leaving the nest to forage. In the morning (8:00 to 9:30) bees were commonly observed half-way out of the nest, presumably warming up flight muscles, as occurs in L. (D.) aeneiventre. Bees that were captured while they were in nest entrances

had thoracic temperatures which ranged from 27 to 30.5 °C [$\bar{x} = 29.4 \pm 1.41$ (S.D.), $n = 5$], as measured with a thermocouple probe inserted into the thorax. After ~ 30 secs of flight in a net, the temperature increased to 34.0°C (S.D. = 1.43, $N = 4$).

Pollen from pollen balls consisted mainly of Melampodium divaricatum (Asteraceae), as well as Croton bilbergianus (Euphorbiaceae), Solanum? (Solanaceae), and an unknown Compositae sp. (D. Roubik, in litt.); another sample contained pollen from at least two different kinds of Asteraceae. L. figueresi represents the first record of a halictid bee on Melampodium (Moure and Hurd, 1987). Pollen balls ranged from 15 to 48.5 mg (dry weight after drying to a constant weight at 50°C) [$\bar{x} = 30.7 \pm 10.2$ (s.d.), $n = 12$].

SOCIAL BEHAVIOR: Since most L. figueresi females are solitary, they display little social behavior, other than for mating or tending a nest. Adult females are unimodal in size, with a mean headwidth of 2.3 ± 0.09 (S.D.) ($N = 93$, C.V. = 4.196), and there are no obvious seasonal size differences among females throughout the year, based on reared females (Figure 2.11).

The percentages of nests with 2 females during the provisioning phase for the various years ranged from 9 to 21% (Table 2.2), and did not differ significantly between years or localities. Fewer two-female nests, however, were found in August. Solitary bees [$\bar{x} = 2.4 \pm 0.22$ (S.D.), $N = 20$]

were not larger than females from two-female nests [$\bar{x} = 2.32 \pm 0.13$ (S.D.), $N = 14$]; among the latter, mated females ($\bar{x} = 2.312 \pm 0.14$, $N = 11$) were the same size as unmated ones ($\bar{x} = 2.36 \pm 0.115$, $N = 3$). I examined the spermathecae of both females in seven 2-female nests: in 4 pairs both females were mated, and in 3 pairs one female was mated and one was not (among the latter, there were insignificant size differences).

Based on mature nests excavated after provisioning ceased in February, 1986, the number of cells per nest for single-female nests ranged from 0 - 14 [$\bar{x} = 8.9 \pm 3.37$ (S.), $N = 24$, "Near site"], while nests known to have 2 females contained up to 24 cells (see Figure 2.12). Two-female nests had a greater number of cells per nest [$\bar{x} = 11.6 \pm 8.24$ (S.D.), $N = 6$] than known one-female nests, but the difference was not significant.

NATURAL ENEMIES OR ASSOCIATES: The principal natural enemy of L. figueresi at all aggregations was the phorid fly, Phalacrotophora halictorum (Melander & Brues) [details of the parasitic and courtship behavior of this fly are given in Wcislo (in press)]. At one site ("Nice view," 1987/1988), approximately 16% of 171 cells from 25 nests were destroyed by these fly larvae. As with L. aeneiventre, many cells contained fungi, but again it is usually not clear whether a fungus is the agent of morbidity, or whether it represents a secondary invasion. Other associated natural enemies were an undetermined species of Conopidae (Diptera) (one female had a conopid larva in its abdomen), Sphecodes sp.

(Hymenoptera: Halictidae) (one adult ♀ collected, no immatures), and an undetermined Mutillidae wasp (larvae were collected in three cells, but were not successfully reared). At all sites ants were remarkably absent, and were rarely observed doing great damage. Occasionally during nest excavations a bee's tunnel became an ant nest, so the bee's cells were probably destroyed by scavenging ants. Based only on mature nests with known numbers of adult females, single-female nests had 21% (S.D. = 0.231, N = 34 nests) of all cell contents destroyed, while two-female nests had 20% destruction (S.D. = 0.117, N = 8 nests) (pooled from mid-February-April, 1985- 1987).

Lasioglossum (Dialictus) aeneiventre (Friese)

NEST SITES: Several aggregations of L. aeneiventre were observed on a farm approximately 1 km west of San Antonio de Coronado, San José Province (9°59' N, 84°00' W, elevation = ~1380 m):

Area cafetal: Bees nested in an aggregation in flat to gently sloping (<10°) bare earth within a clearing with sparse to no surface vegetation in a field of coffee (Cafe) plants.

Area casa: Bees nested in an aggregation in flat to gently sloping bare earth in an area free of vegetation near a home. This site was approximately 100 m from Area cafetal.

Area desagüe: Bees nested in flat or sloping (45° angle) ground near a drainage ditch in a field.

Iglesia: An aggregation of L. aeneiventre was briefly studied by WTW in 1985 in an earthen bank (elevation = ~1300 m) approximately 3 km south of the Iglesia de San Isidro de Coronado, ~ 2 km from the above sites. Bees nested in a 1 X 3 m section of a nearly vertical, earthen, south-facing, and fully-exposed 2 m tall bank along the drainage ditch beside a paved road in a residential area. The nests seemed to be uniformly distributed over the surface of the bank (NND data not collected); the bank was sparsely covered with grasses, dandelions, and lichens.

These observations show for L. aeneiventre the lack of a strict requirement for substrate orientation, as is known for other Dialictus (Sakagami and Michener, 1962), including L. figueresi.

NESTS: Females nested mainly in horizontal ground, but occasionally in vertical banks (above). Nests were observed clumped together in aggregations, but within one aggregation (Area cafetal) the distribution of nests did not differ significantly from random [$r_A = 19.71$, $R = 0.9$, $c = 0.87$, $n = 21$ nests, $p > 0.5$].

The entrances to active nests on flat ground were frequently surrounded by a symmetrical mound of earth (tumulus) piled around each entrance. These usually wash away after rains, and the nest entrance constrictions were repaired. On horizontal ground nests entered the soil at a 90° angle, and continued downward, usually with only slight meanderings. Mature nests sometimes contained branches of the main

tunnel, beginning at 12 to 20 cm depth. Cells were found beginning at ca. 4 cm below the surface. A summary of nest characteristics is given in Table 2.3, and representative examples are illustrated in Figure 2.13. Features of nest architecture did not differ appreciably from those of other Dialictus (refs. above). Nests were of the type O(Ch-i)ⁿB (subtype IIIb, of Sakagami and Michener, 1962). Cells were of the usual halictine shape, 10 to 12 mm long, 3 to 4 mm in diameter at the widest part, and tapered to 2 mm at the collar that was sealed with a 2 mm plug. Cells usually were connected to the main tunnel without laterals. Cells apparently were not re-used, since old cells with feces were filled with soil, while others were simply closed off. At least young nests in vertical banks are similar to those described above, except that tumuli do not accumulate around nest entrances, which are flush with the bank. The burrow is perpendicular to the vertical bank, and extended 10 to 18 cm into the bank.

Pollen is mixed with nectar and formed into a pollen loaf (~ 3 X 4 X 3 mm. An index of the amount of pollen stored was estimated by multiplying the L X W X H for pollen balls, and is given in Figure 2.14. Pollen balls in late March are larger than those from mid-February, but the differences are not significant ($p > 0.5$, Mann Whitney U-test). In multi-female nests cells are cooperatively provisioned, since returning foragers marked with different colors of powder, deposited their different colored powders into the same cell. Furthermore, nests in which several females

were pollen collectors had only a single partially provisioned cell.

Eggs are placed on the top of the pollen loaf, and measure 0.49 ± 0.05 in width at the anterior end, 0.325 ± 0.034 in width at the posterior end, and 1.97 ± 0.106 in length ($n = 13$).

SEASONAL CYCLE: Lasioglossum aeneiventre is a eusocial species with up to several broods per year. It is active nearly year-round, except for October and November when strong rains result in nests being temporarily closed (Figure 2.6).

Recently active nests with a single female each were abundant at the beginning of the dry season in late November, December, and January. The foundresses had mainly unworn wings and mandibles, and their nests were typically shallow burrows with few or no cells (Table 2.3). Some nests were re-activated from the previous season as shown by cells with dried fecal material (3 of 6 nests in October; 11 of 13 nests in February, before brood began to emerge). In each re-activated multi-female nest, there was usually one female with greatly worn wings and mandibles, while the other females were mainly unworn (5 of 6 nests for February). The worn females evidently were survivors from the previous generation. In the dry season nests were gradually enlarged until they contained up to 66 cells and 12 females by the end of the dry season in May. These large colonies became senescent and died at the end of the dry season. A small number of new nests were established throughout the dry

season (Figure 2.17) by unworn, presumably recently emerged, bees.

New nests without or with few cells were again abundant in April - June (e.g., Figure 2.13 B), and followed a cycle similar to that described above for the first generation. The brood produced from these nests emerged in September and became foundresses. In September and October, 5 of 8 nests consisted of only tunnels, and the others contained a few (<3) cells. Females were largely inactive, although they collected pollen and provisioned cells during infrequent brief periods of favorable weather (2 of 6 nests with ≥ 1 pollen ball each). These females probably survived until January; their offspring emerged and either initiated new nests at the start of the dry season, or became workers or replacement queens.

LARVAL AND COLONY DEVELOPMENT: The seasonal development of nests is summarized in Figure 2.15. Newly constructed empty cells, as well as those with pollen balls and eggs, were found at all times throughout the year when observations were made. There was general synchrony in life-cycles within the favorable periods, although some nests were out-of-phase.

On the basis of periodic nest excavations, coupled with rearing in the laboratory in January, the durations of the various life history stages are given in Table 2.4. The total duration for egg to adult development is ca. 35 days, comparable to that for other halictines (see Table 2.1), and quite different from that of L. figueresi.

MALES: Males were found throughout the active cycle. Male pupae were present in the first brood to emerge in late February, and were observed in nests whenever female pupae were collected. The seasonal abundance of males was not quantified, although males seemed more abundant in April. Data on sex ratio are anecdotal: a large nest (40 cells with 10 adult ♀♀) excavated on 6 April contained 11 ♂♂ and 3 ♀♀ pupae (younger stages were not sexed); a nest (27 cells and 7 adult ♀♀) excavated on 1 March had 2 ♂ pupae and 1 ♀ pupa.

Details of mating were not recorded at the cafetal site. At the vertical bank males flew in a manner similar to other Dialictus (e.g., Wcislo, 1987b), but mating was not observed. Throughout the year roughly half of the females in a nest, on average, are mated and half are not (Figure 2.16), again suggesting that at least some males are present at all seasons.

DIEL ACTIVITY: The diel foraging activity of female bees began between 7:30 and 8:00 on clear or partly cloudy days, and continued until 14:30 or 15:00 (see Figure 2.9). Most of the pollen foraging was concentrated in mid-morning hours. In general, flight activity began when the air temperature exceeded 18°C. During periods of inclement weather (rain or very low misty clouds), the bees were not active outside the nest. Bees departing from the nest often lingered for long periods, partly out of the entrances,

presumably warming up, as did L. (D.) figueresi. When active, bees foraged for pollen and nectar, and concentrated their foraging in the first half of the day. The pollen that bees used was not identified, although at least two colors of pollen were recorded, suggesting that these bees use a variety of floral resources, as do other Lasioglossum (Moure and Hurd, 1987).

SOCIAL BEHAVIOR: The most complex social development in L. aeneiventre is "primitively eusocial" (see Michener, 1974; Wilson, 1971), but many life-history details need to be studied. Nests founded by single females at the beginning of the dry season (or in late October followed by a brief quiescent period) produced offspring which emerged throughout late January and February. Some remained in the nest, did or did not mate, and became workers, replacement queens, or auxiliary queens. Other females left their natal nests to initiate new nests as foundresses (see Michener, 1990 for terminology). The proportion of solitary nests increased throughout the dry season (Figure 2.17), but small sample sizes in June and October preclude statistical analyses. Solitary foundresses usually had sperm in their spermathecae: 35 of 47 foundresses were mated ($X^2_{ADJ} = 10.29$; $p \ll 0.05$), and had oocytes beginning to develop.

For a study of seasonal or caste differences in size, females were grouped as solitary; group-living with sperm; and group-living without sperm (Figure 2.18). Solitary females are larger (headwidth: $\bar{x} = 2.02 \pm 0.13$ mm, $n = 43$) than females in multi-female nests ($p < 0.0001$, $t = 4.362$, $df =$

232), regardless of whether the latter are mated (headwidth: $\bar{x} = 1.93 \pm 0.12$ mm, $n = 85$) or not ($\bar{x} = 1.92 \pm 0.13$ mm, $n = 109$) ($p > 0.5$, $t = 0.603$, $df = 196$). The majority of solitary females were taken in April and May, with a few in October. Within multi-female nests females with sperm are not larger than females without sperm. Females in multi-female nests were more likely to have unworn wings and lack pollen in the crop if not mated than if mated (Table 2.5; G-test, $p < 0.001$), presumably because recently emerged females were included in the samples.

There is no positive relationship between size and degree of ovarian development. For multifemale nests with dissection data for all individuals, the female with the most developed ovaries was the largest bee in 6 nests, tied for largest in 4 nests, and was smaller than a nest-mate in 15 nests. Large-ovariole bees (\bar{x} headwidth = 1.97 mm [SD = 0.9, $n = 12$] [March]; 1.95 mm [SD = 0.11, $n = 11$] [April], and 1.76 mm [SD = 0.16, $n = 2$] [May]) did not have a larger headwidth than the other bees in their nests ($\bar{x} = 1.9$ [SD = 0.123, $n = 60$] [March]; 1.9 [SD = 0.127] [April]; 2.02 [SD = 0.153] [May]) (test statistics for March and April respectively, are $t_s = 1.225$ [$df = 70$], $p = 0.225$; and 1.147, $p = 0.255$).

Large solitary females each first produced a brood of smaller females. As seen in Figure 2.19, the size of the females produced did not change significantly throughout the dry season, until late April and May when the emerging females were as large as the solitary females, including

those taken in October. Similar seasonal size variation is known in temperate species of eusocial halictid bees (Batra, 1966; Michener, 1974, 1990). Females living as solitary foundresses had a headwidth range of 1.7 to 2.5 mm [$\bar{x} = 2.02 \pm 0.132$ (S.D.), C.V. = 6.55, N = 43]. By comparison, females in multifemale nests were not significantly smaller, and ranged in size from 1.6 - 2.3 mm [$\bar{x} = 1.92 \pm 0.125$ (S.D.), C.V. = 6.495, N = 191 ($p > 0.5$, Mann Whitney U-test)].

For 49 nests (pooled from all sample dates) the number of females per nest ranged from 0 to 14 ($\bar{x} = 2.677$). The number of cells per nest was 0 to 81 ($\bar{x} = 13.5 \pm 1.744$) (S.E.). Nests with more females usually had more total cells (Spearman's $r_s = 0.77$ ($p < 0.0001$)). After excluding old cells with feces, the correlation between the number of active cells per female and the number of females in the nest is significant ($r_s = 0.49$, $p < 0.001$), suggesting groups might be slightly more efficient at building and provisioning cells than solitary females.

Data on ovarian development for the three groups are given in Figure 2.20. Solitary females tended to be larger, with sperm in the spermathecae, yet tended to have undeveloped ovaries, probably because many were collected in October and April when the bees were either inactive, or activity was just beginning. The length of the longest oocytes in solitary females ($\bar{x} = 0.69 \pm 0.52$, $n = 47$) was not significantly different than the corresponding length from un-mated group-living females ($\bar{x} =$

0.37 \pm 0.33, n = 120 (p > 0.4, Mann Whitney U-test); both groups had oocytes that were shorter than mated group-living females (\bar{x} = 1.28 \pm 0.42, n = 85), which were the reproductively dominant females.

NATURAL ENEMIES: Natural enemies of L. aeneiventre were incidentally studied. Of 930 active cells, 4.5% (42 cells in 21 of 97 nests) were destroyed due to usually unspecified morbidity factors. During excavations fly larvae (Diptera) were periodically collected. One larva was found internally in a dead bee and was probably Conopidae. Two adult females were parasitized by a Strepsiptera. One cell contained nematodes. The majority of the destroyed immatures were filled with mold and fungi, but it is unknown if the fungi killed the bees, or secondarily invaded the cells. No other parasites or predators were recorded at the sites. An analysis of rates of mortality by month reveals no seasonal effects, but the sample size is too small for meaningful conclusions. I observed female parasitic flies, Phalacrotophora sp. (Diptera: Phoridae), flying at the vertical nest site, but they were not abundant. In 6 cases (in June and October) marked females entered nests which were being used by other bees at the time, and usurped the nest tunnels, and were later seen entering the nests with pollen.

DISCUSSION

There are few ethological and ecological studies of solitary L. (Dialictus), yet knowledge of their behavior is critical for understanding

social evolution in these bees (cf. Michener, 1990). L. (D). figueresi is a mainly solitary bee, and most females are mated and have developed ovarioles. Nearly all females construct a nest, although some re-use old nests. Approximately 10 - 20% of all nests contain 2 females (one nest had 3 females) during the provisioning phase. By contrast, a series of nest excavations of L. aeneiventre showed that the social organization includes solitary foundress nests, monogynous nests with few or many workers, as well as large or small polygynous nests. A comparison of ethological attributes related to social behavior for two species of sweat bees reveals a high degree of behavioral uniformity, except for a few unusual features. These features are considered below as they relate to the possible advantages and disadvantages associated with group-living.

Ethological comparisons

A list of attributes related to social behavior (modified from Michener, 1974) and nest architecture is given in Table 6****, with character states for L. figueresi and L. aeneiventre.

Nest architecture:

Features of nest architecture are generally not related to social evolution (Sakagami and Michener, 1962; but see Eickwort and Kukuk,

****It would be useful for other biologists studying the ethology of Apoidea to present summaries in a standard format to facilitate systematic comparisons as the data base increases.

1986 for a different view), and are similar for these two species (see Table 6). Among differences are construction of nest turrets, re-use of old cells, and digging >1 cell early in the season prior to using all of them by female L. (D.) figueresi. These features are rare in other Dialictus and Halictinae (Michener and Seabra, 1959; Sakagami and Michener, 1962; Sakagami and Moure, 1967). Tepedino et al. (1979) show how empty cells in mud nests of wasps can theoretically reduce rates of parasitism due to hole-searching parasites.

Social organization:

The social organizations of L. figueresi and L. aeneiventre varies among nests. Some nests have a weakly differentiated social organization and some nests are more structured (i.e., distinct workers and queens). In many nests of L. aeneiventre several or most females have well-developed ovaries and are mated. Other nests are more hierarchical in their social organization. Nests of L. aeneiventre with two bees usually (88%) contained one mated and one unmated female, while the corresponding figure for two-bee nests of L. figueresi is 50%. As discussed below, there are no discernible ecological correlates with either class of behavior within populations.

Costs and benefits of social behavior

For the mostly solitary D. figueresi the mean number of active cells per female was not different for solitary females as compared with bees in

2-female nests (see Michener, 1964; Schwarz, in prep.; Wenzel and Pickering, 1991 for some other primitively social insects). Rates of parasitism did not vary greatly for either solitary or social nests. Within a population, on the basis of productivity and rates of parasitism, solitary females do as well, on average, as do average group-living females. Energetic savings relating to nest excavations are probably not substantial, since cells and new burrows are dug only when the soil is moist and workable. A smaller proportion (~5%) of the offspring of the social species, L. aeneiventre, were destroyed by natural enemies, while for the solitary L. figueresi the corresponding figure is ~20%. This finding suggests social benefits due to mutualism (Lin and Michener, 1972), but data are not comparable since they are not from the same population.

An important advantage to group-living females involves "assured fitness returns", which vary with the length of the time period that young are dependent on adults for survival (Gadagkar, 1990 b). These social benefits are undoubtedly lower for mass-provisioning animals than for progressive provisioners. Species such as L. figueresi probably gain little from this mechanism (although some benefit is obviously better than none): the period of dependency lasts from the beginning of cell construction to final closure, which is relatively brief, on the order of 1 or 2 days (e.g., Wille and Orozco, 1970; Danforth, 1989). This low value is very near the threshold in Gadagkar's (1990 b) model for any assured

fitness returns.

The evolution of solitary behavior?

Temporal patterns of the life-cycle of D. figueresi were unusual for solitary bees, and probably are not related to seasonal patterns of resource availability. Adult L. figueresi females behave in ways reminiscent of spring gynes of temperate eusocial halictine species (refs. in Michener, 1990), or like gynes of some seasonally active neotropical species (e.g., Wille and Orozco, 1970). A temperate-zone gyne emerges in the spring, provisions several cells (~4 - 8), and waits inside her nest for brood to emerge; she dominates them and they become her workers (or replacement gynes). In like manner, female D. figueresi begin excavating nests at the start of the dry season, and provision cells; then they quit provisioning in the middle of the dry season (at a time when other Dialictus and many other bees are flying). Female D. figueresi continue to wait, perhaps effectively functioning to protect the brood against enemies, and occasionally forage, until they die. Meanwhile, the larvae develop into pupae and eventually eclose, beginning in mid-April, but they remain as adults inside the open cells for long periods of time. There is excellent synchronization of activity among individuals within and among aggregations of D. figueresi (for another halictid, see Michener and Lange, 1958a), and in contrast to species such as D. aeneiventre (also Michener and Lange, 1958b).

The proximate mechanism underlying the slow egg-to-adult development time is not known. A more usual range of developmental durations for halictines is 20 to 35 days, similar to those of D. aeneiventre. There is some inter-specific variability in estimates of development times (Table 2.2), and intra-specifically these vary with temperature and other factors. Temperatures near the D. aeneiventre localities (Coronado) tend to be either slightly cooler or similar to temperatures at localities of D. figueresi, so it is unlikely that low temperatures explain the slow development of the latter. Some other bees with long egg to adult durations include various allodapine bees (Michener, 1971)-- their larvae are fed progressively, and their developmental rates more directly depend on levels of parental activity. [These bees are the only lineage besides Halictidae with species which appear to have lost social behavior.]

L. figueresi use pollen from several plant species, although a major source of pollen is Melampodium (Asteraceae), which is locally abundant. No other halictids have been recorded from this plant (Moure and Hurd, 1987), and it is possible but unlikely that nutritional considerations account for the slow developmental rate. Another bee, Pseudopanurgus aethiops (Andrenidae), has been collected on Melampodium (Krombein et al., 1979), but little is known of its biology.

In general terms "caste determination" may be in part a consequence of parent-offspring conflict (Trivers, 1974). Parents, being

older and usually larger, in some instances may "win" the conflict. In many bees the oldest individual in the nest is reproductively dominant (e.g., Schwarz and O'Keefe, in press; Michener, 1990). Daughters or younger relatives then behave as workers because maternal effects (parental manipulation) leave them disadvantaged for independent living, and this choice maximizes their inclusive fitness. This line of reasoning is used in some hypotheses to explain "helping" behavior by reproductively competent, but functionally sterile, adults (Michener and Brothers, 1974; Alexander, 1974). Halictid bees are mass-provisioners, so after several foraging trips a female provides all the food a developing offspring requires, and the bee needs no further care. A larva cannot directly contest her mother. As an adult, especially if she is small due to a small cache of pollen, a daughter is unlikely to defeat her older, already territorial, mother. An extremely retarded development, however, allows an offspring female to win the conflict, if development is slow enough that the mother dies, or is substantially weakened by senescence. This hypothetical mechanism might explain some secondary origins of solitary behavior in mass provisioned bees, if seasonal resource adaptation can be ruled out.

ACKNOWLEDGEMENTS

I thank the following for their help in various aspects of this study. Alvaro Wille and Enrique Orozco kindly showed me various localities

where they had previously found halictid aggregations, and they generously provided other assistance. William Eberhard and Mary Jane West-Eberhard helped immensely with material and intellectual assistance, and much of this study would have been impossible without their generous help, including help from their children, Andrés, Anna, and Jessica Eberhard. Marla Spivak helped with ideas, assistance in field studies, and in numerous other ways; Bryan Alvarez Spivak sometimes helped with field studies. Orley Taylor loaned a thermistor and thermocouple probe for recording thoracic temperatures. For constructive criticisms on the manuscript or for especially helpful discussions I thank Jeanne Altmann, W. Bell, W. Eberhard, R. Jander, R.L. Minckley, Laurence Packer, M. Spivak, John Wenzel, M.J. West-Eberhard, and especially C.D. Michener.

Financial assistance is gratefully acknowledged from the P.L. Stouse Memorial Scholarship Fund, Department of Geography, University of Kansas (1985 and 1988); a Sigma Xi Grant-in-aid of Graduate Research; the Theodore Roosevelt Fund of the American Museum of Natural History; a Short-term Fellowship from the Smithsonian Tropical Research Institute; a U.S.A. National Science Foundation grant BNS 82-00651 (C.D. Michener, P.I.); U.S.A. National Science Foundation Doctoral Dissertation Improvement Grant (BNS 87-01046); the University of Kansas Graduate College Travel Fund; a University of Kansas Summer Fellowship; and a

University of Kansas Dissertation Fellowship that was generously supplemented by the H.B. Hungerford Fund, Department of Entomology, University of Kansas.

Figure 2.1. Mandible of female Lasioglossum aeneiventre, showing indices of mandibular wear, an indicator of the amount of nest-building work done by a bee.

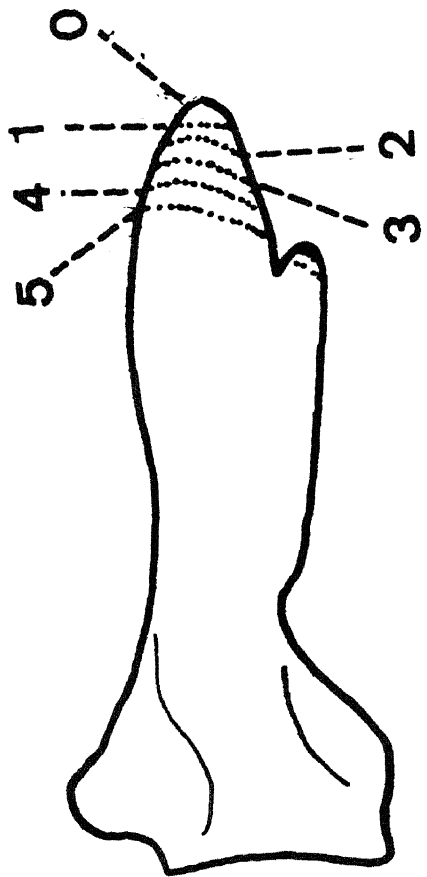


Figure 2.2. Nest-site of Lasioglossum figueresi (San Antonio de Escazú, Costa Rica). In the earthen bank between the foreground and the insect net were nests of several hundred bees. The insect net is ~1.3 m tall.

Figure 2.3. Fused nest turrets of Lasioglossum figueresi (ruler is in mm). All three nests were active at this time.

Figure 2.4. A cell with pollen ball from a nest of Lasioglossum figueresi. The arrow indicates the cell plug.

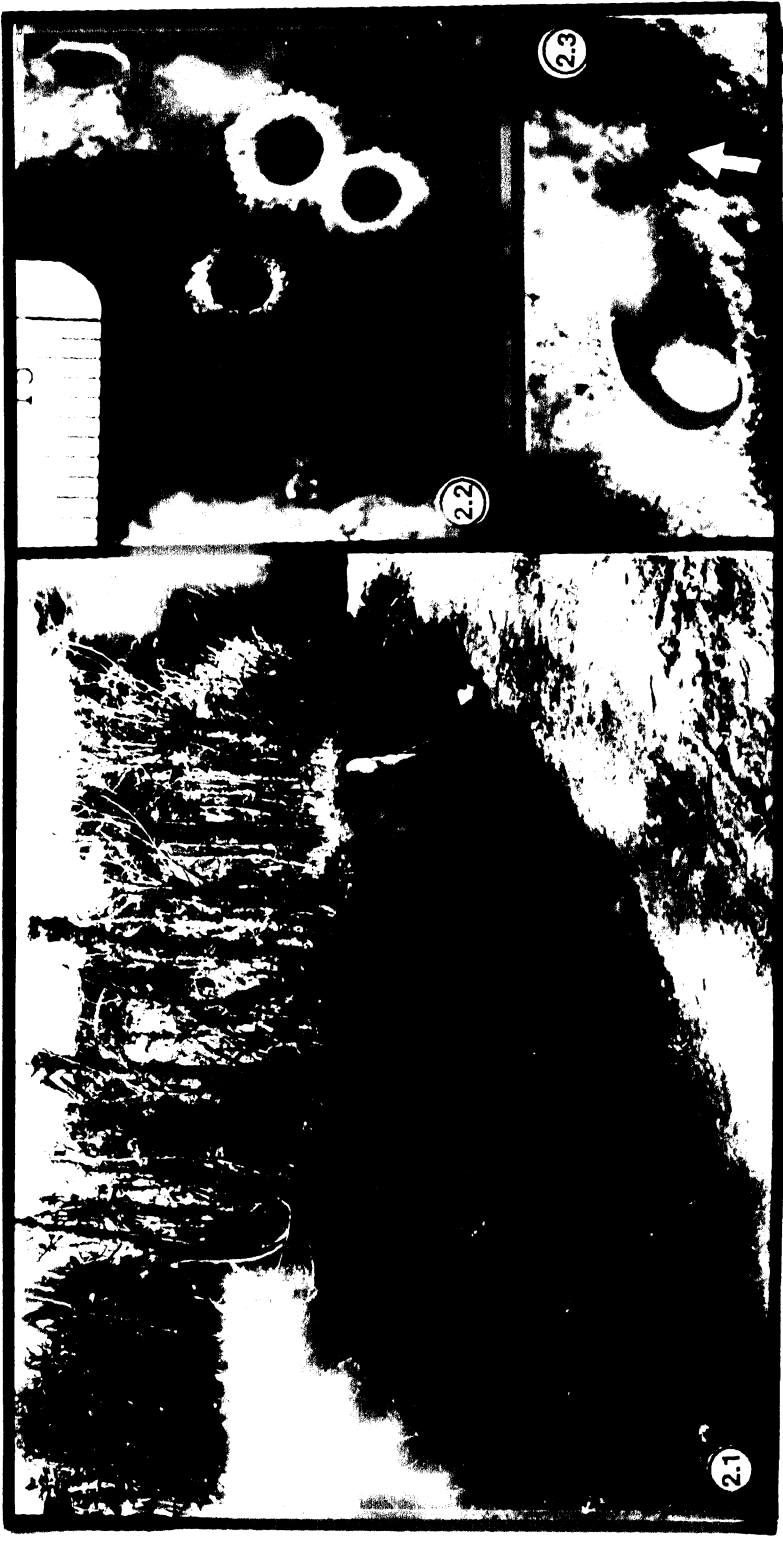
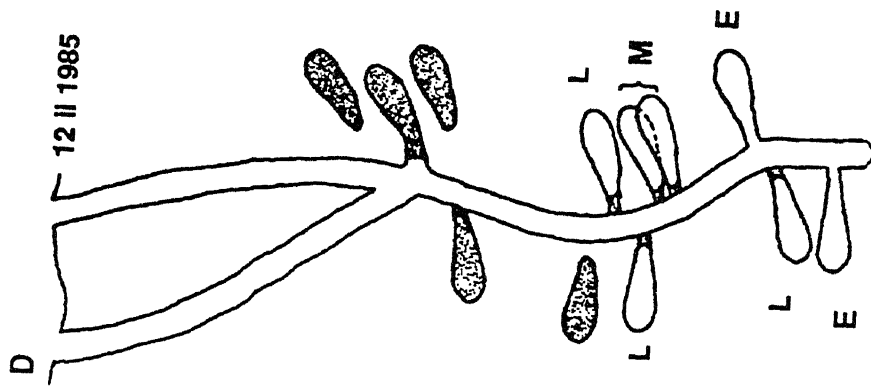
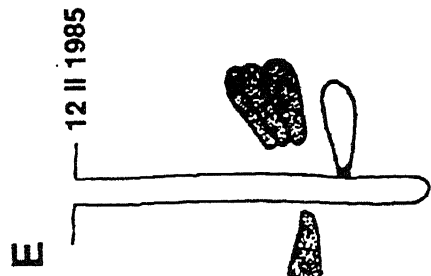
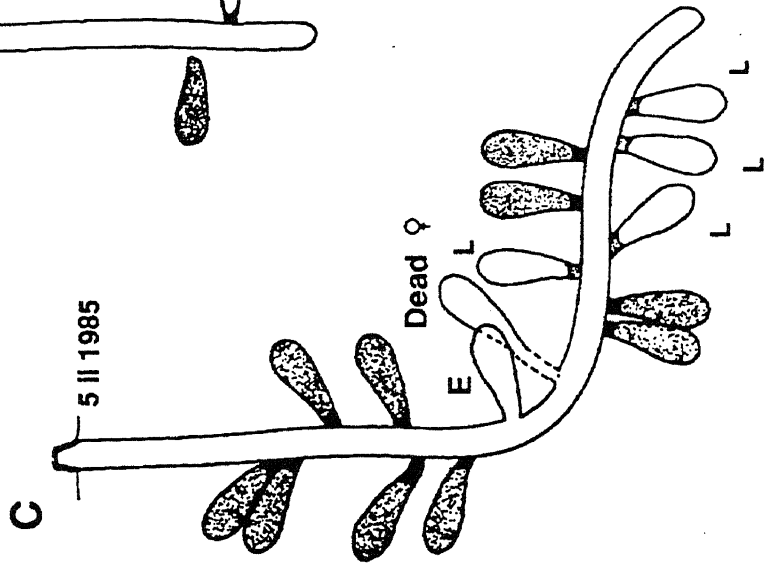
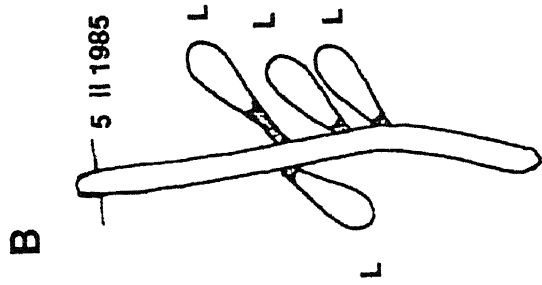
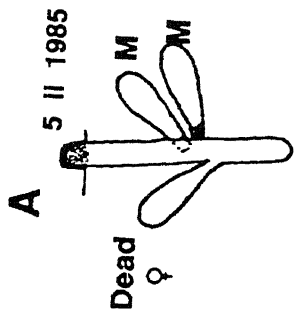
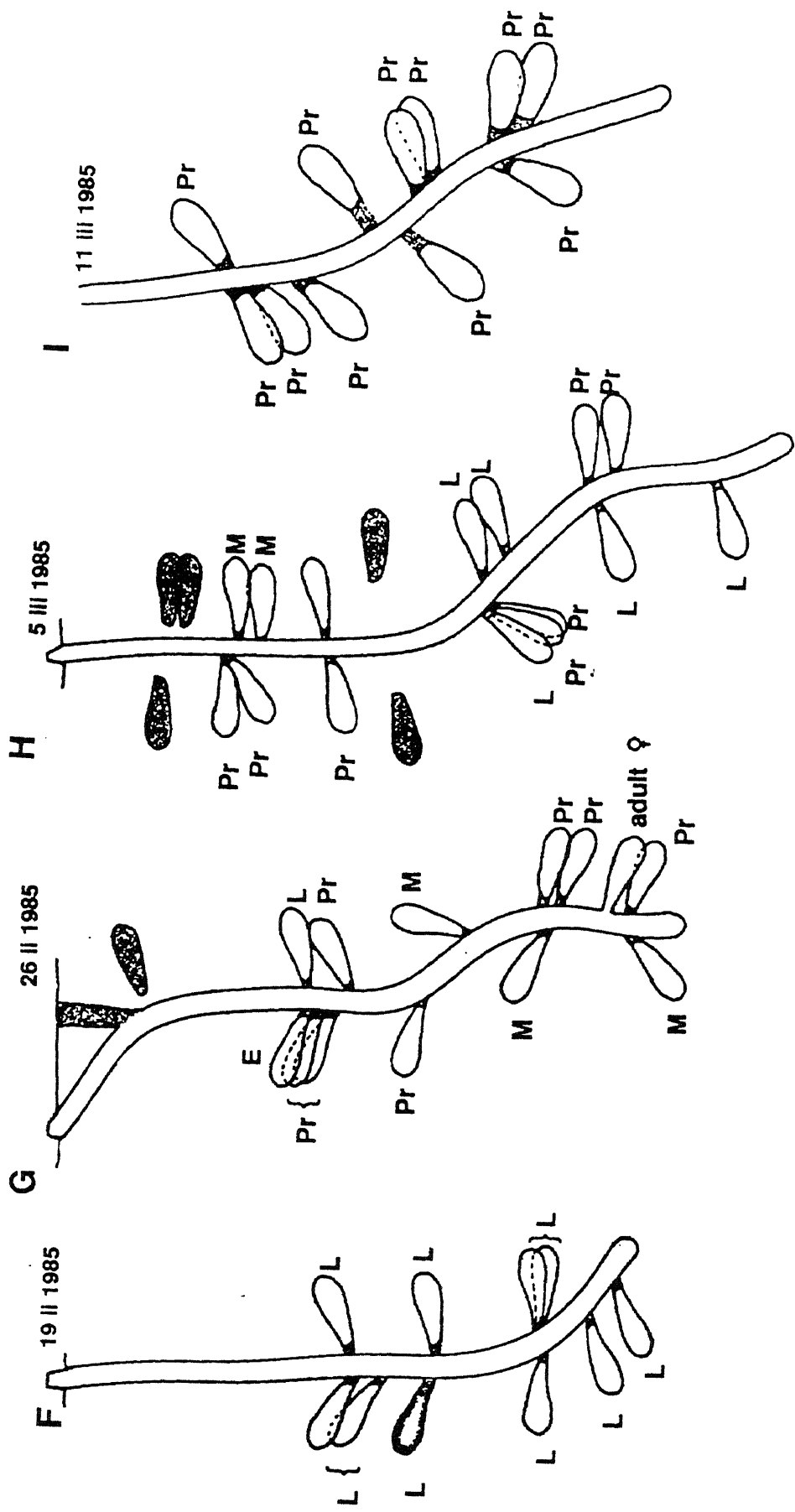


Figure 2.5. Schematic top-view sections of nests of Lasioglossum

figueresi at various times of the year. A-D = 5 Feb.; E = 12 Feb.; F and G = 19 Feb.; H and I = 26 Feb.; J = 5 March; K - M = 11 March; N and O = 18 March; P = 3 April; Q = 9 April. Nests J and L had two adult females; nests D, F, I, K, M, N, O, P and Q all were known to have one female. Shaded cells were old cells with dried feces, usually filled with soil. Scale = 5 cm.





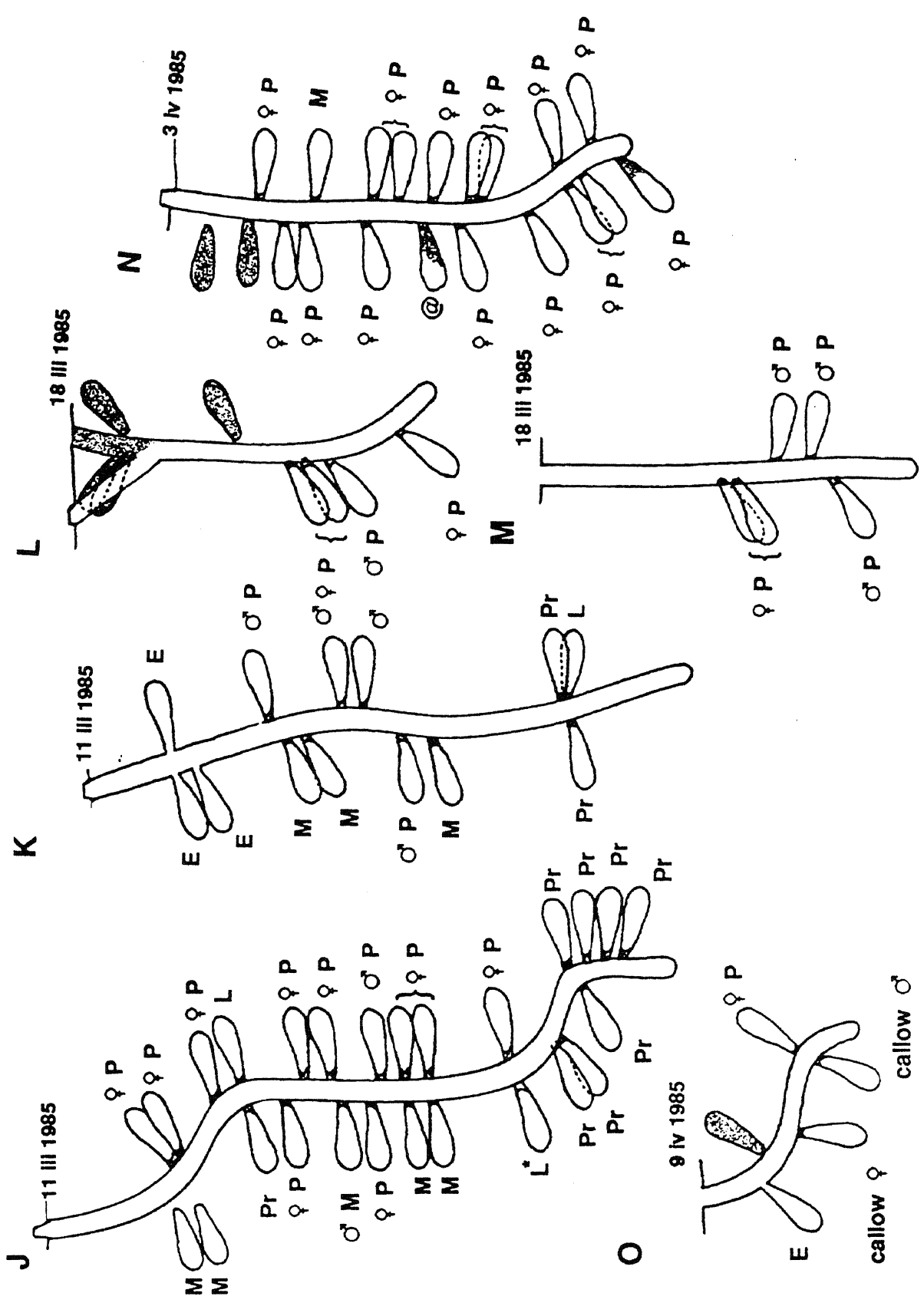
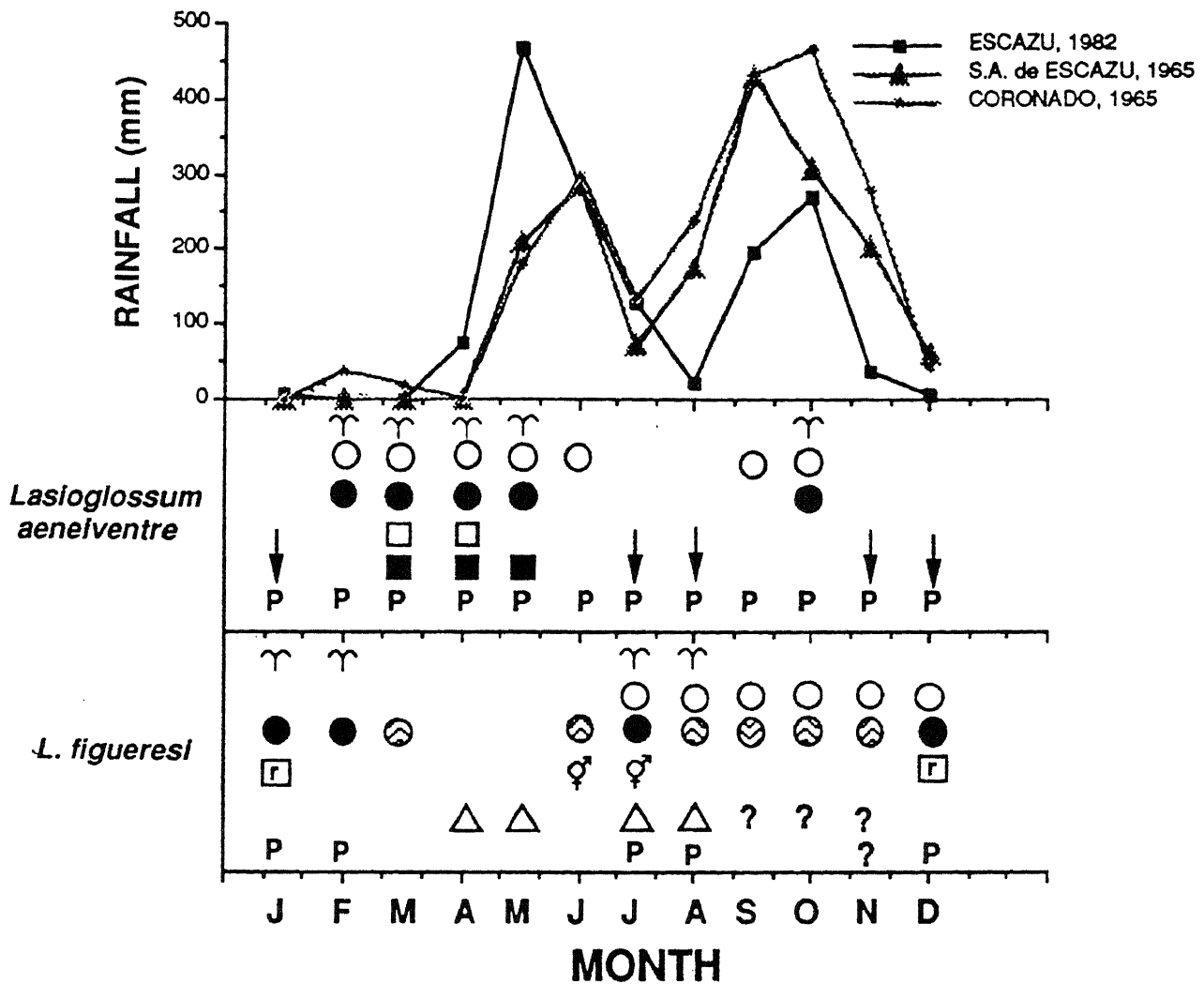


Figure 2.6. Diagrammatic representation of the nesting phenologies and social organizations of Lasioglossum figueresi and L. aeneiventre, along with seasonal precipitation in Escazú and Coronado, Costa Rica. Symbols: OPEN CIRCLE = burrows only with no cells; CLOSED CIRCLE = active nests each with a solitary female; SHADED CIRCLE = nests contain a solitary female that is intermittently active during favorable weather; OPEN SQUARE = nests contain > 1 mated female, and few unmated workers; OPEN SQUARE + r = as above, but are rare; CLOSED CIRCLE = nests contain > 1 mated female and >3 unmated workers; WING = a nest with a single mated female and ≥ 1 unmated worker; TRIANGLE = a nest containing recently emerged, unmated adults (presumably siblings) which cohabit a nest during an unfavorable period; one p = females observed entering nests with pollen; \downarrow = no nests were excavated; ♂^{\uparrow} = adult males and mating.



SOLITARY

○ BURROWS ONLY

● ACTIVE

⊗ SPORADIC
ACTIVITY

♀ MATING

P COLLECTING
POLLEN

△ PRE-REPRODUCTIVE
ASSEMBLAGE

□ POLYGYNOUS,
FEW WORKERS

[r] = occurs rarely

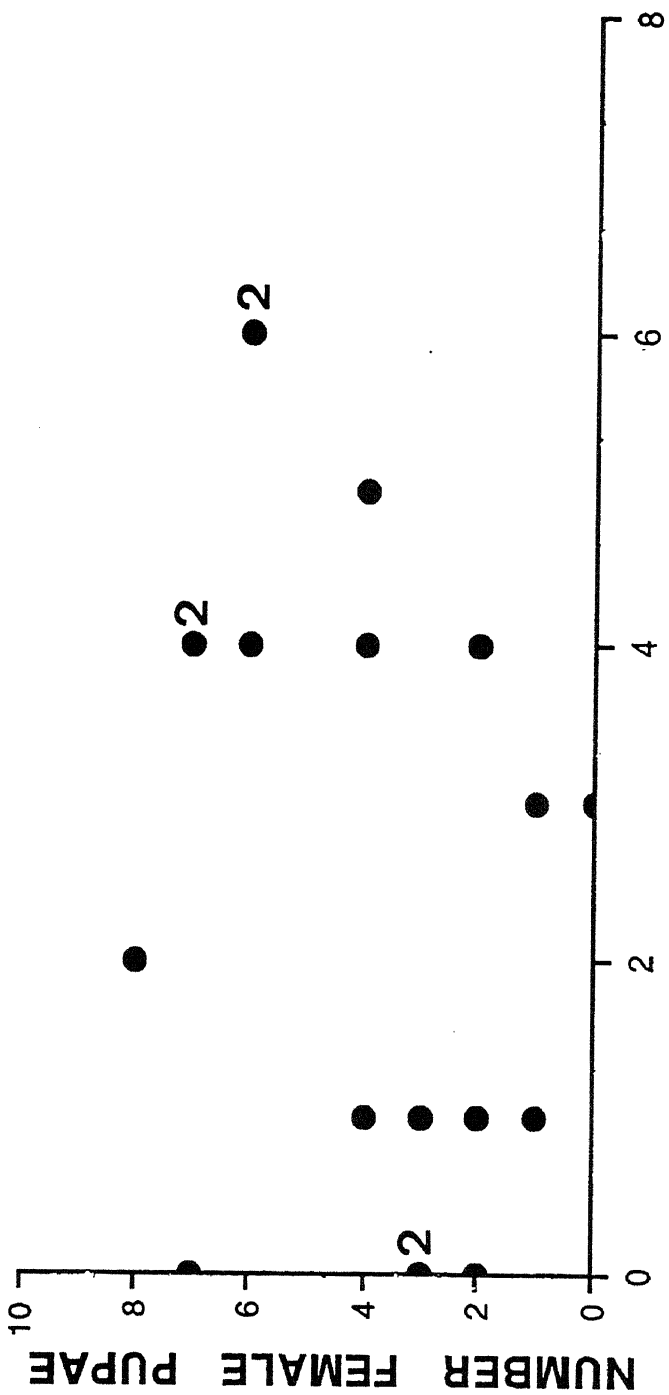
■ POLYGYNOUS,
MANY WORKERS

∩ MONOGYNOUS
(> 1 unmated ♀)

↓ NO NESTS
EXCAVATED

Figure 2.7. Population-level summary of developmental stages of brood of Lasioglossum figueresi.

Figure 2.8. Scatter plot of the number of male pupae versus the number of female pupae in a nest of Lasioglossum figueresi.



NUMBER MALE *L. figueresi* PUPAE IN NEST

Figure 2.9. Diel provisioning activity of Lasioglossum figueresi and L. aeneiventre.

FEMALES ENTERING NESTS WITH POLLEN

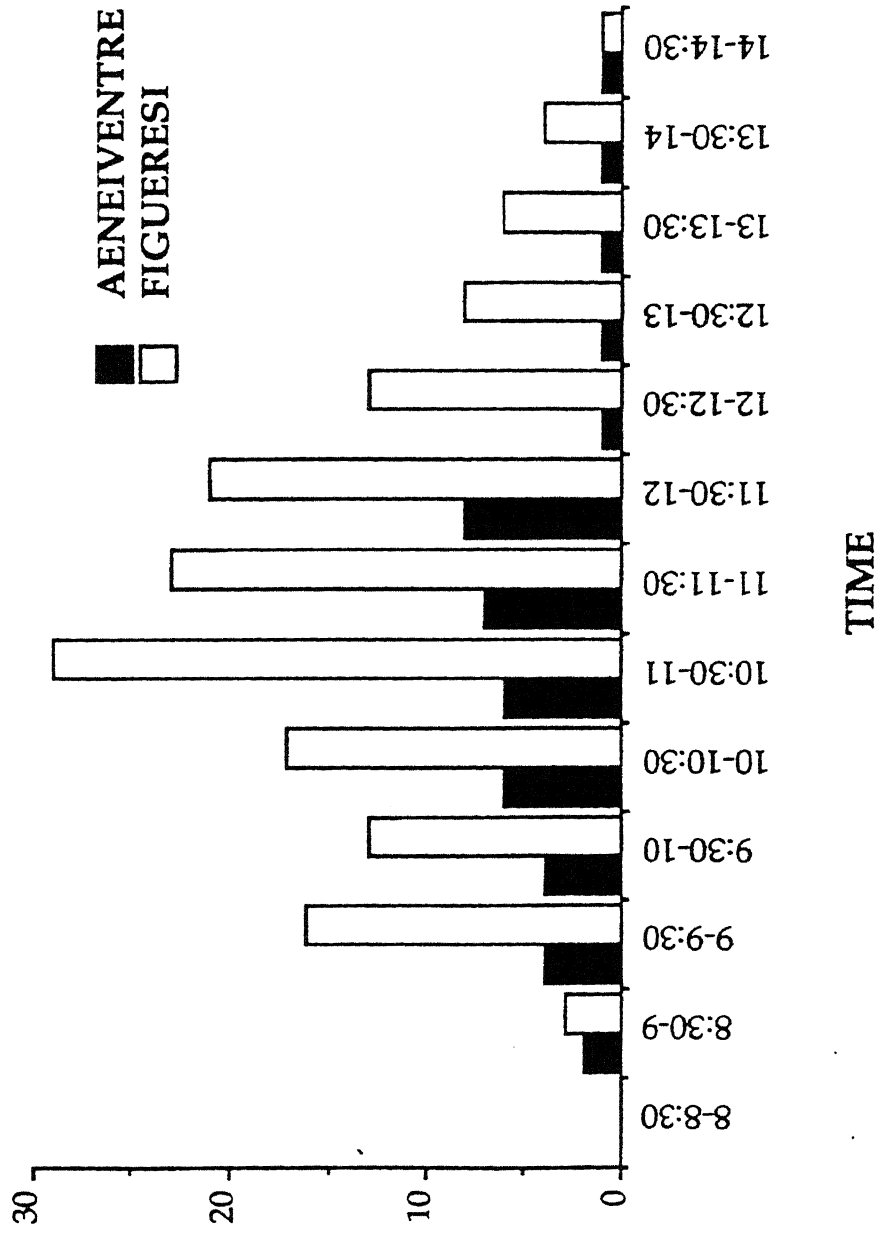


Figure 2.10. Distribution of the durations of pollen-gathering foraging trips by female Lasioglossum figueresi.

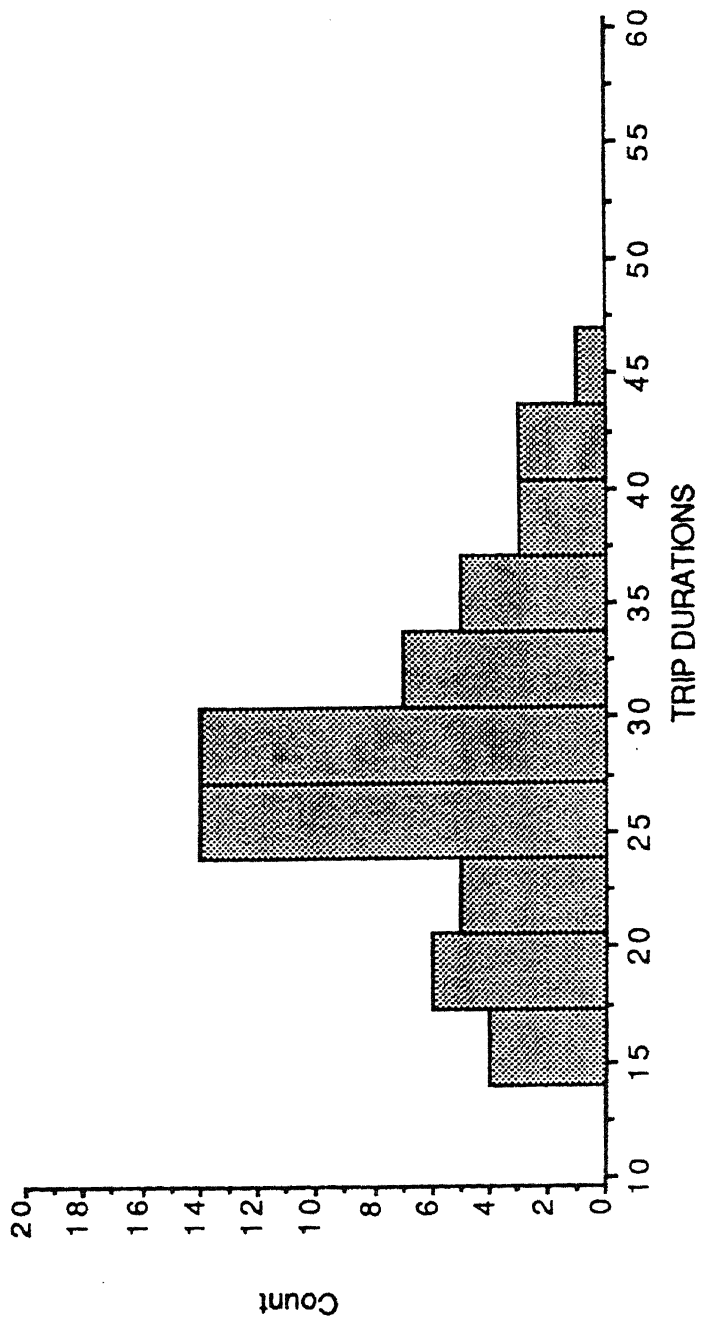


Figure 2.11. Head-width of female Lasioglossum figueresi as a function of the date the bee was collected. The inset figure gives corresponding data for females with unworn wings; each point represents a mean of 3-5 values. f = February; a = April; m = May; jn = June; ag = August.

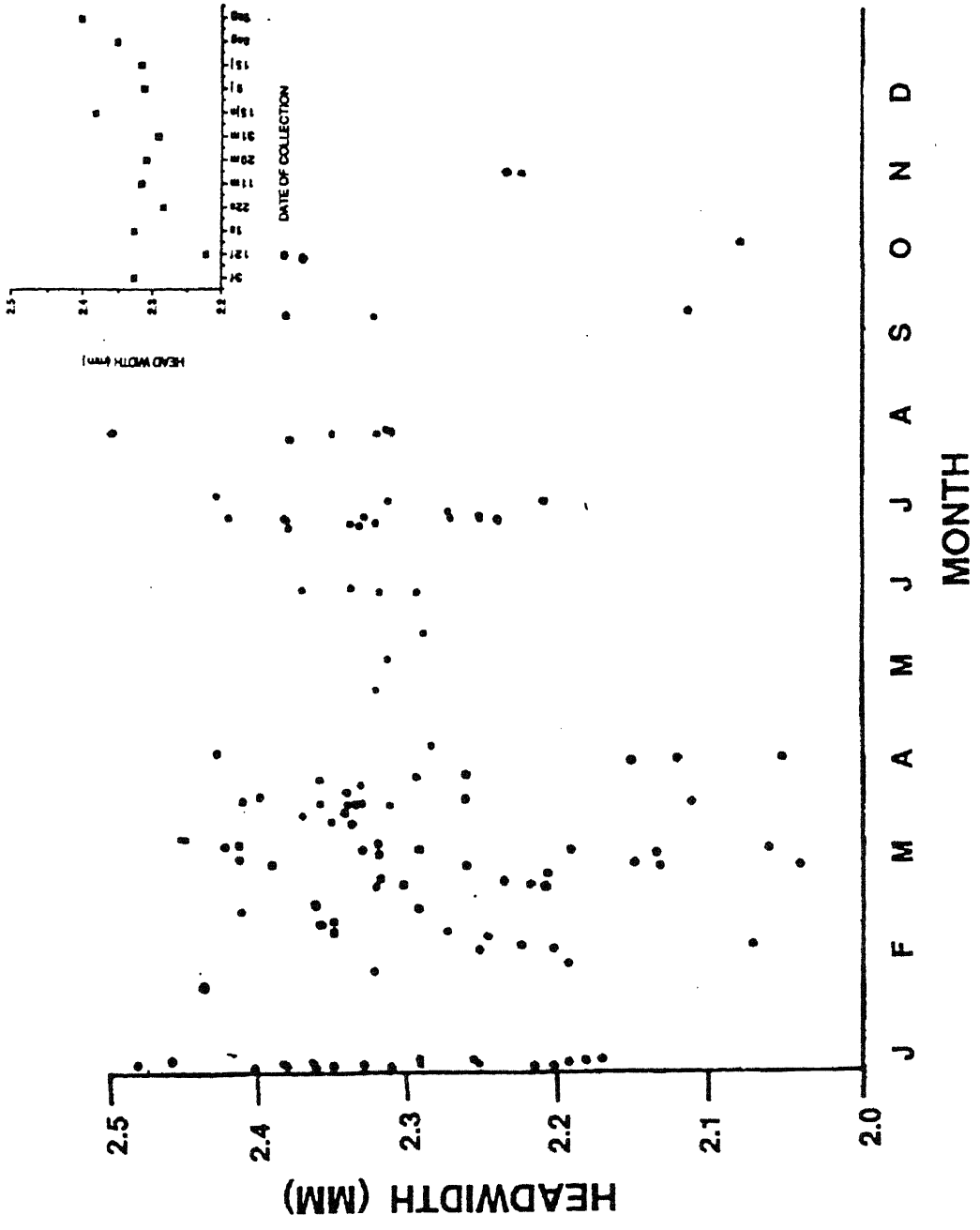


Figure 2.12. The number of cells per nest of Lasioglossum figueresi, for nests with one, two or an unknown number of females (1986).

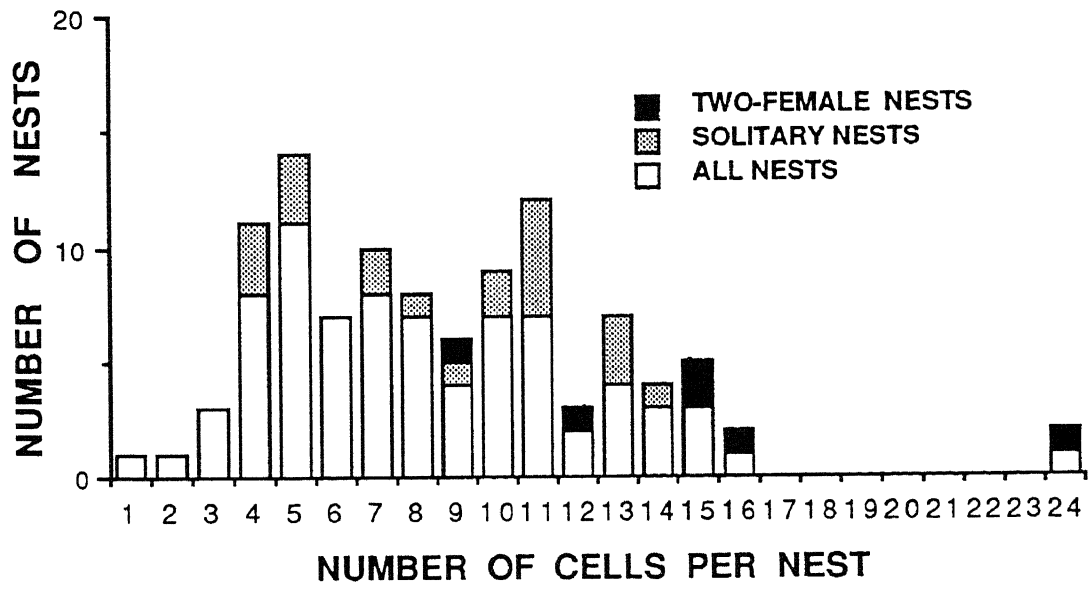


Figure 2.13. Schematic representations of nests of Lasioglossum

aeneiventre. A = 11 March, 2 ♀♀; B = 19 Feb., 2 ♀♀; C = 19 Feb., 1
♀; D = 26 Feb., 4 ♀♀; E = 1 March, 1♀; F = 11 March, 2 ♀♀; G = 7
April, 4 ♀♀, 5♂♂, 2 callow ♀♀; H = 3 April, 1♀; I = 10 May, 1♀ ; J
= 1 Oct., no adults; ♀ = 1 Oct., 1♀.

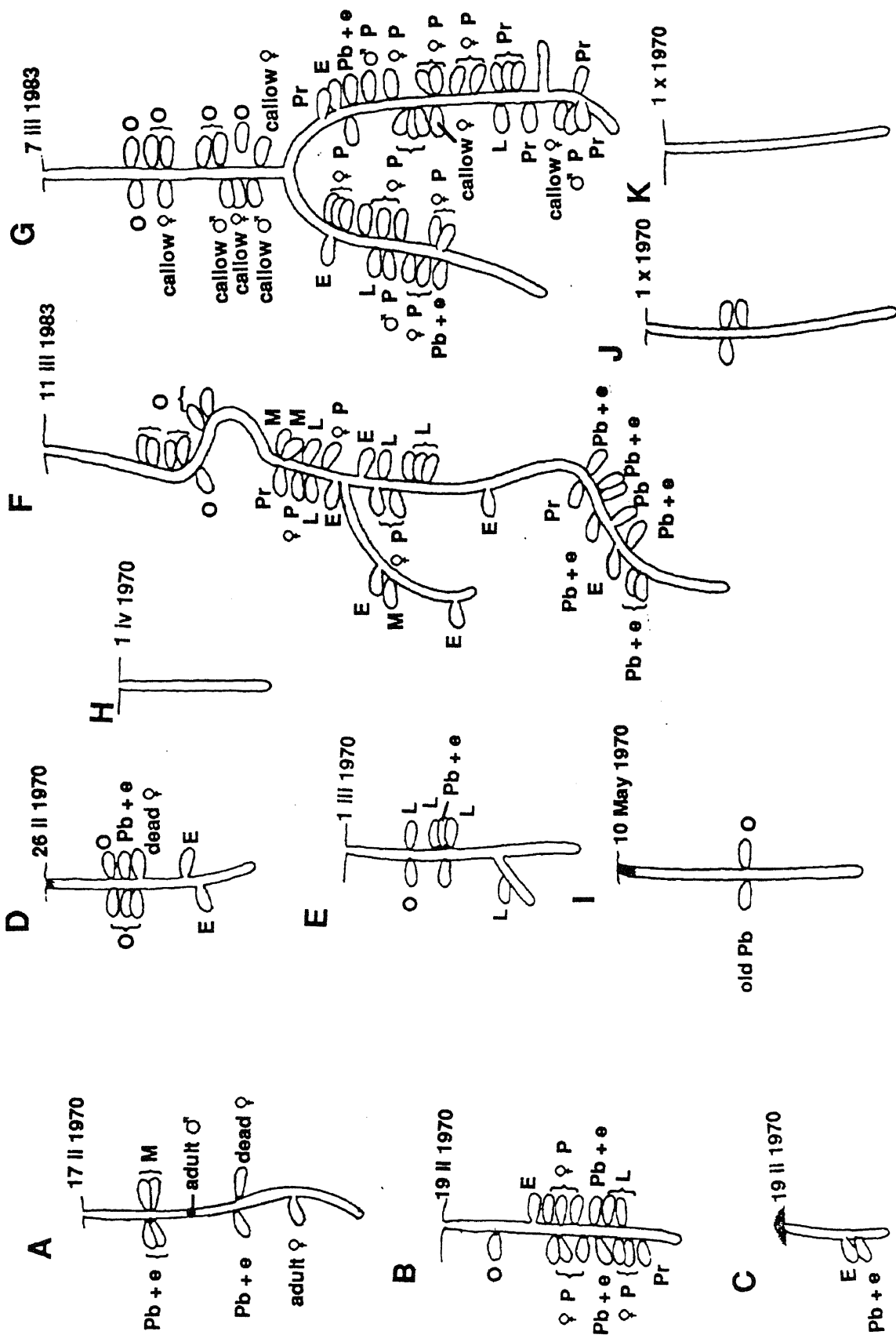


Figure 2.14. Histogram of an estimate of pollen ball size (L x W x H, mm) for Lasioglossum aeneiventre, showing a unimodal distribution.

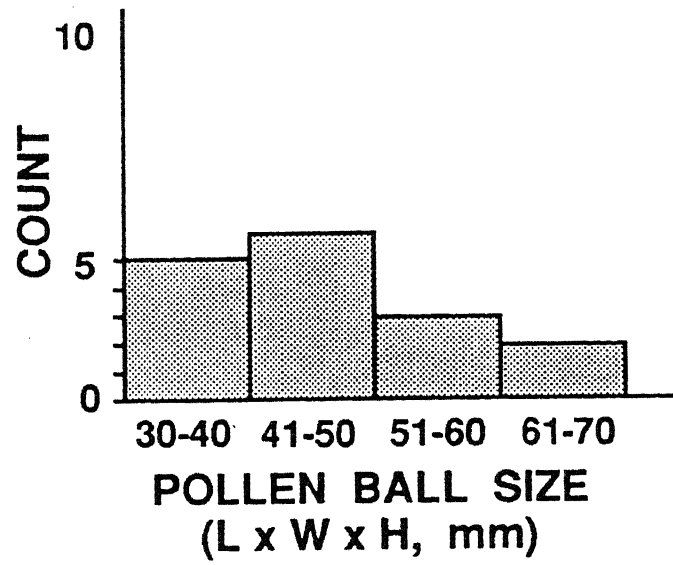


Figure 2.15. Population-level summary of seasonal changes in developmental stages of brood of Lasioglossum aeneiventre.

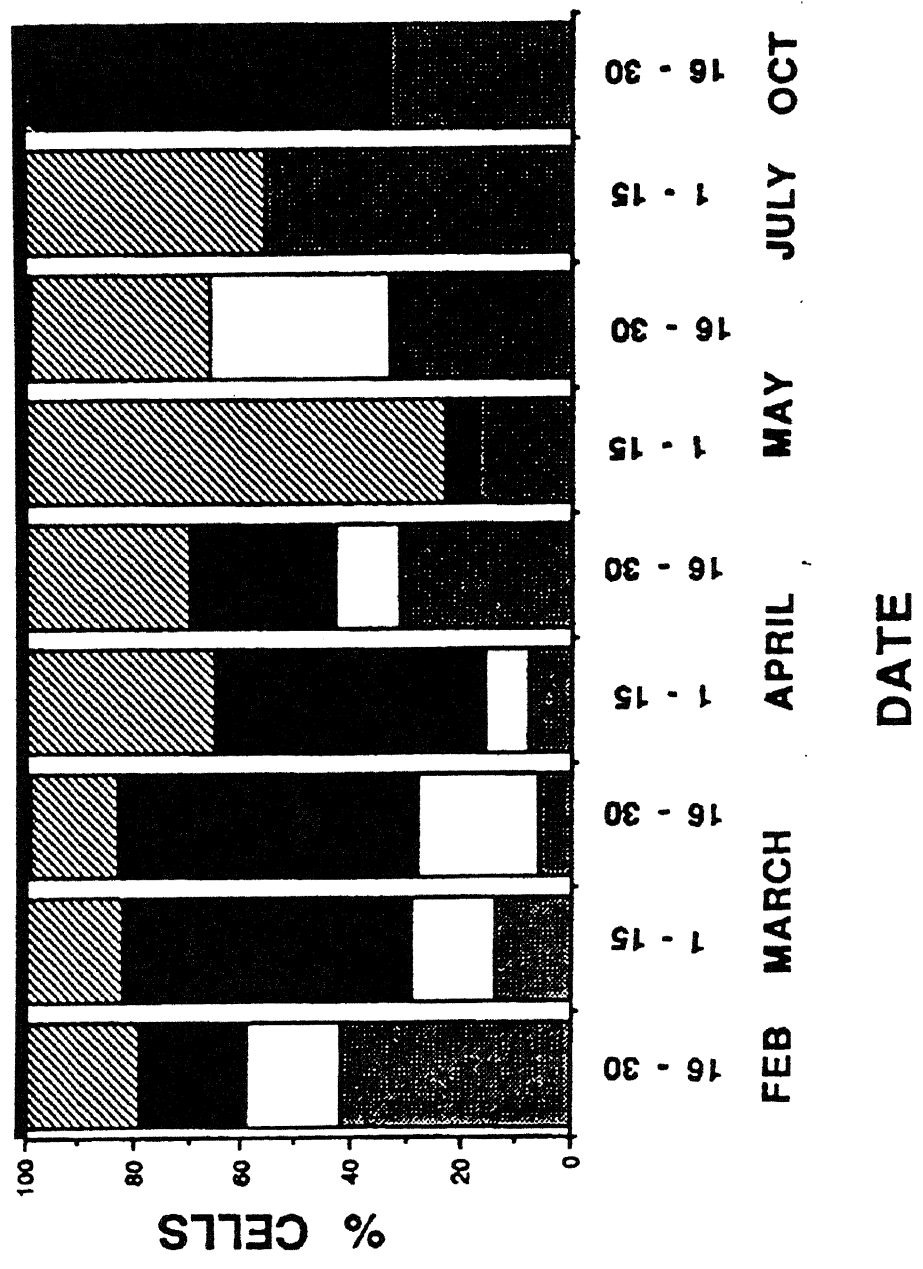


Figure 2.16. Seasonal variation in the proportion of fertilized females per nest of Lasioglossum aeneiventre; none of the values are significantly different from 50% mated. No samples were taken in November, December, and January (indicated by "N").

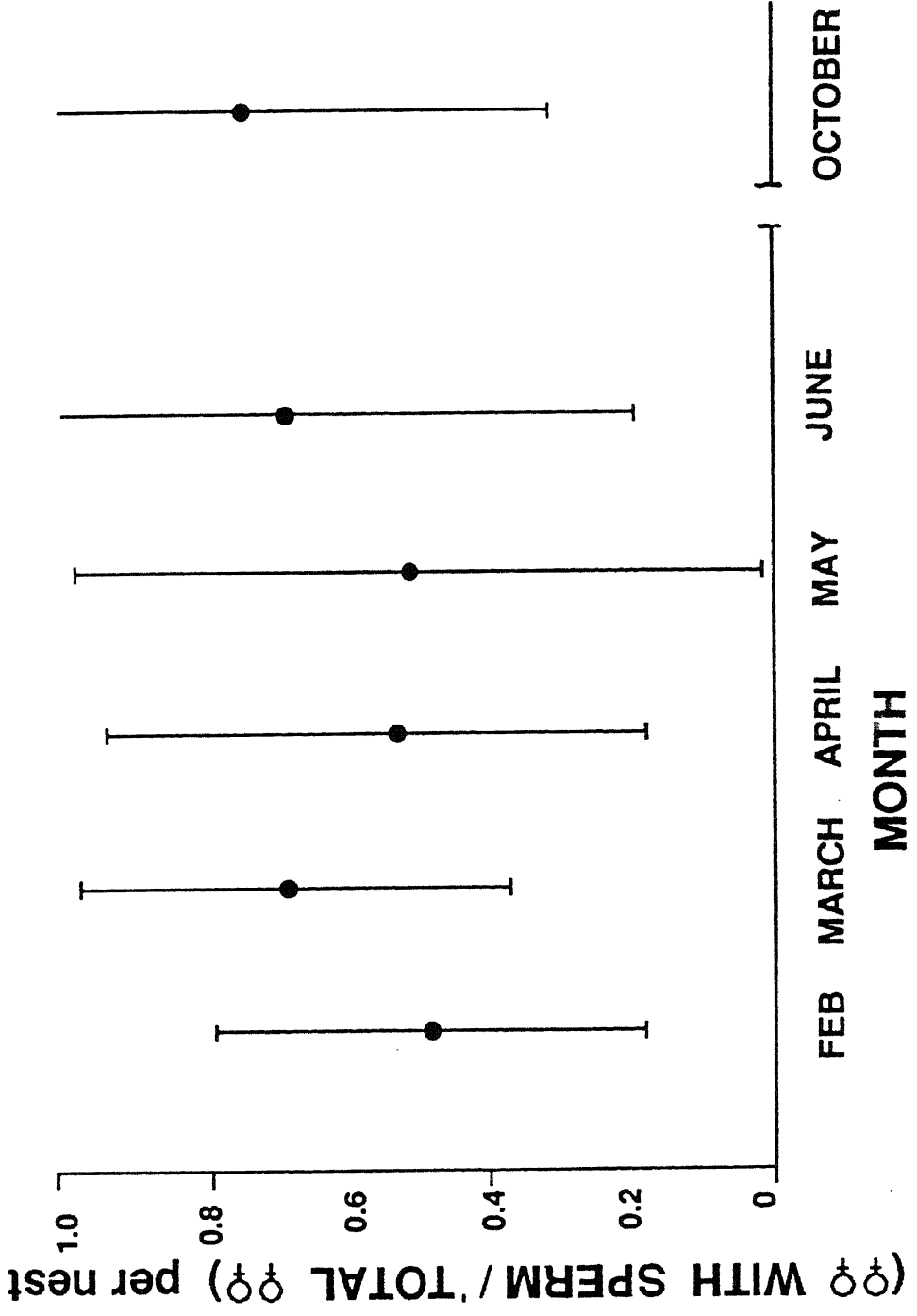


Figure 2.17. Seasonal variation in the total number of nests (circles) of Lasioglossum aeneiventre (pooled over aggregations), showing a marked increase in April and a smaller increase in October. The proportion of solitary nests (bars) also increases throughout the year (especially in April - June, and October), suggesting the overall increase in population size is due to new nest founding.

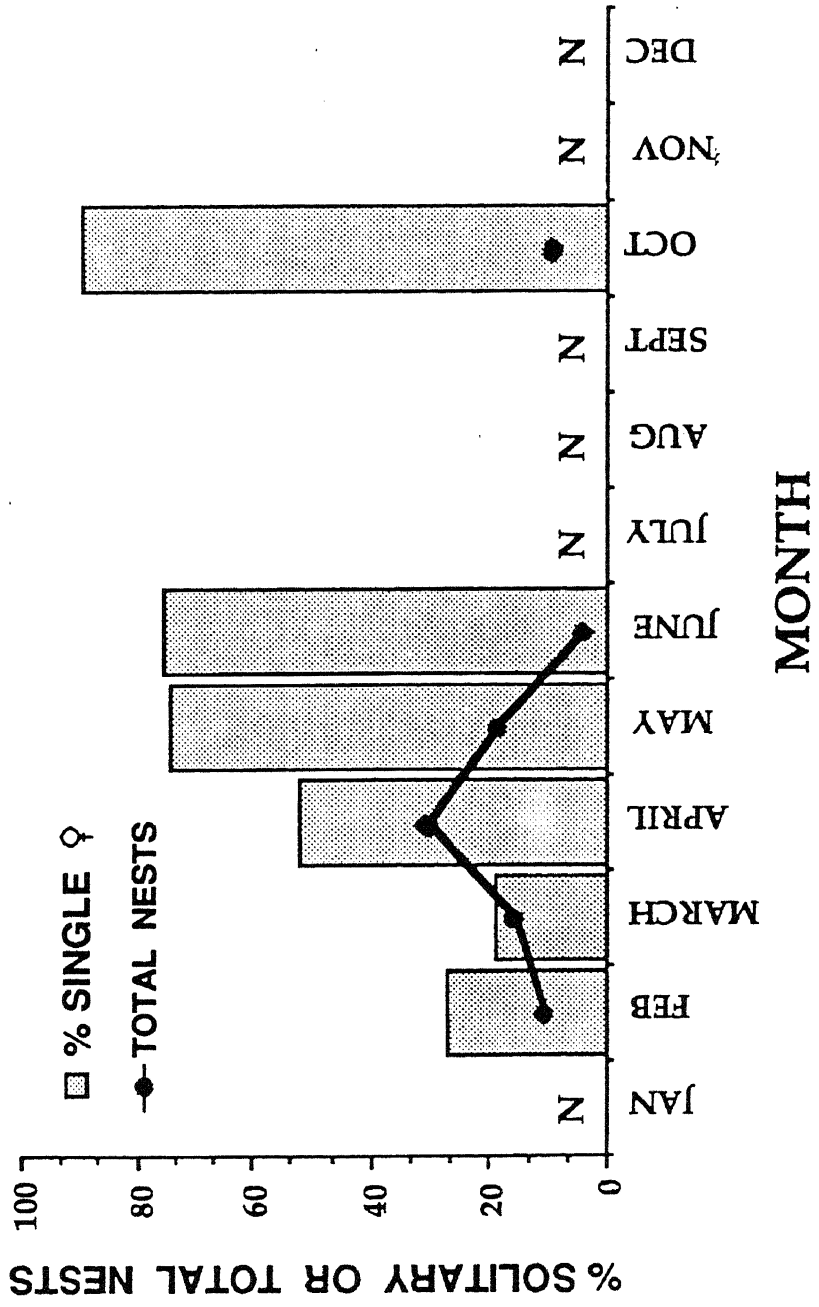


Figure 2.18. Distributions of head-widths for female Lasioglossum
aeneiventre, according to whether she was a solitary female,
mated and living in a group, or unmated and living in groups.

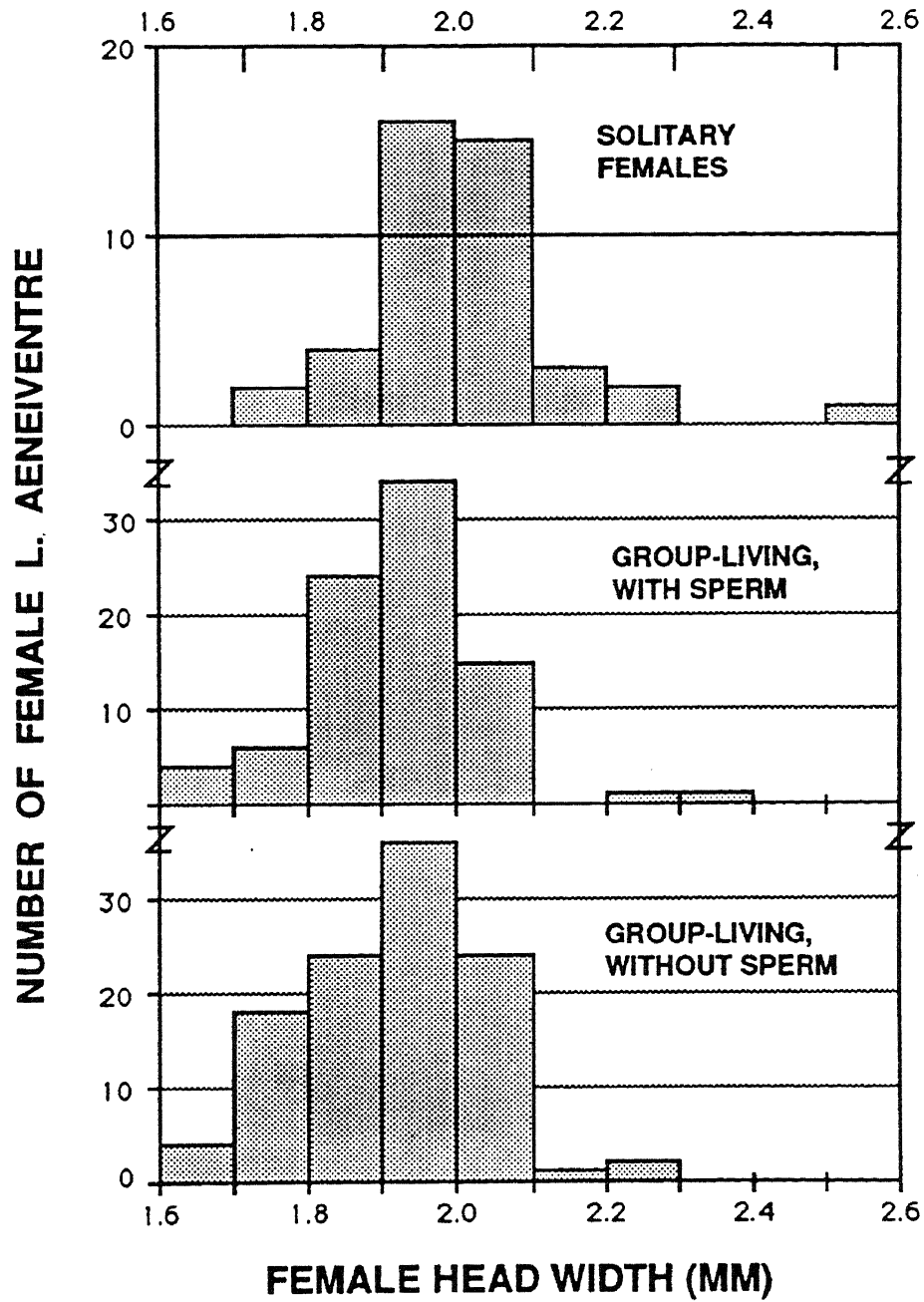


Figure 2.19. Seasonal variation in mean head-width of female Lasioglossum aeneiventre. Females in May and October are larger than females produced in the first brood, but the differences are not significant.

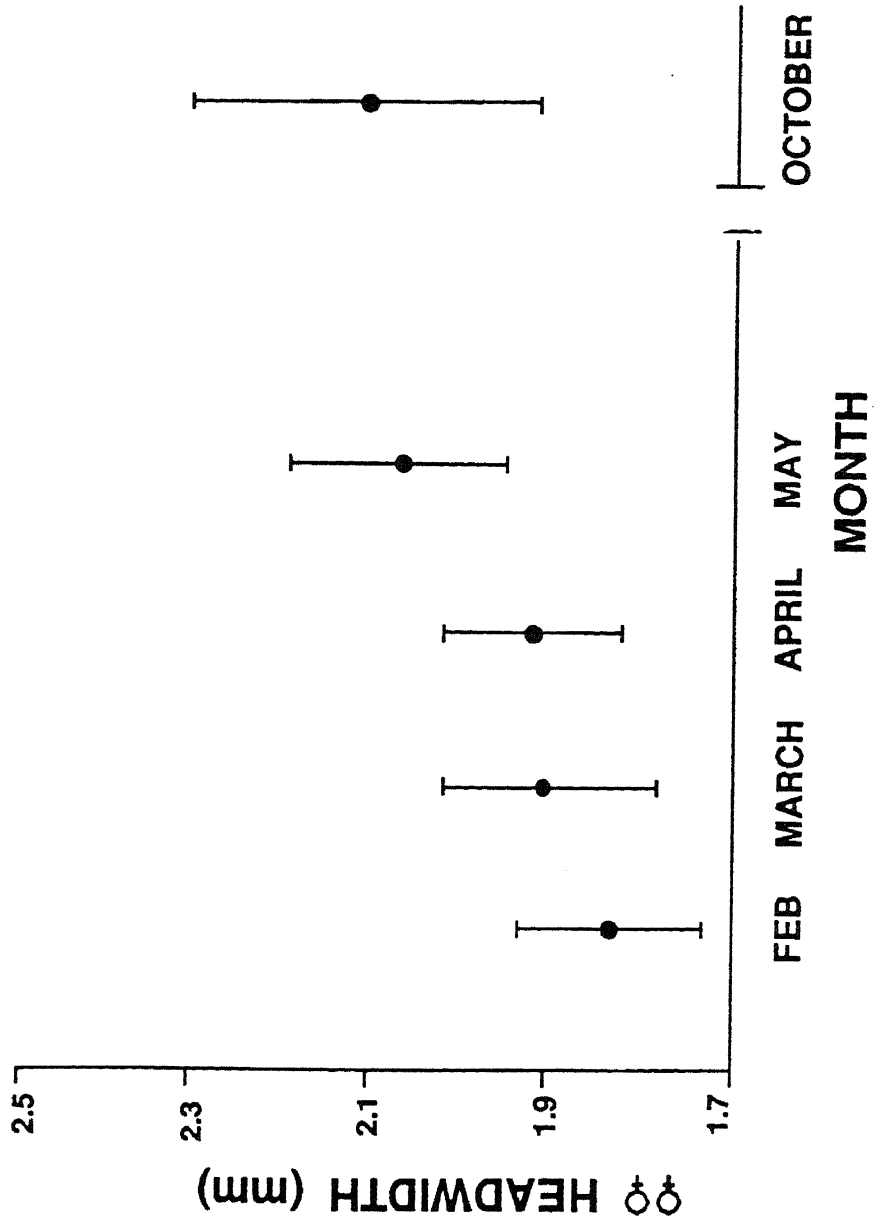


Figure 2.20. Distributions of lengths of longest oocyte in female Lasioglossum aeneiventre, according to whether she was a solitary female, mated and living in a group, or unmated and living in a group.

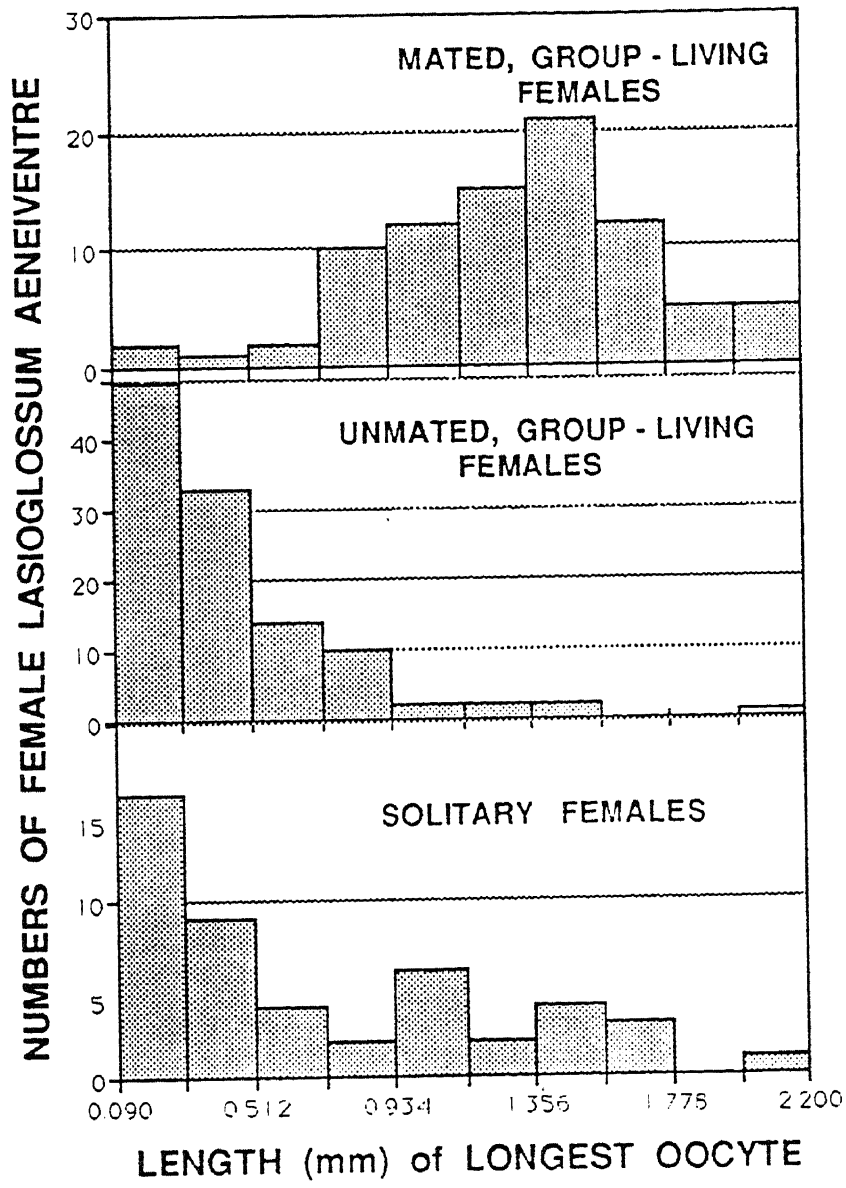


Table 2.1. Egg to adult developmental rates for various halictid bees from different localities. In most cases the data given are approximations extrapolated from published illustrations. D = duration in days for development from egg to adult.

SPECIES	LOCALITY	D	REFERENCE
<i>Lasioglossum versatum</i>	Kansas	30	Michener, 1966
<i>L. imitatum</i>	Kansas	35	Michener & Wille, 1961
<i>L. rohweri</i>	Kansas	30	Breed, 1975
<i>L. zephyrum</i>	Kansas (25°C)	21	Batra, 1966
<i>L. zephyrum</i>	Kansas (21°C)	24	Kahm, 1974
<i>L. zephyrum</i>	Kansas (26°C)	23	op. cit.
<i>L. zephyrum</i>	Kansas (30°C)	18	op. cit.
<i>L. ohei</i>	Hokkaido, Japan	50	Sakagami et al. 1986
<i>L. affine</i>	Fukuoka, Japan	35	Sakagami, 1982
<i>L. sakagami</i>	Morioka, Japan	40	Sakagami et al. 1986
<i>L. duplex</i>	Sapporo, Japan	31	Sakagami et al. 1986
<i>L. duplex</i>	Sapporo, Japan	38	Sakagami et al. 1986
<i>L. linearis</i>	Paris, France	40	Knerer, 1983
<i>L. umbripenne</i>	Damitas, Costa Rica	22	Wille & Orozco '70
<i>L. figueresi</i>	Escazú, Costa Rica	80	Results
<i>L. aenieventre</i>	Coronado, Costa Rica	35	Results
<i>L. laevissimus</i>	Maryland	51	Batra 1987
<i>L. allodatum</i>	Sapporo, Japan	50	Sakagami et al. 1986
<i>Agapostemon texanus</i>	Kansas	32	Roberts 1969
<i>A. virescens</i>	New York	>30	Abrams & Eickwort, 1981
<i>Augochlorella striata</i>	Kansas	29	Ordway, 1966

Table 2.2. Numbers and percentages of multi-female nests in Lasioglossum figueresi during the active provisioning phase. Nests with unknown or uncertain numbers of females were excluded. Number of nests per sample are given in parentheses.

	PERCENTAGE OF NESTS WITH TWO FEMALES		
	NEAR SITE	STATION 9	NICE VIEW
I-V, 1985	16 (25)	14 (7)	---
I-IV, 1986	21 (28)	20 (5)	--
XII, 1987-I, 1988	19 (16)	20 (5)	26 (15)
VI-VII, 1988	9 (21)	---	13 (15)

Table 2.3. Summary of nest characteristics of Lasioglossum aeneiventre. Standard

deviations are given in parentheses; the number of nests excavated per sample is given in brackets.

DATE [# nests*]	TOTAL CELLS	NEW CELLS	OLD CELLS	NEST DEPTH (cm)
Feb. [13]	8.0 (4.1)	1.2 (0.8)	3.2 (2.0)	10.0 (3.1)
March [19]	23.6 (16.7)	1.2 (1.5)	5.2 (4.5)	18.1 (9.8)
April [32]	20.3 (21.7)	0.7 (0.9)	5.5 (8.2)	16.5 (7.0)
May [21]	5.3 (9.6)	0.09 (0.3)	3.7 (7.8)	12.3 (5.6)
June [6]	6.5 (7.3)	0.6 (0.9)	5.2 (5.7)	18.1 (7.7)
October [6]	1.2 (1.5)	0.2 (0.4)	0.2 (0.5)	7.4 (2.5)

* The mean (\pm SD) number of females per nest was: Feb., 2.7 ± 1.1 ; March, 4.1 ± 3.4 ; April, 3.3 ± 3.8 ; May, 1.6 ± 1.8 ; June, 1.3 ± 1.0 ; October, 1.0 ± 0 .

Table 2.4. The durations of life-history stadia during the development of female Lasioglossum aeneiventre, based on laboratory rearing near San José, Costa Rica.

LIFE-HISTORY STADIA	NUMBER OF DAYS AFTER OVIPOSITION
from EGG	
--> HATCHING	3
--> PREPUPA (=post-defecating larva)	16
--> PUPA	20
--> BLACK-EYED PUPA	27
--> PIGMENTED PUPA	31
--> CALLOW ADULT	35

Table 2.5. Association between mated status, wing wear, and pollen consumption in Lasioglossum aenieventre.

	WING WEAR?		POLLEN IN CROP?	
	YES	NO	YES	NO
SPERM PRESENT	44	36	43	37
SPERM ABSENT	11	101	32	90

Table 2.6. Comparison of behavioral attributes for Lasioglossum (Dialictus) figueresi and L. (D.) aeneiventre. Attributes 1 - 28 are from Michener (1974: table 20.2).

VARIABLES OR CHARACTERISTICS	<u>L. figueresi</u>	<u>L. aeneiventre</u>
1. Maximum normal number of females per nest	1 (1-3)	1 - 12
2. Sex ratio in early colony (nest) growth	1:1	1:1?
3. Frequency of reduced reproductivity in females	?	?
4. Queen (or lone female) foraging	yes	yes/ no ^a
5. Social dimorphism	no	no
6. Excess gynes	none	none
7. Queen (or lone female) ovarian specialization	none	none
8. Queen (or lone female) longevity	none	none
9. Worker fertilization	much < 1 year	much < 1 year
10. Worker laying of reproductive eggs	< 50%	~50%
11. Larval food	?	?
12. Eggs and larvae closed in cells	pollens & nectar	pollens & nectar
13. Progressive feeding of larvae	yes	yes
14. Food storage for adults	no	no
15. Food exchange among adults	no	no
16. Removal of wastes from larval quarters before pupation	no	no
17. Secretion of cell construction material	yes	yes
18. Re-use of cells	occasionally	no
19. Stages of caste determination	adult	adult

(Table 2.6, continued)

VARIABLES OR CHARACTERISTICS	<u>L. figueresi</u>	<u>L. aeneiventre</u>
20. Communication as to food sources	no	no
21. Defense at entrance	yes	yes
22. Young (cells) in clusters	no	no
23-24. Temperature control	no	no
25. Alarm pheromones	no	no
26. Survival through unfavorable periods	fertilized female ^b	fertilized female
27. Response to emergency conditions such as starvation	death	?
28. Generations of workers and queens	same	same
29. Nests in aggregations?	yes	yes
30. Nests in vertical earthen banks?	yes	yes
31. Nests in horizontal ground?	no	yes
32. Nests in wood?	no	no
33. Nest architectural formula	O(Ch-i) ⁿ B	O(Ch-i) ⁿ B
34. Nests with turrets?	yes	no

CHAPTER 3

NEST RECOGNITION IN A SOLITARY SWEAT BEE, LASIOGLOSSUM (DIALICTUS) FIGUERESI (HYMENOPTERA: HALICTIDAE), AS AN ENABLING MECHANISM FOR SOCIALITY

All insects with vision use visual cues for spatial orientation, and some use them for home-range orientation. "Homing" is known for some damselflies and dragonflies (Odonata); butterflies and moths (Lepidoptera); flies (Diptera); and is especially well-developed in bees, wasps, and ants (Hymenoptera, Aculeata) (refs. in Wehner, 1981). Bees and other nesting Hymenoptera make numerous trips afield to gather food for their young, and return from long distances to a nest. Homing occurs among solitary, social, and brood parasitic species, in diverse lineages of Aculeata (e.g., Graenicher, 1906; Turner, 1923; Frisch, 1967; Rosenheim, 1987; Wcislo et al., 1988).

Various authors have linked homing abilities to brood care and the repeated evolution of hymenopteran social behavior (e.g., Wheeler, 1928; Wilson, 1971; Michener, 1974; Evans and West-Eberhard, 1970; Eickwort, 1981). Homing behavior, however, involves several components, and not all are relevant to understanding social evolution. The directional component of long-distance homing in flying Hymenoptera often involves the visual sense (refs. above). This modality is of little

importance in integrative social relationships (Kennedy, 1927), which are usually modulated by chemo-tactile cues in aculeates (e.g., Wilson, 1971; Fletcher and Michener, 1987; Hölldobler and Wilson, 1990).

Since the sign stimuli for social behaviors are in part chemically based, are there chemical sign stimuli for nest-related behaviors in solitary species? The near-nest components of homing are relevant to social evolution because they require an ability to localize and identify an individual nest entrance, and then distinguish it from other nearby entrances, or similar holes. Olfactory recognition capabilities are ubiquitous in insects, and are especially well-developed in social Hymenoptera. Sweat bees (Halictidae), for example, are known to recognize kin, nests, and mates on the bases of chemical cues (references in Kukuk et al., 1977; Hölldobler and Michener, 1980; Michener, 1982; Michener and Smith, 1987; Wcislo, 1987a; Greenberg, 1988).

This paper concerns experiments on visual and olfactory cues used for nest recognition by a solitary sweat bee, Lasioglossum (Dialictus) figueresi Wcislo. The Discussion considers the relationships among the use of glandular secretions in nest construction, individual recognition, and social evolution.

Synopsis of Nesting Biology and Study Site

Most L. figueresi are solitary bees. Females dig tunnels in soil of vertical banks, and excavate cells to the sides; cells are provisioned with

pollen and nectar collected from flowers during foraging trips; the entrances are usually surrounded by chimney-like turrets, more or less perpendicular to the bank (photograph in chapter 2; length of turrets: 0-25 mm). On sunny or partly cloudy days females began flying at about 9:00 hours, making between 1 and 5 foraging trips per day of activity (for details, see Chapter 2).

Experiments were made from 25 December 1985 to 8 February 1986, and from 2 January to 10 February 1987 at two nesting aggregations of L. figueresi near San Antonio de Escazú, San José Province, Costa Rica: (1) "Near site"-- Bees nested in a west-facing bank of an earthen road passing through agricultural fields (elevation = 1450 m); and (2) "Station 9"--Bees nested in a north-facing bank of an earthen road passing through open pasture and agricultural fields (elevation = 1600 m) on the way to the summit of Cerro San Miguel. At both sites there are fences, shrubs, and trees at the top of the bank, so many complex visual landmarks are available.

Experimental studies

Prior to experimental manipulations bees were individually marked on the thorax with enamel paints. All data are based on observations of pollen-laden females returning to their nests. Observations were timed with a watch, described, and quantified as follows:

Duration of entry = duration in seconds beginning when a marked female first approached her nest (from 1 m away), and ending when she entered it. If a bee entered a nest directly, then a value of $T = 5$ secs was used when calculating statistics; because of this estimate, non-parametric statistics were used.

Number of approaches = the number of approaching flights a female made before she entered her nest. An approach is the flight path of a returning bee from a point of visibility to an observer (ca. 1 m from the bank) to <10 cm from the nest entrance. A returning bee usually made one approach and then entered her nest. If there was some perturbation, the returning bee often briefly hovered (<5 secs) 1-5 cm in front of the bank near her nest. In these cases she flew away beyond my visibility and in a few seconds returned to begin another approach flight (Figure 3.2).

Unless otherwise stated, central tendencies are given as medians with ranges. Comparisons were made using Mann-Whitney U tests, or Wilcoxon signed rank tests (Sokal and Rohlf, 1981); pertinent computer software was developed by R. Roggero (University of Kansas).

Experiment 1: The role of visual cues in nest recognition.

Objects were placed near nest entrances to study the use of visual cues in nest recognition: (1) Six wooden discs, each with a diameter of about 2.5 cm and a height of about 1 cm, were painted white with a 5 mm black diagonal band, pierced with nails, and placed in a circular formation

(diameter = 8 cm) centered on the nest entrance. Discs were about 4 cm above the surface of the bank (Figure 3.1). Earlier trials used a circle of six green coffee fruits, each of which was pierced with a pin and placed as described above. [At least some bees have trichromatic vision, including green color receptors, e.g., Menzel et al., 1988]. Painted discs were used to standardize the objects. Unless otherwise indicated objects were left in place at least 6 days prior to further manipulations, which are described below. The bees' first foraging flights of the day were used, unless otherwise stated.

Experiment 1 a: For 39 trials (nests), cues were presented prior to bees' daily exploratory flights, and then removed before the bees returned from those first flights (i.e., a deletion of an added cue).

Experiment 1 b: Cues were placed around nest entrances after the bees' locality studies and left in place (N = 38). Six to 9 days later both the ring cues + nest turrets were moved from 1 to 30 cm (left or right) during a bee's first foraging flight of the day.

Experiment 1 c: Cues were presented as described in experiment 1 b, although different bees were used. After a training period of 7 to 9 days the cues and turrets were shifted 1 cm to the right or left (N = 15). In these trials the true nest entrance was covered with a paste of mud made from soil collected at the nesting site. A second turret was pinned into the soil 1 cm to the other side of the true entrance (i.e., 2 cm from the shifted turret).

Following various numbers of approaches by a returning bee the mud plug was removed.

Experiment 1 d: In these trials a large bush (1 x 2 x 2 m) was placed above the bank where bees were nesting (site 1, N = 21 bees), or about 1 m in front of the bank (N = 20 bees). For all trials the cues were put in place after bees had made locality studies.

Experiment 2: The role of turrets in nest recognition.

Displacement: Turrets were broken off at their bases and moved 1-30 cm to the right or left as determined by a coin flip (N = 40), where they were supported by two pins in the soil (Figure 3.3). Turrets were moved after females left their nests.

Substitution: The turrets from 10 pairs (N = 20 bees) of neighboring nests (1 - 4.2 cm distant, $\bar{x} = 2.4$, $s = 1.22$) were exchanged, while bees were away foraging.

Deletion: Turrets were removed from nests (N = 25) while bees were foraging.

Experiment 3: The role of olfactory cues in nest recognition.

Experiment 3 a: The inner walls of the outer 5 cm of the nest entrances (including turrets) were washed with a cotton swab repeatedly dipped in hexane (N = 30). This wash was done immediately after a female exited from her nest. These nests are referred to as "washed nests." The time between the application of hexane and the return of the bee ranged

from 7 to 46 minutes (Chapter 2). Hexane is highly volatile and presumably dissipated during this time. The same individuals were observed on all the foraging trips made on the day of application. As a control, the same volume of hexane was applied to the outer surface of the turret and the surrounding soil (N = 15). Additionally, for N = 15 trials the inner surface of the entrance was rubbed with a cotton swab that did not have hexane.

Experiment 3 b: Turrets were removed at their bases. The entrances then were washed with hexane as described above. Upon a bee's return, following one approach flight, the unwashed turret was replaced over the entrance by resting it on two pins (N = 31).

Experiment 3 c: A ring of visual cues (see Experiments 2) was put around a nest entrance. Bees were allowed to forage for 6 to 9 days; a trial began after a bee left a nest, and the ring of cues plus the unwashed nest turrets were shifted from 1 - 3 cm, and the nest entrances (without turrets) were washed with hexane (N = 45) (i.e., a deletion of the chemical cues + a perturbation of the visual ones).

Experiment 3 d: Female bees were collected at distant (> 3 km) aggregations, and placed in groups of 10 into clean glass vials with 5 ml hexane, and stored overnight in a freezer; this volume was reduced to 2 ml by evaporating the hexane. These whole-body extracts were applied to nest entrances (N = 25) that had been previously washed as described

above (see Expt. 3 a).

RESULTS

Exploratory Behavior

Each day before the first foraging flight females made brief exploratory flights (median = 7.0, range = 4-17 secs, N=50) in the vicinity of the nesting area. A female departed from her nest head first and usually walked onto the turret and faced the bank. She took flight facing the nest, and returned in a gradually widening serpentine pattern. After flying 1-2 m away from the bank, the bee flew directly towards the entrance and briefly hovered about 5 cm in front of it. This loop was repeated 2 to 5 times, in different directions from the nest, before the bee flew away. Similar flights have been described for other aculeate Hymenoptera (refs. in Introduction), and have been described as "locality studies" or "orientation flights." In the absence of experimental manipulations females never made such flights on subsequent foraging trips on a given day.

The importance of visual cues

Visual objects put in place prior to exploratory behavior did not disorient returning bees and did not induce exploratory behavior on subsequent flights during that day (expt. 1a; Table 3.1). This finding contrasts with responses to objects placed after exploratory behavior (expt. 1b). These manipulations disoriented bees, as evidenced by the

significantly longer elapsed duration for entry (Table 3.1), as well as by the induction of exploratory behavior not different in duration from daily exploratory flights (median = 7.0 secs, range = 4-15, N = 50; $p > 0.1$, Mann-Whitney U test; see section on "Exploratory behavior"). After this visual disturbance, 31 of 39 females entered their nests immediately after contacting their own turret ($p < 0.01$, $\chi^2 = 6.78$, $df = 1$), suggesting an ancillary visual or chemical role for the turret in nest recognition (expt. 1b, 1c).

Larger visual objects play some role as landmarks, since their addition delayed the entering bees (expt. 1d); there was no significant difference between the delay time resulting from small-scale or large-scale cues ($p > 0.01$; Table 3.1). A bush placed in front of the bank disoriented bees, although eventually they found their entrances. The addition of a bush above the bank did not disorient bees. The latter finding probably means little as there were many other potential cues above the bank (e.g., fence posts, trees) for bees to use, and it was not possible to manipulate these objects.

The importance of turrets

Turrets do not provide necessary visual information, since re-moving them (cue deletion) did not significantly increase the duration for entry (Table 3.2, expt. 2), and did not cause any deviations in their flight paths or number of approaches. Shifting ring cues + turrets resulted in a

significantly longer duration for entry (Table 3.2, expt. 1 c). After turret manipulations, bees never explored before leaving for other foraging trips. In the dry season turrets commonly erode or break off, and are repaired only early in the dry season when the soil is malleable (Chapter 2).

Turrets do, however, provide some olfactory information. In one set of experiments (expt. 1 c) the nest entrance was covered with a mud paste such that it appeared visually indistinguishable to me from the nesting substrate. In conjunction with this manipulation ring cues and turrets were shifted, and bees given a choice between their own and an alien turret. During these trials bees flew directly toward the pasted entrance and briefly contacted the mud plug, and then usually hovered in front of it. Following this, the bees would usually fly away to begin another approach sequence, or land on the bank and crawl about in the vicinity of the pasted-over entrance. Searching bees entered their turret upon antennal contact, and sometimes sat inside for up to 3 minutes before backing out. Upon contacting a "foreign" turret bees rarely entered it (Figure 3.4). These findings suggest that some chemical compounds used for nest recognition may be adsorbed onto the turret.

The importance and role of olfactory cues

In the absence of manipulations bees entered their nests directly and without hesitation (Table 3.1). Washing the inner lining of the nest tunnel with a hexane swab produced a significant increase in the duration

for entry and a significantly greater number of approaches (Table 3.3; expt. 3a, c). This delay is also significantly greater than that for hexane applied to the outer surface as a control. The effect of this delay gradually decays throughout the day such that bees enter nests more rapidly on subsequent foraging trips on the same day (Table 3.3). No effects were observed on subsequent days. These results are explicable with one of two hypotheses:

(1) Bees recognize their nests by means of chemical signatures which are diluted by the application of hexane. A necessary assumption is that production of the compound(s) is continuous and they are deposited as the bee moves through the tunnel, accounting for the decline in duration for entry and number of approaches; or

(2) Bees simply avoid the odor of hexane, and the progressive decline in duration for entry with each post-hexane foraging trip occurred because the hexane dissipated through time.

Data obtained from the control (i.e., hexane applied to the surface) do not support hypothesis No. 2. When hexane was applied to the outer surface of the nest entrance both the number of approaches and time for entry were not significantly different from that obtained for no manipulations (cf. Table 3.1).

In another experiment (expt. 3 B) turrets were removed from nests and the burrows were washed with hexane. Following this manipulation the median time for one approach to the turret-less nest was 48 sec. After

the bees departed to begin another approach flight the turret was replaced: the median time for this approach was significantly shorter, and 24 of 31 bees ($p < 0.05$, $X^2 = 4.66$, $df = 1$) entered their nests following replacement of the turrets (Table 3.4). These data suggest that chemicals adsorbed onto the nesting substrate are used as cues by the bees to recognize their nests.

The deletion of chemical cues (above) increases the delay time for bees entering nests. The addition of a cue (i.e., whole-body extracts of alien females) results in a similar delay for the first approach flight (median = 43, range = 29-78, $p > 0.1$, Mann-Whitney U test, expt. 3d). There is a significant correlation between "time for the first approach flight" and total "time for entry" (Spearman's $\rho = 0.57$, $p = 0.003$, $n = 25$). Overall, however, the effect of this kind of cue addition is not as great as for cue deletions [total time for extracts: median = 111 secs, range = 17-283; versus hexane washes: median = 192 secs, range = 53-245 ($p < 0.001$, Mann-Whitney U Test)].

DISCUSSION

The Discussion first reviews mechanisms of nest recognition in other Apoidea, and then discusses the relationship among contextual changes and social evolution.

Mechanisms of nest recognition

Animals use information from one or more of their senses as they move about (e.g., refs. in Carthy, 1956; Jander, 1975; Schöne, 1984; Bell and

Carde, 1984; Bell, 1990). Objects placed near the nest entrance prior to exploratory behavior never disturbed a provisioning Lasioglossum figueresi, although the same objects disoriented her when put in place after exploration. The latter manipulation induced another locality study prior to the next foraging flight while the former did not. These bees, and other nesting Hymenoptera, learn spatial relationships among objects in their nesting area during exploratory flight behavior (see Wehner, 1981).

The fidelity of bees and wasps to a particular place is well-known, and homing individuals alter their flight paths in response to alterations in spatial positions of local landmarks. In contrast, female L. figueresi homed to their nests following the displacement of very local visual cues. These bees may localize their nests using larger-scale landmarks such as bushes and posts, but these could not be eliminated. Various facts discussed below show that bees perceive visual objects, yet do not necessarily respond to their deletion. Such findings suggest they are capable of multimodal orientation. This "switching" to olfactory signals as additional cues is well-known in honey bees (see Bogdany, 1978; refs. in Bitterman, 1988).

Several lines of evidence support the interpretation that L. figueresi identify their nest entrances in part by chemical cues. Following the application of hexane, bees identified their nests only after some delay. If, however, turrets were removed prior to the application of hexane and

later replaced, then bees entered their nests more directly. In both cases, following the chemical manipulations, bees later exited their nests after depositing their pollen load, and did not perform exploratory behavior before the next foraging trip. Similarly, if the entrance was sealed with mud and the turret shifted several cms (expt. 2 b), a bee almost always entered her turret after antennal contact, but rarely entered similar-looking but foreign turrets, from nearby or distant nests. If, however, turrets were swapped between neighboring nests, then bees made little use of the olfactory information. The application of whole-body extracts of foreign bees significantly delayed bees entering their nests, although this delay was significantly less than that caused by the application of a hexane wash (i.e., deletion of odor cues). Addition of a signal is given greater weight by pigeons than is deletion of a signal (Hearst and Wolff, 1989). Further work is needed on bees since different cues were added and deleted in this study.

The use of chemical signatures at nest entrances for individual recognition has been proposed repeatedly (e.g., Lubbock, 1882; Shinn, 1967). Linsley (1958) even suggested that selection for such abilities might be more pronounced in populations nesting in large aggregations. He also cited Jacobs (1924), noting that cues might be glandular products which in solitary females are associated with mating (Chapter 4). For some bees the presence of individually distinctive Dufour's gland secretions at nest

entrances has been confirmed but bioassays either have not been made (Hefetz et al., 1986; Brooks and Cane, 1984), or did not demonstrate a recognition function (Hefetz et al., 1982). In other cases bioassays demonstrated a recognition function, but detailed chemical analyses are lacking. Excellent studies by Steinmann (1973, 1985, 1990) demonstrated that bees of several species readily discriminated foreign nests from their own (see Table 3.5).

When the odors of foreign bees were applied to nest entrances, these chemicals disrupted identification (a delay in the duration of entry of returning bees into their nests), but did not prevent localization (Results; also Hefetz et al., 1986; Shimron et al., 1985). The number of components in these chemical badges can be high (> 20), theoretically enabling individual nest recognition even in areas of high nest density (Hefetz and Graur, 1988).

In some bees and perhaps many sphecid wasps, nest "recognition" (=identification and discrimination) may be equivalent to nest localization. "Topographic nest recognition" may occur in relatively simple habitats such as the "Philanthus plains" of Hulshorst (Tinbergen, 1958), or in areas where nests occur at low densities. Mason bees (Chalicodoma spp., Megachilidae), for example, build mud nests on cliff faces, rocks, or buildings. Fabre (1914) shifted nests short distances (< 30 cm) and a bee always returned directly to the spot where its nest had been.

A searching bee ignored its nest when it passed nearby (< 2 cm). He also reciprocally switched nests from pairs of nearest-neighbors; in all cases bees returned to the place where its nest had been, and continued working on the foreign nest it found there. For some Chalicodoma, therefore, the mechanisms of nest localization, identification, and discrimination probably involve mainly vision (other megachilids use olfaction too-- see Table 3.5).

In an active nesting aggregation of a hunting wasp, Ammophila, Baerends (1941) buried soil-filled biscuit cans in which wasps nested. He then replaced nest-containing cans with only soil-containing ones; these experimental manipulations, analogous to Fabre's (above), indicated that no olfactory attractants originated from the nest. To date, the only evidence for chemical nest recognition in a sphecid wasp is Steinmann's (1976) studies of Psenulus (Pemphredoninae) which marked their nest entrances with individually distinctive odors. These wasps are in the only subfamily of Sphecidae known to use glandular secretions in nest construction (Malyshev, 1968; pers. obs. of unpubl. film by W.L. Rubink, courtesy of H.E. Evans, Colorado State University); this is the only sphecid taxon with eusocial species (refs. in Wcislo, 1990b).

As seen above, studies addressing olfactory nest recognition in Sphecidae are needed because olfactory cues are used by these wasps in many contexts: some sphecid wasps are remarkably successful in finding

their nests, even after local landmarks have been completely trampled underfoot [although landmarks on the horizon usually are available (van Ieserl, 1975)]; digger wasps use chemical cues for prey recognition when hunting (Tinbergen, 1972; Steiner, 1983), but do not use them for prey recognition at the nest site (e.g., to recover lost prey items--Baerends, 1941); female wasps (Sphecius) may respond differentially to familiar individuals (Pfenning and Reeve, 1989); and parasites are attracted to wasp nests in part by olfaction (Wcislo, 1986; Rosenheim, 1987).

Recognition, Contextual Changes, and Social Evolution

As discussed by Jaisson (1985), a major feature of insect social evolution involves the controlled use of olfaction in modulating social integration and homeostasis (e.g., Verlaine, 1924, 1925; Frisch, 1967; Butler et. al., 1969, 1970; Kukuk et. al., 1977; Foster and Gamboa, 1989; Breed et al., 1989; Espelie et al., 1990). Among solitary bees, are there material sources of inherited variation to permit the evolution of chemo-recognition and modulation abilities?

Comparisons between a solitary bee, L. (D.) figueresi (Results; Chapter 2), and a congeneric social species [e.g., L. (D.) zephyrum] show that both species use chemical cues for nest recognition, guarding, and mating. One might conclude that sensory systems for recognition evolved in some context other than a group-living one. This interpretation however, cannot be supported because, based on morphology and

behavior of congeners, L. figueresi may be secondarily solitary (Wcislo, 1990 a).

The evolutionary transfer of signal usage from one context to another is wide-spread (refs. in Hölldobler and Carlin, 1987; West-Eberhard, 1984), so it is nonetheless likely that the origin of kin recognition abilities had little to do with group-living per se, but was related more to the parental investment in nest structures, stored food, etc., or to behaviors associated with mating, as discussed in Chapter 4. Indeed, olfactory learning predates the evolution of the Aculeata since it has been demonstrated in numerous Parasitica (Hymenoptera) (e.g., Papaj and Vet, 1990). Once evolved, the use of olfaction for mate and nest recognition may facilitate the development of more complex societies, due to an ability to segregate along lines of kinship (cf. Hamilton, 1964). A related example of social signal transfer involves the burrow entrances of desert isopods (Hemilepistus reaumuri) which are surrounded by embankments of feces, analogous to the bee turrets. These embankments allow isopods to discriminate their own burrow from an alien's, possibly using the same chemical badges used to recognize kin (Hoffmann, 1985; review: Linsenmair, 1987) [for other examples, see Pedersen and Blass (1981), Free (1987), and Hölldobler and Wilson (1990)].

The origins of social behavior and the learned abilities to recognize individuals (things or conspecifics) are related in Hymenoptera. Bees are a

derived group of "sphecoid" wasps which often line their nest cells with glandular secretions, while most sphecid wasps do not (Malyshev, 1968; Michener, 1964, 1974). This difference may relate to the greater apparent use of olfactory information by bees relative to sphecids to modify their behavior at the nest. In turn, this difference relates to the phyletic distribution of sociality: one lineage of Apoidea (bees with > 20,000 species) has independently evolved variably complex social and parasitic behavior many times, while other lineages (digger wasps with > 7,700 species), often living in the same areas, remained mostly solitary or communal, despite its greater antiquity, and despite both lineages having undergone much speciation (Wcislo, 1990b).

Evolutionarily, the perception of compounds used initially only to line brood cells may facilitate the evolution of social recognition mechanisms, including those for mating. The use of the same mixture in different contexts facilitates the evolution of communication, as explained by Haldane and Spurway (1954) for aural signals and vocal mimicry in birds. The chemicals and sensory systems used for nest recognition are probably transferred for use in social contexts (see Hölldobler and Carlin, 1987). Within Apoidea, in situations where group-living is advantageous (Lin and Michener, 1972), some bees may make use of these compounds to associate with kin, permitting the evolution of more highly integrated societies.

ACKNOWLEDGEMENTS

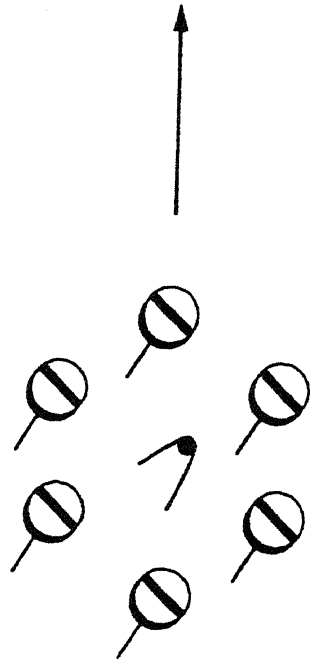
I am especially grateful to Andrés, Anna, Jessica and William Eberhard and Mary Jane West-Eberhard for much help and hospitality while I did field studies; Bryan Alvarez Spivak and Marla Spivak also were very generous and helpful. I thank the following people for useful discussions or criticisms: William Bell, Donna Conlon, W. Eberhard, George Eickwort, Rudolf Jander, Robert Minckley, Laurence Packer, M. Spivak, Erwin Steinmann, Jan Tengö, M.J. West-Eberhard, Doug Yanega, and especially Charles Michener. Howard Evans generously provided film of a nesting pemphredonine wasp. R. Jander kindly allowed me to read his thorough and insightful review of exploratory behavior in aculeate Hymenoptera. Financial support was provided by a Smithsonian Tropical Research Institute Short-term Fellowship; a Sigma-Xi grant-in-aid for graduate research; the P.L. Stouse Memorial Fund, Department of Geography, University of Kansas; a U.S.A. National Science Foundation Doctoral Dissertation Improvement Grant (BNS 87-01046); and the Theodore Roosevelt Fund of the American Museum of Natural History.

Figure 3.1. Diagram showing six painted discs placed in a ring centered on the nest turret of Lasioglossum figueresi. Ring cues are left in place during a training period (top), and then shifted a given distance during experimental trials (Experiment 1 a-c).

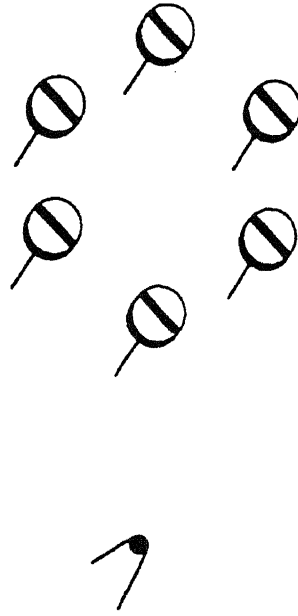
Figure 3.2. Schematic illustration showing the flight paths of three approach flights of a Lasioglossum figueresi female.

3.1

BEFORE



AFTER



3.2

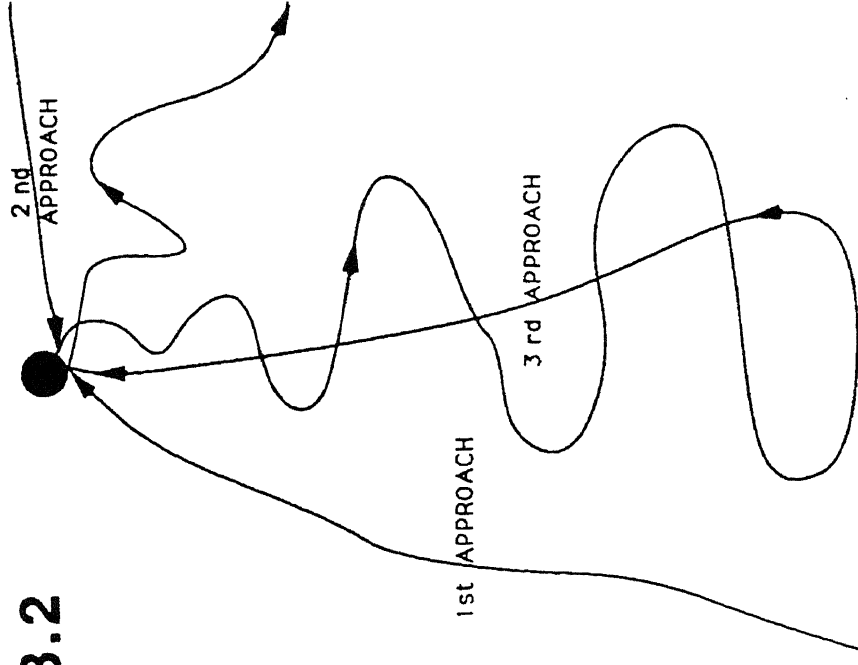


Figure 3.3. Diagram showing a nest turret in situ, as well as the method for supporting the turret during experiments (Experiments 2 and 3).

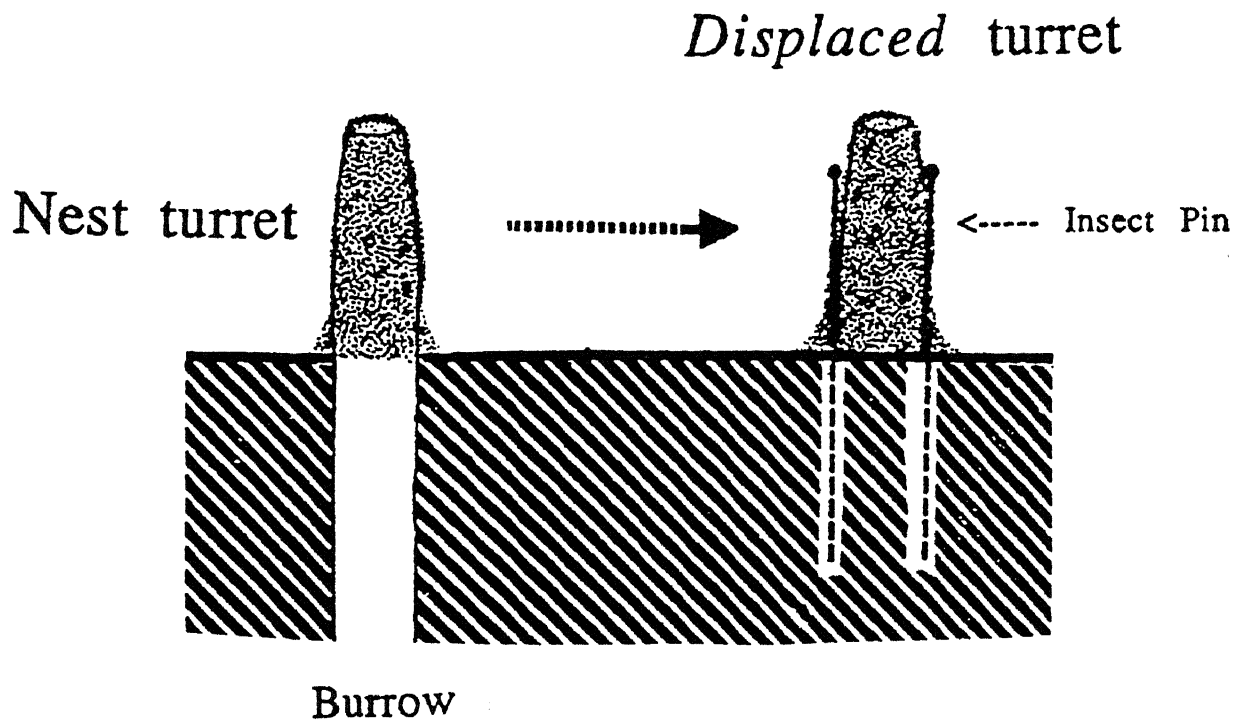
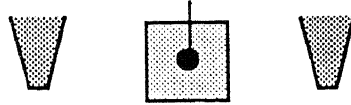


Figure 3.4. Responses of female Lasioglossum figueresi returning to their nests after turrets were removed, and the entrances were covered with a mud paste. The bee's turret and an alien turret were placed to the right and left of the true entrance (as in Fig. 3.3).

MUD - PASTE
COVERED
ENTRANCE



OWN
TURRET

ALIEN
TURRET

CONTACTS TURRET

15

13

ENTERS TURRET

15

4

N = 15 bees

G = 3.28 ($\chi^2_{.05 [1]} = 3.84$)

0.1 > p > 0.05

Table 3.1. Responses by *Lasioglossum figueresi* females returning from foraging to visual objects added near the nests. Median values are given with ranges in brackets; sample sizes are given in parentheses. Within columns, values are significantly different from other values not sharing the same letter ($p < 0.01$).

EXPERIMENTAL MANIPULATION	APPROACHES TO NEST	TIME (SECS) FOR ENTRY INTO NEST	EXPLORATION INDUCED?
No manipulation (49)	1 [1-2] ^a	6.0 [5-15] ^a	NO
Ring cues before locality study (39)	1 [1-2] ^a	9 [5-20] ^a	NO
Ring cues after locality study:			
1st return trip (38)	4 [2-7] ^b	138 [64-219] ^b	YES
2nd return trip (37)	1 [1-2] ^a	11 [5-29] ^c	NO
Bush above bank (21)	1 [1-2] ^a	7 [5-16] ^a	NO
Bush in front of bank (20)	4 [3-7] ^b	168 [42-230] ^b	YES

Table 3.2. Responses by Lasioglossum figueresi females to manipulations involving nest turrets. Other information as for Table 3.1.

EXPERIMENTAL MANIPULATION	APPROACHES TO NEST	TIME (SECS) ENTRY INTO NEST	LOCALITY STUDY INDUCED?
No manipulation (49)	1 [1-2]	6 [5-15] ^a	NO
Turrets deleted (25)	1 [1-2]	7 [5-16] ^a	NO
Turrets shifted < 1 cm (40)	1 [1-2]	9 [5-21] ^b	NO
Neighbor turrets swapped (10 pair; 20 bees)	1 [1-2]	11 [5-19] ^{b,c}	NO
Ring cues & turrets shifted 1-30 cm (45)	1 [1-3]	14 [5-25] ^c	NO
Ring cues & turrets shifted + mud patch (15)	7.11	not measured	NO/YES ²

¹The number of approach flights depended on when the mud-paste patch was removed.

²Eleven of the bees did not make a locality study on the next flight, while 4 bees did.

Table 3.3. Median number of approach flights and time of entry for several foraging trips on the same day following the application hexane to the inner linings of bee tunnels; ranges are given in brackets, and sample sizes are given in parentheses. To maintain an experiment-wise error rate of 0.05, an adjusted significance level of $0.05/6 = 0.008$ was used.

SAME - DAY FORAGING TRIPS AFTER ONE HEXANE APPLICATION	APPROACHES BEFORE ENTRY	TIME (SECS) FOR ENTRY INTO NEST
Control (15)	1 [1-2] ^a	8 [5-18] ^a
First trip (30)	5 [2-12] ^b	192 [70-262] ^b
Second (30)	3 [2-5] ^c	112 [63-247] ^c
Third (15)	2 [1-4] ^a	84 [48-128] ^d
Fourth (8)	1 [1-2] ^a	33 [16-73] ^e

Table 3.4. Median time for one approach flight during a return trip by a female Lasioglossum figueresi following the application of hexane to the inner lining of the nest tunnel; after one approach, the nest turret was replaced and times were recorded for subsequent approach flights, until bees entered their nests. Ranges are given in brackets, and sample sizes are given in parentheses.

MANIPULATION	TIME (SECS) FOR ONE APPROACH FLIGHT	NUMBER BEES ENTERING NESTS AFTER APPROACH
Hexane wash (31)	48 [22-82] ^a	0
Turret replaced:		
1st Approach (31)	7 [5-39] ^b	26
2nd Approach (5)	5 [5-15] ^b	4
3rd Approach (1)	5	1

Table 3.5. Partial list of known mechanisms for nest localization and identification among free-living bees and hunting wasps (Apoidea); numerous taxa are known to use visual cues for nest localization (see Wehner, 1981), but these have been excluded for all cases where the authors do not report information on the possible use of olfactory cues for nest identification.

TAXON	VISUAL CUES?	OLFACTORY CUES?	GLANDULAR PRODUCTS IN NEST?	REFERENCE
BEES (APIFORMES)				
<i>Apis mellifera</i>	YES	YES	YES	Free, 1987; Butler et al., 1969, 1970
<i>Bombus occidentalis</i>	YES	YES	YES	Foster & Gamboa, 1989
<i>Xylocopa imitator</i>	YES	YES	YES	Anzenberger, 1986
<i>X. pubescens</i>	?	YES	YES	Hefetz et al., 1990
<i>X. virginica</i>	YES	YES?	?	Rau, 1929
<i>Mesotrichia caffra</i>	YES	YES?	YES	Skaife, 1952
<i>Melissodes</i> sp.	YES	YES	YES?	Turner, 1908
<i>Anthophora plagiata</i>	YES	YES	YES	Steinmann, 1985
<i>Eucera palestinae</i>	YES	YES	YES	Shimron et al., 1985
<i>Heriades truncorum</i>	YES	YES	YES?	Steinmann, 1976

(Table 3.5, continued)

TAXON	VISUAL CUES?	OLFACTORY CUES?	GLANDULAR PRODUCTS IN NEST?	REFERENCE
<i>Osmia cornuta</i>	YES	YES	YES?	<u>op. cit.</u>
<i>O. bicornis</i>	YES	YES	YES?	<u>op. cit.</u>
<i>O. rufa</i>	YES	YES	?	A. Raw, ms.
<i>Chalicodoma</i> spp.	YES	NO?	YES	Fabre, 1914
<i>Megachile centuncularis</i>	YES?	YES	?	A. Raw, ms.
<i>Andrena vega</i>	?	YES	YES	Steinmann, 1990
<i>Anthidium manicatum</i>	?	YES	?	A. Raw, ms.
<i>Lasioglossum</i> (D.) <i>zephyrum</i>	YES	YES	YES	Kukuk et al., 1977; WTW, pers. obs.
<i>L. (D.) figueresi</i>	YES	YES	YES	Results
<i>L. (E.) malachurum</i>	?	YES	YES	Ayasse, 1990; Hefetz et al., 1990

(Table 3.5, continued)

TAXON	VISUAL CUES?	OLFACTORY CUES?	GLANDULAR PRODUCTS IN NEST?	REFERENCE
HUNTING WASPS (SPHECIFORMES)				
<i>Ammophila campestris</i>	YES	NO	NO	Baerends, 1941
<i>Bembix</i> spp.	YES	NO (YES?)	NO	van Iersel, 1975; Nielsen, 1945
<i>Philanthus triangulum</i>	YES	NO	NO	Tinbergen, 1972
<i>Cerceris</i> spp.	YES	NO?	NO	Tsuneki, 1965
<i>Sceliphron caementarium</i>	YES	NO	NO?	Ferguson & Hunt, 1989
<i>Psenulus fuscipennis</i> (Pemphredoniae)	YES	YES	YES	Steinmann, 1976

CHAPTER 4

MATE ATTRACTION AND MATING BIOLOGY OF SOLITARY HALICTID BEES

Hymenoptera--especially Aculeata--are well-known for their sophisticated learning abilities, but these are usually studied in females. Female worker bees (Apis), for example, learn information about floral shapes, colors, and odors, and also learn of numerous stimuli related to social behavior (e.g., Frisch, 1967; Lindauer, 1985), including the recognition of nest-mates (refs. in Fletcher and Michener, 1987). Wheeler (1919) described male aculeates as "ethological non-entities" (see Evans and O'Neill, 1988). In fact, however, in terms of their goal (mating), the repertoire of male aculeates is rich, and their behavior is often dependent on local conditions (e.g., body size, or distributions of female abundance) (Alcock et al., 1978; Thornhill and Alcock, 1983; Evans and O'Neill, 1988). Males of a eusocial bee, Lasioglossum zephyrum (Smith) (Halictidae), for example, habituate to odors of nest-mate females, and of unreceptive females, and use this information to modify their behavior in situation-appropriate ways, under both laboratory and natural conditions (Barrows, 1975; Greenberg, 1982; Smith, 1983; Smith and Ayasse, 1987; Wcislo, 1987 b; reviews, Michener and Smith, 1987; Greenberg, 1988).

Most studies of mating behavior in aculeate Hymenoptera have

been totally unrelated to studies of social evolution, which is surprising given the high level of interest in the evolution of worker sterility. The reasons why many halictid workers do not mate are poorly understood, in part due to the general neglect of mating biology mentioned above.

Furthermore, as discussed in Chapter 3, there is considerable interest in understanding the evolutionary origins of the recognition systems which permit cohesive social groups (also West-Eberhard, 1989). One hypothesis postulates that such kin recognition systems arose in a solitary ancestor in a functional context of sexual behavior in solitary ancestors (Jacobs, 1924, cited in Linsley, 1958). In particular, males are hypothesized to learn odors of nest-mates, which they then avoid to avoid close inbreeding (Hölldobler and Michener, 1980; Michener, 1982; refs. above). Nothing is known, however, concerning simple learning behavior in solitary species or populations. Bioassays on solitary halictid bees, Lasioglossum (Dialictus) figueresi Wcislo (Halictinae) and Nomia triangulifera Vachal (Nomiinae), were made to ascertain if males learn individually different female-produced odors. Similar studies on a eusocial species L. (D.) zephyrum (Smith) (Halictini) were made by Wcislo (1987 b).

This chapter also presents ethological data on the mating behavior of N. triangulifera, to define the environment with which learning might occur. Empirical and theoretical studies of sexual selection support the hypothesis that many features of a male's behavior and morphology

function at a proximate level to provide stimulation to a female so that she completes mating with him (Richards, 1927; Eberhard, 1985). This hypothesis predicts that occurrence of complex pre-copulatory behavior should be associated with relatively simple male genitalia and little species-level genitalic diversity among related species. Species without preliminary courtship should have complex and species-specific genitalia. N. triangulifera is unusual because of its extremely complex pre-copulatory courtship behavior, combined with its modified legs, metasomal sterna, and genitalia, which are species-specific among Nomia (e.g., Cross, 1958; Michener, 1965; pers. obs.).

NATURAL HISTORY AND BACKGROUND INFORMATION

Lasioglossum figueresi (Halictinae)

The natural history of female Lasioglossum figueresi in Costa Rica is given in Chapter 2, together with an account of nesting sites. An overview of male behavior is briefly given here to clarify the reasons for experimental studies.

Male and female brood are present in equal numbers, and develop throughout the dry season (December to April), and they eclose as adults beginning in mid- to late April. Adult bees remain in opened cells in nests until they emerge from the nests in mid- to late-June during a characteristic lull of the wet season (veranillo) (see Fig. 2.6, Chapter 2). Males leave their natal nests and patrol among bushes along a vertical

bank opposite the bank where females are nesting (the two banks are ~ 3 m apart, and both the nest aggregation and the length of the patrolled area was ~15 to 20 m; "Nice view" site of Chapter 2). At four other nest aggregations males were never observed patrolling near the nest site, although they were seen leaving nests in the morning, and returning to them in the afternoon or before rains. Nights are spent within nests. Males became progressively less abundant throughout July, and are rare by the end of the month.

Flight patterns were generally less frenetic than those of some smaller Dialictus, such as D. zephyrum or imitatum (Batra, 1966; Michener and Wille, 1961; pers. obs.). A male approaching a female has a characteristic posture with his antennae directed forward (see Figure 4.1), and flies in a serpentine flight path. Males pounce on females that land on a leaf, twig, or the surface of the bank, and the pair then falls to the ground. In only one of 17 such cases was it possible to definitely observe copulation (except with dead females, see below). In this one case, mating was brief (~43 secs), as in some other Dialictus (Barrows, 1975). Males also sometimes pounced on other males, small pompilid wasps, beetles, etc.

Nomia triangulifera (Nomiinae)

I studied the mating behavior of Nomia (Epinomia) triangulifera at large aggregations of nests at a farm on a floodplain along the south bank of the Kansas River between Eudora and Lawrence (Douglas Co.), Kansas

(38° 57' 30" N, 95° 7' 30" W). Female bees emerged from, and nested in, fields where crop plants [corn (Zea mays), soy beans (Glycine max), and alfalfa (Medicago sativa)] were rotated annually, or the fields were left fallow. Nomia have been nesting at this site at least since 1972 (Mr. Gregory Shipe, pers. comm.) (details of the site, and female nesting biology, are given in a paper with R. Minckley, W. Wcislo, S. Buchmann, and D. Yanega, in prep.).

N. triangulifera is active from mid to late August through September in eastern Kansas. A portion of the male population is protandrous, such that some males emerge before any females, but thereafter the distributions overlap. Males flew in great numbers over areas where females emerged, and were also abundant on the plant (Helianthus annuus) from which females gather pollen and nectar. Males have elaborate courtship (also Wcislo et al., in prep.). After mating, females establish nests which they provision with sunflower pollen. Approximately 2 to 3 weeks after initial emergence, males become scarce at the site and much rarer on flowers.

The genus Nomia contains 20 New World species, which are placed in several smaller groups, N. (Acunomia), N. (Curvinomia), and N. (Epinomia + Dieunomia) (Hurd and Moure, 1987). Many Nomia have highly modified legs, sterna, and genitalia, which provide useful taxonomic characters, although their functions are mainly unknown.

Voucher Specimens

Voucher specimens of the bees are in the Snow Entomological Museum, University of Kansas; audio and video samples of the courtship behavior will be deposited in the Library of Natural Sounds, Cornell University (Ithaca), and the Archives of the Kinsey Institute for Sex Research, Indiana University (Bloomington), respectively.

METHODS

Lasioglossum figueresi

Cage experiments on the role of olfaction in mate location, and individual female odors

Male and female pupae were collected in mid-April from nest cells (see Chapter 2). Pupae were transferred to plastic tissue culture trays, with 1 or 2 females and 2 or 3 male pupae per plastic cell; pupae were mixed from different natal nests. All bees, therefore, had social experience following eclosion. Callow adults were kept together for ~48 hours, and periodically fed honey-water solution (1:1). Female bees (N = 19) were then transferred to individual 6 dram glass vials, and were killed by freezing; they are called unextracted females below. An additional 11 female bees killed as described above, were placed in three washes of excess hexane, baked in a ~50°C oven for 24 hours, and then frozen in individual glass vials. These females, called extracted females, were presumably devoid of any volatile chemicals. Eleven males were transferred to an

inverted "fish cage" (16 X 12 X 12 cm), and were given honey-water ad libitum (methods in Greenberg, 1982); the cage was placed on an island in a pan of water to prevent ant attack. Males used in the tests were between 48 and 96 hours after becoming adults.

To determine if males respond to female-produced olfactory cues, their behavior was compared when they were presented with frozen unextracted females versus extracted females. Females were coded so that during tests I did not know their class. A test involved taking a frozen female from a vial, sticking a #2 or 3 insect pin through the thorax (see Figures 2 and 3), and then inserting the pin in the cage floor so that the bee was ~2-3 cm above the floor of the cage, which was placed in bright sunlight in still air. The numbers of males approaching the pinned female and those contacting her were counted using hand-held counters for each minute during a 4 minute period.

A Contact is unequivocal, and varies from a male momentarily touching or landing on a female, to extended attempts to copulate; frequently a male everted his genitalia and attempted to insert them in the female, sometimes successfully (Figure 4.2). An Approach involves both a characteristic male flight posture and the flight pattern: the male oriented to the female, antennae directed forward (Figure 4.1), and flew within 5 cm of her, hovering and zig-zagging along a serpentine flight path (after Kullenberg, 1973; Smith, 1983; Wcislo, 1987 b).

Field studies on the role of olfaction in mate location and male learning

Some of the experimental studies planned for L. (D.) figueresi [described below for Nomia; also Wcislo (1987 b)] require several groups of naive males. I located only one population of active males, so first I needed to determine if marked males ranged over the entire area where males patrolled, or if flight paths were restricted so that there were "sub-groups" of males.

Male patrolling: To ascertain the size of the areas that males patrol, males were captured, individually marked with enamel paints on the thorax, and released (N = 33; 29 June- 3 July, 1988). On each of 2 subsequent days, at seven stations (A - G), each 5 m apart, all male bees that flew by in a 5 minute period were captured, inspected for color marks, and released.

Male learning: Experiments on the role of learning used protocols similar to that described for the cages studies, with the modifications described below. Adult females bees (N = 20) were collected from nests at "Near site," placed individually in glass vials, and killed by freezing. Frozen bees were stored overnight in a freezer, and the next day were carried to the "Nice view" nest aggregation in a cooler with frozen "ice substitute" (Coleman's® Chillers). Females were pinned and placed at the ends of branches in the bushes along the bank (Figure 4.3) where males patrolled; the experimental site was mid-way between the ends of the area where most males patrolled. Responses were scored as above (Cage studies),

except that responses are reported per minute for each 4 minute period. Not all males were marked, so it was not always possible to distinguish between the same male contacting a female twice, and two different males doing so once each. An additional five unextracted females were left exposed to air (away from females) for 30 to 60 minutes before they were presented to males to determine if attractants dissipated after exposure to air at field temperatures (23 to 27°C).

Nomia triangulifera

Since Nomia triangulifera males were abundant at the emergence site, more details of its mating biology are known.

Emergence phenologies and operational sex ratio

The intensity of intra-sexual competition is influenced by the operational sex ratio (OSR), or the ratio of the number of males present to the number of receptive females. Daily measures of the OSR were obtained through patterns of the emergence phenologies of males and females in 1989 and 1990. Emergence phenologies of bees were determined by placing three 1 X 0.5 m and one 1 X 1 m emergence traps (see Wcislo and Minckley, in prep.) over areas where bees nested the previous year. These traps covered a total area of 2.5 m². Traps were checked daily, the numbers and sexes of emerging bees were recorded, and the bees were removed. The operational sex ratio was estimated by determining the number of emerging, receptive females per day, divided

by the cumulative number of males that had emerged up to that date (assuming males live 11 days).

Male patrolling behavior

The areas in the fields where bees emerged covered up to 2.8 hectares. There was yearly variation in the locations and sizes of the areas that males patrolled, but this was mostly a result of crop rotation in these fields. On 19 August 1986 a mark-recapture study was initiated to estimate the fidelity of males to particular areas. A portion of the site was divided into two 15 X 15 m quadrats, and two 2 X ~50 m quadrats (running along an access road) (each quadrat was separated from the others by ≥ 50 m). Quadrats were sampled simultaneously by me and three others. All the bees that were collected in each quadrat between 9:00 and 11:00 hr were marked with colored paint on the thorax, a different color for each quadrat, and released into the air in their quadrats of origin (green = 161 bees; purple = 173 bees; white = 92 bees; orange = 147 bees). Bees were then collected to determine the frequency of marked individuals during 15 minute periods in each quadrat on 20, 22, and 26 August. A smaller-scale study was undertaken on 23 August 1986. Two adjacent 3 m² quadrats were chosen and all the bees that passed through were collected and marked (yellow = 62; blue-white = 39), and then released approximately 20 m away up-wind.

Male learning of female odors

The protocol for N. triangulifera was the same as that used for L. figueresi, except as indicated below. The use of female odors as sex pheromones was studied by comparing the relative attractiveness of frozen unextracted females (N = 20) versus hexane-extracted females (N = 20). To localize the source of potential pheromones, heads, thoraces, and abdomens were individually crushed onto 2 x 4 mm black velvet rectangles, which were then tested as for frozen unextracted females (N = 30 for each tagma).

Results indicated that individual females differed in their overall attractiveness to males. To better understand this variability I compared the relative attractiveness of newly emerged (presumably unmated) females, with older (presumably mated) females. The criterion used to discriminate between these classes was whether females carried pollen. Pollen-collecting females usually have developed ovaries and are mated, while females that have not yet begun to provision cells usually were not mated (as determined by lack of sperm cells in spermathecae) or had undeveloped ovaries. Females (N = 15) without pollen were collected and frozen as described above, as were females with pollen (N = 15). Females were tested as described above, except that each female was tested at three different field sites. Five pollen-collecting females were likewise collected and frozen; as much pollen as possible was removed with an insect pin,

and the bees were washed in distilled water, and returned to the freezer. Subsequently, they were presented to males as described above.

Male learning of individual female odors was studied by presenting frozen females to males at three sites, A, B, and C (indicated by A1, B1, etc.); these same bees then were presented a second time at A and B (indicated by A2 or B2) (N = 30 females each) (methods from Wcislo, 1987 b, and references therein). Sites A and B were approximately 100 m apart on a line parallel to the direction of the prevailing winds, and site C was ~ 500 m away at the other end of the fields. Responses of males to an additional 34 frozen unextracted females were recorded on videotape and later analyzed to determine the waning of response through time.

Social facilitation

To determine the role of social facilitation (Clayton, 1978), 25 randomly chosen one-minute periods of video were divided into 60 events each. Every one-second event was scored as either "yes" or "no," depending on whether a male approached the frozen female during that time. [Males that remained and courted the dead female were counted only once].

Flight paths

Representative flight paths of "approach" and "contact" are shown in Figure 4.4. These were made by copying the path of the bee from a horizontal video image to a computer by means of a digitizing bit-pad; as

the bee's image moved a cursor pen was used to follow its path, which was inputted at 11 data points per second.

Courtship and mating behavior

Details of the courtship and mating behavior were studied by numerous hours of direct observation of hundreds of mating pairs. While copulating the bees are largely oblivious to all else, and can be approached within one cm (a 10X handlens was sometimes used in the field); without much care a mating pair could be picked up. Mating was video-taped (3.5 hrs) using a Panasonic videocamera with close-up lens, and tripod (in 1987 and 1988); or filmed with a Paillard Bolex 16-mm film camera with an Yvar 150 mm macro-lens, and tripod (in 1986)*. Mating pairs were picked up and quickly placed on a platform (which sometimes consisted of a microphone) set up in front of the camera. Approximately 7 hours of audio recordings were made using a Uher reel-to-reel tape recorder (tape speed = 19 m/s), with a standard microphone (this often served as the platform for filming). Preliminary analyses of sound recordings were made using a Kay Elemetrics DSP Sona-graph (Model 5500), connected to a Uher 4000 reel-to-reel recorder via a Krohn-Hite mode 3550 filter (LP = ~575 Hz).

*Approximately 1.5 hours (out of 10 hours shot) of 16 mm film recordings provided useful details; analyses of some of these frames are included in Wcislo et al. (in prep.).

To examine size-related patterns of mating behavior, I measured the sizes of females and their male partners (N = 20 MM and 20 VV), males patrolling at the emergence/nesting site (N = 44), and males patrolling at flowers (N = 51). Size (inter-tegular distance) was measured using a Wild microscope (10X) with an ocular micrometer. Some males (N = 21) were also dried to a constant weight at 50°C (Thermolyne Oven/Incubator), and weighed on a Fisher electronic balance to the nearest 0.001 g; for these males I also measured the lengths at the longest point of the inner face of the expanded hind tibiae.

The receptivity of females was studied as follows. After being courted, there are obvious behavioral signs (to an observer, see below) that indicate whether a female is sexually receptive. I observed mating pairs to determine the receptivity status of females: "receptive to 1st male & mated" females mated with the first male I introduced to them (N = 34); "unreceptive" females refused to mate with the first male (N = 18); and "receptive to 1st male & unmated" females were receptive to the first male, but the pair was separated before intromission (N = 26). Females from these classes were individually introduced to 3 - 5 males in either a fish cage (above), or a 1 X 0.5 X 1 m enclosure (an emergence trap) to ascertain receptivity. Additionally, the spermathecae of 11 "receptive and unmated" and 14 non-receptive females were dissected successfully and examined for presence of sperm cells in the spermathecae.

RESULTS

Lasioglossum figueresi

Cage experiments on the role of olfaction in mate location

In small laboratory flight cages newly eclosed (48 to 96 hours old) adult males pounce on unextracted females much more frequently than they do on extracted ones (Table 4.1), showing that the presence of olfactory cues reduces a male's threshold to respond to other cues, despite the fact that newly eclosed males and females in nature are not yet sexually active. Among living individuals, although several males made attempts, no females were sexually receptive.

The rate of pouncing on dead females (0 to 5 contacts per 5 minute period) was much lower than observed later, under more natural conditions (below), and may relate to the onset of sexual maturity. Ovaries of these females were slender. Two frozen unextracted females were completely unattractive to males (no contacts); of the 17 contacted females, 8 were sufficiently attractive to cause the male to evert his genitalia, and remain mounted on the dead female for 12 to 244 seconds (\bar{x} = 73 + 73.9 secs. (SD), N = 10 males). Males did not perform any visible courtship behaviors while mounted on the female.

Field studies on the role of olfaction in mate location

Males leave their natal nests in mid-June, and (at least at one site) patrol among vegetation along a bank across the trail from the bank where

females are nesting (and where males return at night and during inclement weather); 3 marked males returned to the same burrow on up to 5 different nights, but I do not know if they preferentially use their natal nests. Males were not obviously aggressive to one another while flying, but would vigorously push other males which were crawling on frozen females (Figure 4.3).

Male patrolling range: Males began flying at 9:00 on clear, sunny days, and continued to fly until it rained or became heavily overcast. Forty males were marked individually, and 11 of these males were caught at both ends of the area where males patrolled. Several males were also caught during collecting periods at stations beyond where most males were captured.

These findings indicate that males do not restrict their flight paths to a subset of the area where males are found, as do some other species of Dialictus (Kukuk, 1989; Wcislo, 1987 b). Males were caught most frequently at Station B, which was a brightly sunlit spot of vegetation, and consistently had the greatest number of males flying about.

Male response to female odors, and male learning: Free-flying males were attracted to females when stimulated by chemical cues. The mean number of contacts/approach/minute for all presentations (n = 76) of 20 frozen extracted females was greater ($\bar{x} = 0.348$; SD = 0.168) than the comparable rate in the cage experiments. As before, a significant observation is the tremendous variability seen in "female attractiveness":

some females were highly attractive and others were infrequently contacted.

The mean (\pm SD) number of contacts per approach (C/A) for L. figueresi is given in Figure 4.5 for each of 4 minutes during a presentation; Figure 4.6 gives a sampler of male responses to individual females. The mean C/A for the first minute ($\bar{x} = 0.49$) was significantly greater than the C/A for the second minute [$T_s = 14$, $p = 0.001$, Wilcoxon sign rank test; Conover (1971)]; there is a trend towards decreasing response in the remaining minutes, but the decreases were not significant.

The decay in responsiveness of male L. figueresi to frozen females can be interpreted with one of the following hypotheses (modified from Wcislo, 1987b): (1) males mark females with an "antiaphrodisiac" prior to intromission (cf. Kukuk, 1985); (2) males learn that pinned females are not receptive and during subsequent encounters they tend not to respond to those learned odors; (3) female odors dissipate rapidly and are less pronounced during subsequent presentations; (4) males learn to avoid the places at which unreceptive females are presented; (5) males deposit individually distinctive marks enabling them to recognize and ignore females already contacted [this differs from No. 1 in that males do not respond to marks from other males]; and (6) Male motivation decays spontaneously after initial activation [if females are perceived as a class]. For L. figueresi several of these possibilities could not be tested, since only

one population of males was available, and at least some individual males were found at both ends of the area where males patrol. As discussed below for Nomia (also Wcislo, 1987 b), it is necessary to have other populations of naive males to test certain of these hypotheses. Males sometimes remained on females for long periods of time (up to 126 secs), as with caged trials, and they displayed such behavior throughout trials, so it is unlikely that females per se become progressively less attractive (No. 3). Females exposed to air (away from males) for > 30 minutes were as attractive to males (C/A, $\bar{x} = 0.46 \pm 0.12$ [SD], N = 15) as females that were frozen until the time of testing ($p > 0.5$, Mann Whitney U test). Therefore, dissipation of odors is probably not responsible for the decay in responsiveness. Site learning (No. 4) and motivational changes (No. 6) are probably not important since in every case the presentation of a novel unextracted female again attracts males. It is, therefore, possible to eliminate hypotheses Nos. 2, 3, 4, and 6 (above), while Nos. 1 and 5 could not be tested, and cannot be rejected.

Nomia triangulifera

Emergence phenologies and operational sex ratio

Males began emerging in mid-August, and emergence continues for ~2 weeks; this emergence is followed by female emergence, and male and female emergence periods overlap. The emergence sex ratio varies from equality to slightly male-biased (Figure 4.6). The operational sex ratio, in

contrast, was always heavily male-biased, even at times of peak female emergence (Figure 4.7). Males are, on average, smaller than females, as measured by inter-tegular distance (Figure 4.8) ($p < 0.0001$, Mann Whitney U test); for males this measure positively correlates with dry weight (Kendall's $t = 0.5$, $p < 0.01$, $N = 21$) (dry weights for females not measured).

Male patrolling

The entire site where receptive females emerge covers ~10 hectares, although emerging females were not uniformly distributed. Males do not patrol over the entire aggregation, but at least for short periods of time restrict their flight activity to particular sections of the nesting site. Mark-recapture studies show that up to several days after marking, at least some males are still found within in the small area (~100 m²) of previous capture (Table 4.2).

Courtship and mating behavior

Males search for receptive females at the emergence site and at sunflowers. Males that were flying over the emergence/nesting site were not, on average, different in size from males collected at sunflower plants or males collected with females in copula (Figure 4.9).

The courtship behavior involves motions of the antennae, all three pairs of legs, sternal protrusions on the abdomen, and presumably the dorsoventral flight muscles. Several details do not fully agree with the description of courtship behavior by Cross and Bohart (1960) based on a

Utah population; descriptions by those authors are parenthetically italicized for comparison, indicated by "C&B":

Courtship and mating occurred most frequently on the ground at the emergence site in all years; males also patrolled at the females' food source (sunflower plants) and pounced on females and courted them, but I never observed successful matings on flowers, even on plants close to the emergence site. In the nesting area males rapidly fly over the ground where females are emerging, and frequently stop to inspect or enter holes.

Upon discovering a female, a male rapidly climbs on her, and wraps his hind legs around the latero-ventral portion of her metasoma near sterna 1-3 (C&B: "*His hind legs lock beneath the posterior portion of her abdomen*"). The tibia of these legs are greatly expanded, and the inner faces are contoured and fit the general shape of the female metasoma. Males with larger inter-tegular distances have larger faces on their inner hind tibiae (Kendall's $t = 0.516$, $p = 0.002$, $N = 21$). Throughout the courtship, but especially soon after pairing, other males fly at and pounce on the mating pair, and sometimes there can be a ball of up to 8 males crawling over a mating pair. The expanded male tibiae effectively prevent a male from being knocked off a female, and prevent a female from "escaping." I never observed a male in copula displaced from a female by other males.

A male's mid-legs are held nearly parallel to the female's venter,

and are directed posteriorly (C&B: "[mid-legs are locked]...*between her fore and hind wings and under her propodeum*"); and the forelegs are placed either on the pronotum, or sometimes on the front edge of the female's front wings (C&B: "[a male]...*locks his forelegs beneath her mesothorax*").

A schematic description of the precopulatory courtship behavior is given in Figure 4.10. The female is nearly motionless throughout, except for occasionally grooming an antenna; sometimes (subsequently unreceptive) females walked around the surface with a male mounted on her back. The following time durations are for 30°C:

The antennae are slowly moved downward in a motion lasting 1.07 secs (SD = 0.1, N = 9), and then are rapidly flung upward (\bar{x} = 0.33 secs (SD = 0.1, N = 9), repeating about once per second, giving the appearance of an asymmetric metronome (C&B: ".*[there is]...alternate vertical and lateral jerking of the antennae*").

The male's first pair of legs is used to rapidly tap the female's pronotum, followed quickly by rubbing the pleural area or mid-legs, and then repeating those movements; this entire sequence is repeated once per 1.3 - 2.0 seconds (*not reported by* C&B).

Without flexion the extended mid-legs are rotated 90° around the coxae to be brought forward and downward to stroke the female's pleural region (the exact position varies with the position of the male's body); the legs are then contracted and lifted up, which again strokes the female; the

legs are then counter-rotated and extended to their starting position. After courtship has begun, the mid-legs often quiver when they are in the extended "starting" position. This sequence is repeated every 1.3 - 2.0 seconds (*not reported by C&B*).

Male metasomal sternum 5 has a modified pair of protruding stubs which have a contoured surface (there are species-specific modifications on this sternum in numerous species of Nomia; e.g., Cross, 1958; Michener, 1965). These knobs are large enough to be points of contact when the male rapidly drums the dorsal surface of the female's metasoma. A series of 4 - 6 taps is delivered rapidly in succession by the male's metasoma. These taps are forceful, as evidenced by the displacement of the female's body following contact; in slow motion it is obvious that each tap does not land in the same place, but the male moves to the left and to the right of center.**

Following a "drumming bout," the male produces a loud "buzz" (600-1000 Hz), presumably from the dorso-ventral flight muscles (Figure 4.11) (*not reported by C&B*); during this time the male has mandibles open and in contact with the female's scutum or scutellum (*not reported by C&B*). After these vibrations, the metasoma again taps the female one

**Co-incidentally, females collect pollen from the large open head of sunflowers by tapping or drumming with the metasoma.

or two times. This courtship sequence is repeated up to 114 times (*not reported by C&B*). The final sequences increase in intensity, such that drumming bouts are often accompanied by wing fluttering.

After courting, a female either indicates receptivity by slightly raising her abdomen, and the male then flutters his wings, and inserts his genitalia (inflating membranous structures; A. Roig, in prep.). During copulation the male is motionless, except for periodic contractions of the abdomen, each of which occurs with a loud higher-frequency (1200 Hz) buzz (Figure 4.12) (*not reported by C&B*; these authors reported that during copulation the male "*strokes the female with his antennae at a rate of about one stroke per second*"). Alternatively, an unreceptive female curls her metasoma downward and forward and the male is unable to insert his genitalia; she often bites at his legs until he lets go.

The duration of precopulatory courtship lasted from 37 - 149 secs (\bar{x} = 70.58, SD = 27.47, N = 55), although several homosexual courtings were much briefer. The duration of actual copulation was 9.95 secs (SD = 4.32). For mating pairs collected at the same temperatures ($\pm 1^\circ\text{C}$), there is a significant positive correlation between the duration of the courtship and the duration of the copulation ($r = 0.64$, N = 19). The durations of precopulatory behavior were not different for males with receptive or unreceptive females ($p > 0.2$).

Females that were captured as they entered emergence traps (above)

were allowed to mate, and then given subsequent opportunities to mate again. Table 4.3 shows that already unreceptive and recently mated females are not receptive to subsequent males; females receptive to the first male, but not allowed to mate with him, were subsequently receptive to a second male. Such bioassays suggest that females do not mate multiply. Dissections of receptive and unreceptive females supports this interpretation. Receptive females tended to lack sperm in spermathecae (3 of 11), and unreceptive females were mated (12 of 14).

Courtship behavior was briefly observed at small aggregations (near the levee, north of the entrance to River Front Park, Lawrence; and a site near "Nesting site #1" [5 mi. NW Lawrence] of Cross and Bohart, 1960), and was similar to behavior described above (Results).

Male learning of female odors

Male response to female stimuli is increased by the presence of female odors, as shown by comparing the mean number of C/A on frozen unextracted females ($\bar{x} = 0.7 \pm 0.15$ [SD], $N = 30$, for site A1) versus extracted ones ($\bar{x} = 0.101$ SD = 0.098, $N = 20$) ($p < 0.0001$, Mann Whitney U test). Young females, not yet carrying pollen, were contacted per minute more frequently ($\bar{x} = 5.6 \pm 0.76$ [SE], $n = 45$, pooled for first presentations of 15 females at each of three sites) than older females already carrying pollen ($\bar{x} = 1.1 \pm 0.183$ [SE]) ($p < 0.0001$, $t = 4.55$; $N = 45$ for presentations of 15 females). Pollen-carrying females from which most of the pollen washed

off with water were also less frequently contacted per minute ($\bar{x} = 1.2 \pm 0.24$, $n = 15$ [5 females, 3 sites]). This finding suggests that the color of pollen does not deter males (the odors associated with lipids from the pollenkitt could have a masking effect, and were not controlled). A comparison of male responses to the heads of females with and without pollen (below) give parallel results, which suggest that the altered responses in the males is not due to the pollen per se, but rather due to maturational changes in the females. In numerous hours of observations for other studies, pollen-laden females always rejected attempted courting from males.

Bioassays show that a major source of the sex pheromone is in the head and presumably a cephalic gland. The mean number of contacts for "Nomia heads" of newly emerged females was 8.0 ± 0.69 [SE] ($N = 30$), greater than the number of contacts to the corresponding "Nomia abdomen" ($\bar{x} = 3.5 \pm 0.43$ [SE]) ($N=30$) ($p < 0.0001$, $t = 7.9$, paired t-test), and both of these values were greater ($p < 0.0001$; paired or unpaired t-tests) than responses to either "Nomia thoraces" ($\bar{x} = 1.3 \pm 0.22$ [SE]) ($N = 30$), or a blank black velvet square ($\bar{x} = 1.0 \pm 0.19$ [SE]). Heads from females that already were collecting pollen were contacted less frequently ($\bar{x} = 2.1 \pm 0.53$ [SE], $N = 10$) than models with females not yet collecting pollen ($p < 0.05$, Mann Whitney U test).

Based on unextracted newly emerged females in the field (Figure

4.13), the mean C/A for the first presentations at site A is slightly more than those at B1 ($p = 0.011$), and the latter were not significantly different from presentations at C ($p > 0.4$). The fact that females are attractive to males at a more distant (~500 m) site C, despite the fact that each female has already been repeatedly contacted by other males, shows that a male-produced repellent is unlikely. The mean C/A for A1 is significantly greater than for the second presentation at the same site (A2) ($p = 0.004$). In contrast, at site B there was no significant difference in mean C/A between the first (B1) and second (B2) presentations ($p > 0.2$).

The videotaped responses of males to frozen females ($n = 30$) over time at a single site are summarized in Figure 4.14. These analyses show that the number of males approaching frozen females is not significantly different throughout a 5 minute period (Figure 4.14, top). The number of contacts (Figure 4.14, middle), and the number of contacts/approach (Figure 4.14, bottom), however, were significantly less for the second minute compared to the first following initial presentation (both $p = 0.002$), and still less for the third minute ($p = 0.001$), but thereafter were not significantly different ($p > 0.02$).

Social facilitation

Habituation is often broken by novelty, or apparent novelty, if individuals pay attention to the behavior of other individuals who are responding directly to a stimulus. The importance of this simple "social

facilitation" was determined by detailed analysis of video tapes. Records of 25 one-minute periods are summarized in Figure 4.15. Tested individually, in 6 of these 25 periods the distributions of approaches deviated from random ($p < 0.05$), and overall the pooled data are also significantly clumped ($t_s = -7.926$, $p < 0.05$).

DISCUSSION

The comparative mating biology of Apoidea is little known, despite its relevance to theories of both sexual selection and social evolution. This Discussion emphasizes these inter-connections, and shows how a consideration of mating biology improves our understanding of social evolution.

Courtship behavior and sexual selection

Mating in L. figueresi was rarely observed. There are no intricate precopulatory or copulatory behavior patterns, and the behavior agrees with that of other Dialictus (Barrows, 1975; pers. obs.). The courtship of Nomia (E.) triangulifera, in contrast, involved extraordinarily complex behavior patterns for mating in bees. Except for brief observations on N. (E.) nevadensis and N. (A.) melanderi, nothing is known of courtship in other Nomia. The differences between the behavior of the Kansas bees reported here, and the Logan, Utah, bees reported by Cross and Bohart (1960) are especially striking. These authors did not deposit voucher specimens, but Cross (1958) most recently revised the subgenus Epinomia,

so the species determination is probably correct. The movements of the legs, antennae, and abdomen are very noticeable, as are the precopulatory buzzes of bees, which are audible to me from a standing position. It is likely that Cross and Bohart would have noticed and reported such unusual behavior, especially since they described the positions of the legs, antennae, etc. If real, these population differences represent an impressive case of intra-specific behavioral divergence.

By comparison, none of the unusual behaviors seen in N. triangulifera were reported for N. nevadensis (O'Neill and Bjostad, 1987; K. M. O'Neill, in litt.). In N. nevadensis, the initial stages of courtship behavior take place underground, if at all. "Sweet-smelling" females often emerge from the soil with males mounted on them, hind legs wrapped around the female's metasoma. Intromission is accompanied by rhythmic pulsations of the male's metasoma, and often the female is released from the leg grasp. The total duration of copulation for nevadensis ($\bar{x} = 19.2 \pm 8.8$ [SD] secs) is longer than for triangulifera ($\bar{x} = 9.9$ secs, Results); in nevadensis mating is followed by a brief (~22 secs, on average) period when the male remains mounted on the female, but has withdrawn his aedeagus (O'Neill and Bjostad, 1987). After intromission, males of triangulifera never remained with females.

Several analogous elements of the courtship behavior of N. triangulifera also occur in other Apoidea, including Halictidae-- only

Centris pallida (Anthophoridae), however, approaches triangulifera in the complexity of its mating behavior (Alcock et al., 1978; pers. obs.)

[Additionally, analogous elements are widespread in other insects; excellent reviews are Richards (1927) and Gordh and DeBach (1978)].

Rhythmic motions of the antennae, such as occur in male N. triangulifera, are known for some other apoids, as variants on a "waving," "stroking," or "tapping" theme (Barrows, 1976; Eberhard, 1990 a; Longair et al., 1987; Wcislo and Low, ms.; Genise, 1982). Janvier (1960) and Danks (1971) described antennal wavings in pemphredonine wasps, and suggested that they functioned to immobilize females. The antennae of triangulifera are not modified other than the usual sex differences in bees; in other genera or subgenera of nomiine bees (e.g., Acunomia, Spatunomia) the terminal flagellomeres are pointed or greatly flattened.

The use of the fore- or mid-legs in stroking parts of females is less common. Apart from N. triangulifera, leg movements in courtship are known in Triepeolus (pers. obs.), Melissodes (Triplett and Gittins, 1988), and Centris (ref. above). Structural modifications of the legs are widespread in apoids, sometimes for use in courtship, and sometimes for competition (refs. in Wcislo and Low, ms.). Among North American Nomia, claspers on the hind legs can be feebly developed [e.g. N. (E.) boharti], or well-developed [e.g., N. (D.) heteropoda]. Within this large genus there is much diversity in size and shape of this structure, but there

is still not yet enough information to correlate the presence of such structures with particular conditions of sexual selection.

If functional, it is likely that the male buzzes are perceived by the females as substrate vibrations. The occurrence of wing vibrations or stridulations in courtship occurs probably independently in various groups of bees [Colletes (Larsen et al., 1986), Lasioglossum (Dialictus) (pers. obs.; L. Greenberg, *in litt.*), Panurgus (Tengö et al., 1988), Centris (Alcock and Buchmann, 1985), probably Xylocopa (Minckley et al., 1991), and Meganomia (Rozen, 1977)] or other Hymenoptera (Spangler and Manley, 1978; Sivinski and Webb, 1989; Gordh and DeBach, 1978; and Markl et al., 1977). In several species of ants, for example, the stridulations themselves have little communicative function, and instead serve to modulate thresholds in other sensory modalities (Markl et al., 1977). In Nomia triangulifera these pre-copulatory vibrations are at a frequency (~ 600 Hz). A similar frequency artificially applied to honey bee (Apis) combs induces workers nearby to become akinetic (Spangler, 1971 and refs. therein). Hypothetically, the use of this frequency by males may effectively calm the female while males provide tactile and visual stimulation.

The rapid abdominal (metasomal) drumming was always performed by male N. triangulifera, but its function is unknown. Structural differences of the metasoma are widespread in Nomia, and occur sporadically in other bees (e.g., Toro, 1985). The use of the metasoma

by males during courtship to tap or rub the female metasoma occurs in some sphecids, eumenines, and a pompilid wasp (Genise, 1982; Cowan, 1986; Wcislo et al., 1988), but again the function is unknown. Abdominal tapping or drumming occurs as post-copulatory behavior in Centris pallida, and this behavior helps induce changes in females which reduce the latter's receptivity to mating (Alcock and Buchmann, 1985).

Without further comparative data it is not possible to interpret the evolution of the unusual courtship behavior of N. triangulifera. The rationale for treating courtship as communicative behavior is discussed by West-Eberhard (1984), Eberhard (1985), and Dewsbury (1988), and these behavioral and structural traits are likely to have evolved under sexual selection (cf. Darwin, 1872). The main reason for this assertion is that the operational sex ratio is intensely male-biased (Figure 4.7), which provides favorable conditions for sexual selection (Wade, 1987). Although quantitative data are not available, it is likely that a similar situation is true for other Nomia. Males of N. (E.) nevadensis appear to reach females before they emerge above-ground. G.E. Bohart (in litt., to Linsley, 1958) reported that N. (A.) melanderi males are sometimes so abundant on plants that unreceptive females had to forage up to half a mile away because they were harassed by males on plants nearer the nest site. The highly modified hindtibiae of many Nomia inferentially support the idea that intra-sexual competition is important. There are, however, no

obvious size-related advantages for males, nor are there any discernable size-dependent alternative behaviors, as in some other bees (e.g., Alcock and Houston, 1987; Alcock et al., 1978). Males collected patrolling at the nesting site, patrolling at resources, or mating, were not significantly different in size. Tepedino (in litt., 1987) reported that males of N. melanderi patrolling at the nesting site were not larger than males patrolling at plants (crownvetch). More detailed studies are needed for N. triangulifera, however, because results from this study only report information from males and females collected when temperatures were hot (> 30°) and relative humidity high; these are the usual weather conditions in Kansas in August; occasionally there are cool, wet years, but no samples were taken. Larsson (1989a,b) has shown that microclimatic effects differentially influence the reproductive success of small and large individuals of Colletes (Colletidae).

Detailed analyses of individual male behavior are still in progress, so it is not yet possible to discern if there are differences in the behavior of males that induce females to mate a second time.

Mate localization and identification

Results from studies of both Lasioglossum figueresi and Nomia triangulifera show that males display an increased response to female stimuli in the presence of olfactory cues. Female-produced odors that function as sexual releasers are now known in some bees, e.g.,

Lasioglossum, Augochlora (Barrows, 1976; Wcislo, 1987b; Smith and Ayasse, 1987), Perdita (Barrows et al., 1976), Panurgus (Tengö et al., 1988), Centris (Alcock et al., 1976), Eucera (Kullenberg, 1973; Shimron and Hefetz, 1985), Dasypoda (Bergmark et al., 1984), and Apis (Free, 1987). In a sphecid, Trigonopsis, there is anecdotal evidence that males are attracted to females by olfaction (Eberhard, 1974). In some other bees (e.g. Xylocopa, Andrena), and many sphecid wasps (e.g., Philanthus), there are male-produced chemicals which attract females (refs. in Tengö and Bergström, 1977; Minckley et al., 1991; McDaniel et al., 1987). Some male vespid wasps are attracted to female-produced odors (Keeping et al., 1986; Ono and Sasaki, 1987), while in others males mark perches (refs. in Wenzel, 1987).

In general, male bees and sphecid wasps, probably in the presence of female-produced odors, will pounce on small, dark objects that are female-sized (Barrows, 1975; Evans and O'Neill, 1986; pers. obs.). The relative importance of visual and olfactory cues for mate recognition is known for only a few apoids (Eickwort and Ginsberg, 1980). Males of Andrena flavipes are attracted by orange pubescence on the hind legs, which if removed decrease the female's attractiveness; fresh or dead females were equally attractive (Butler, 1965). Panurgus males are more attracted to black & yellow models than they are to black ones alone, but they cannot be trained to associate presence of sugar with color (Meyer-Holzappel, 1987). Models with the large scopae of female Dasypoda altercator are more

attractive to males than are models without the scopae; models with odor were more attractive than models without odor (Bergmark et al., 1984).

Augochlora pura males also used both visual and olfactory cues for locating females (Barrows, 1975). Drone Apis are more attracted to queens with a bright orange "mating sign" (= the genitalia from a previous male) than those without one (Koeniger, 1990). For Nomia triangulifera, the number of males contacting an odorless female was not significantly greater than the number contacting a black rectangle, suggesting that visual cues alone do not provide much stimulation. Similarly, black models with crushed female heads {appropriate olfactory cue + inappropriate visual cue} were contacted more frequently than were the extracted whole females {inappropriate olfactory cue + appropriate visual cue}. Again, these results suggest that olfactory cues are more important than visual ones.

Male learning

In many aculeate species (and other animals) olfaction plays a special role in sexual attraction, although little is known about the development of these perceptual mechanisms, and whether past experience conditions present responses. Habituation, the simplest class of learning (Thorpe, 1963; Macintosh, 1983), occurs in males of the eusocial Lasioglossum zephyrum and L. malachurum, and serves to decrease mating effort (sensu Low, 1978) invested in previously unreceptive

females (Wcislo, 1987b; refs. in Michener and Smith, 1987). Responses of male L. figueresi and N. triangulifera to frozen females at a single site resemble a waning response expected under habituation. After the initial presentation, the responsiveness of males gradually decays. Numerous factors might produce this decay (listed in Results). A similar decay of within-site response occurs in N. triangulifera, with the greatest rate of C/A occurring during the first minute after presentation. As with L. figueresi, both site learning, male repellents, and short-term dissipation are unlikely to account for the decay in response.

One of the more interesting results from these studies with female models concerns the tremendous inter-individual variability in female-attractiveness. Such variability has been reported for L. figueresi, L. zephyrum (Wcislo, 1987 b), and N. triangulifera, and implies that some females are less likely to mate than others, even in the absence of direct maternal manipulation, because they are less likely to attract partners. This intrinsic variability in attractiveness may relate to the general problem in social biology of explaining why some adult females do not mate (e.g., Gadagkar et al., 1990). Even among recently emerged L. figueresi adults, for example, there are some females which were highly attractive, and others were completely unattractive. Other changes in glandular chemistry might be ontogenic, with older bees having different chemical profiles [such changes are common in distantly related Apidae, Engels and

Engels, 1988; Getz et al., 1989]. Additional sources of variation include social facilitation by males, or stochastic differences due to imprecision in the neural control of behavior (Eberhard, 1990 b).

Mating, learned recognition, and social evolution

The impetus for this work was to better understand the origin of social behavior. Simple learning abilities by males of solitary aculeate species have been hypothesized as sources for the origin of kin recognition abilities in social species, possibly to prevent inbreeding; subsequently, this sexual trait is transferred and used in another context to maintain group identity (Michener and Smith, 1987; refs. in Chapter 3). Results for one solitary species (Nomia) demonstrate simple learning, and for the other (Lasioglossum) strongly suggest it, although some alternative hypotheses could not be excluded. As discussed below, however, male learning abilities probably had little to do with the origin of recognition systems.

In N. triangulifera (Results), and probably all bees with scramble competition (see Alcock et al., 1978), sexual selection is likely to be more intense on males than on females (for reasons why, see Trivers, 1972), so selection for refined discriminating abilities in males is never expected to be as strong as in females (a possible exception is Dianthidium ulkei [Frohlich and Parker, 1985]). Under intense competition there will be strong selection to rapidly habituate to cues associated with unreceptive females, coupled with strong selection against males discriminating

among the smaller class of receptive females. In some other species, in contrast, males set up territories and release volatile chemicals that attract females (e.g., Minckley et al., 1991). In these species females fly from one territory to another, and eventually mate with a male. If female choice operates, then females must learn some features of a previous male for comparison with subsequent male(s). These patterns of sexual behavior thus create conditions under which sexual selection operates for improved female discriminatory abilities. If mating patterns and sexual selection are considered, then female-choice represents a more likely sex-related origin for kin recognition in Hymenoptera, than those previously discussed (refs. above) which assume that males will learn in order to be discriminating in matters related to sex!

ACKNOWLEDGEMENTS

Most of the people who helped have been previously acknowledged. In addition to these people, I am also grateful to Dr. H. Spangler of the Hayden Bee Labs (USDA) for help with the analyses of the courtship vibrations.

Financial support was provided by those agencies listed at the beginning of this Dissertation.

Figure 4.1. A male Lasioglossum (Dialictus) figueresi approaching a pinned, frozen female (cropped from photograph) which was 4 cm from the male at the time of the photograph.

Figure 4.2. A male Lasioglossum (Dialictus) figueresi attempting copulation with an unextracted frozen female.

Figure 4.3. Several male Lasioglossum (Dialictus) figueresi crawling over a male that is trying to mate with a frozen female (as in Figure 4.2).

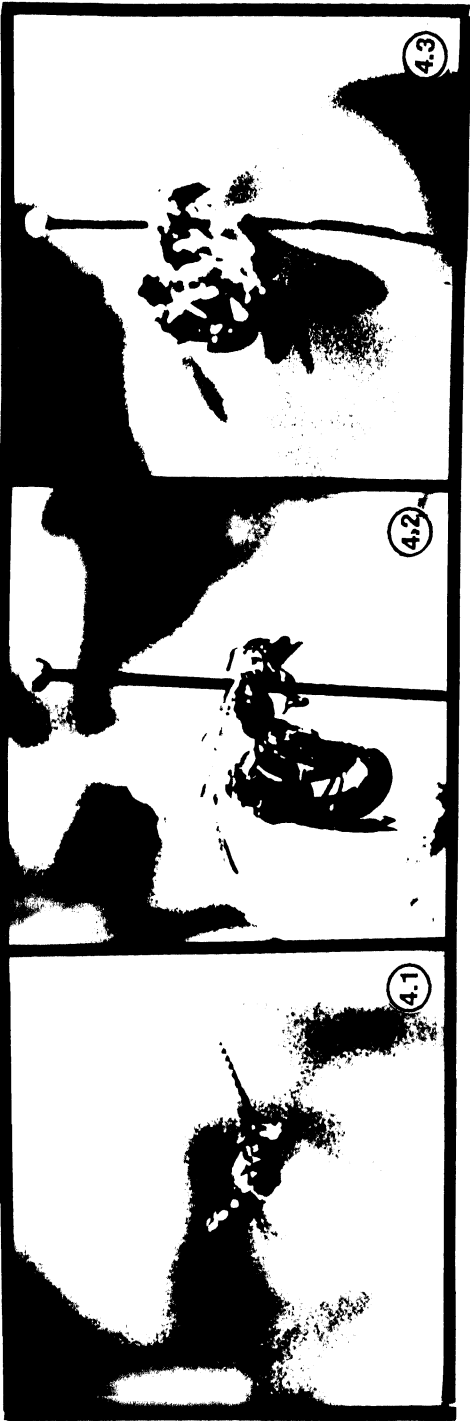


Figure 4.4. Digitized flight paths made from video recordings (August 1986) of male Nomia triangulifera in response to a frozen unextracted female (black circles). Arrows indicate wind direction. Flight paths A and B involve approaches and contacts, while paths C and D involve only approaches. Scale = 50 units.

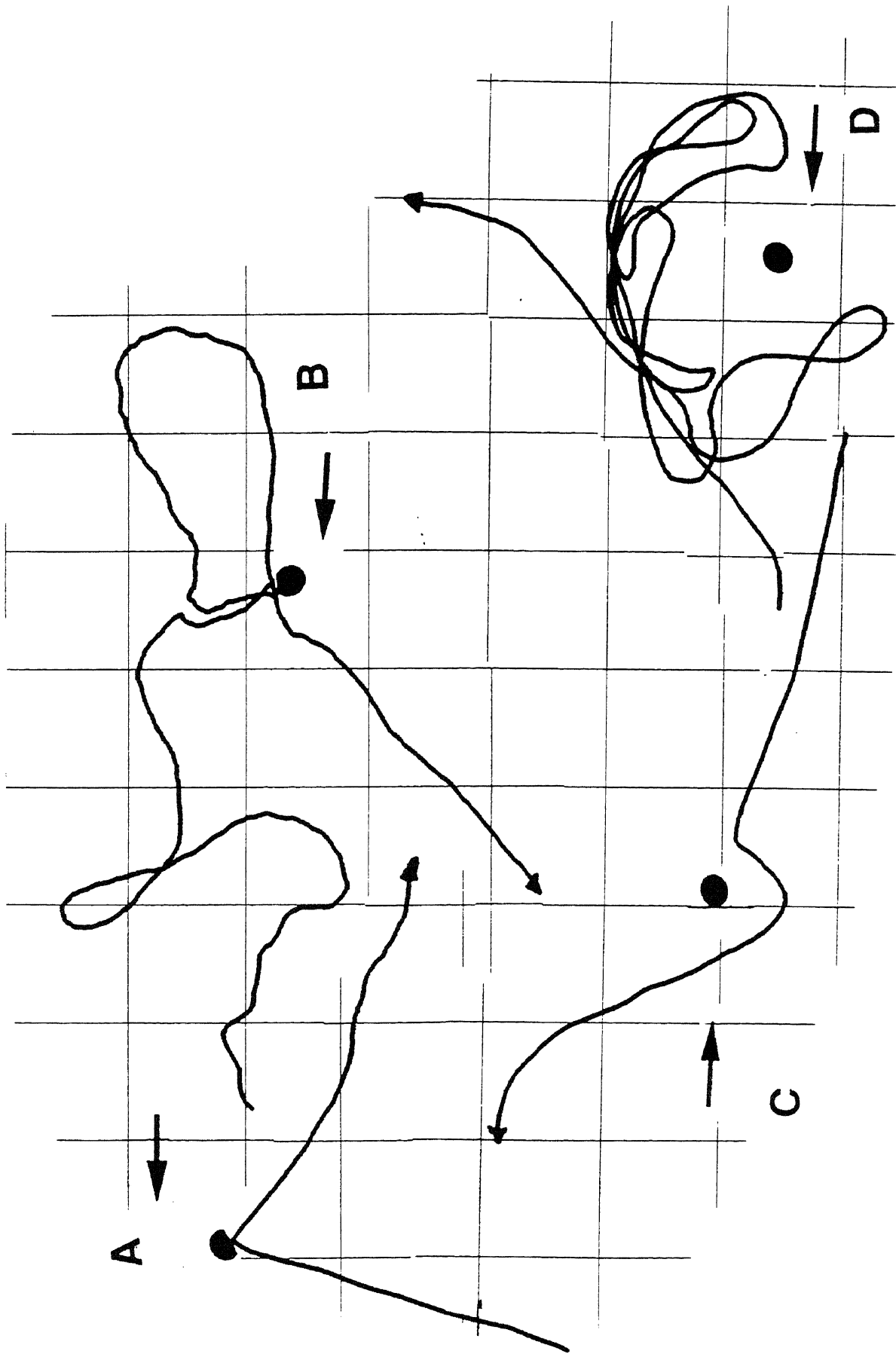


Figure 4.5. The mean (\pm standard deviation) number of approaches (top), contacts (middle), and contacts/approach (bottom) for male Lasioglossum (Dialictus) figueresi presented with the odors of frozen unextracted females. Within each graph, values not sharing the same characters are significantly different at $p < 0.017$.

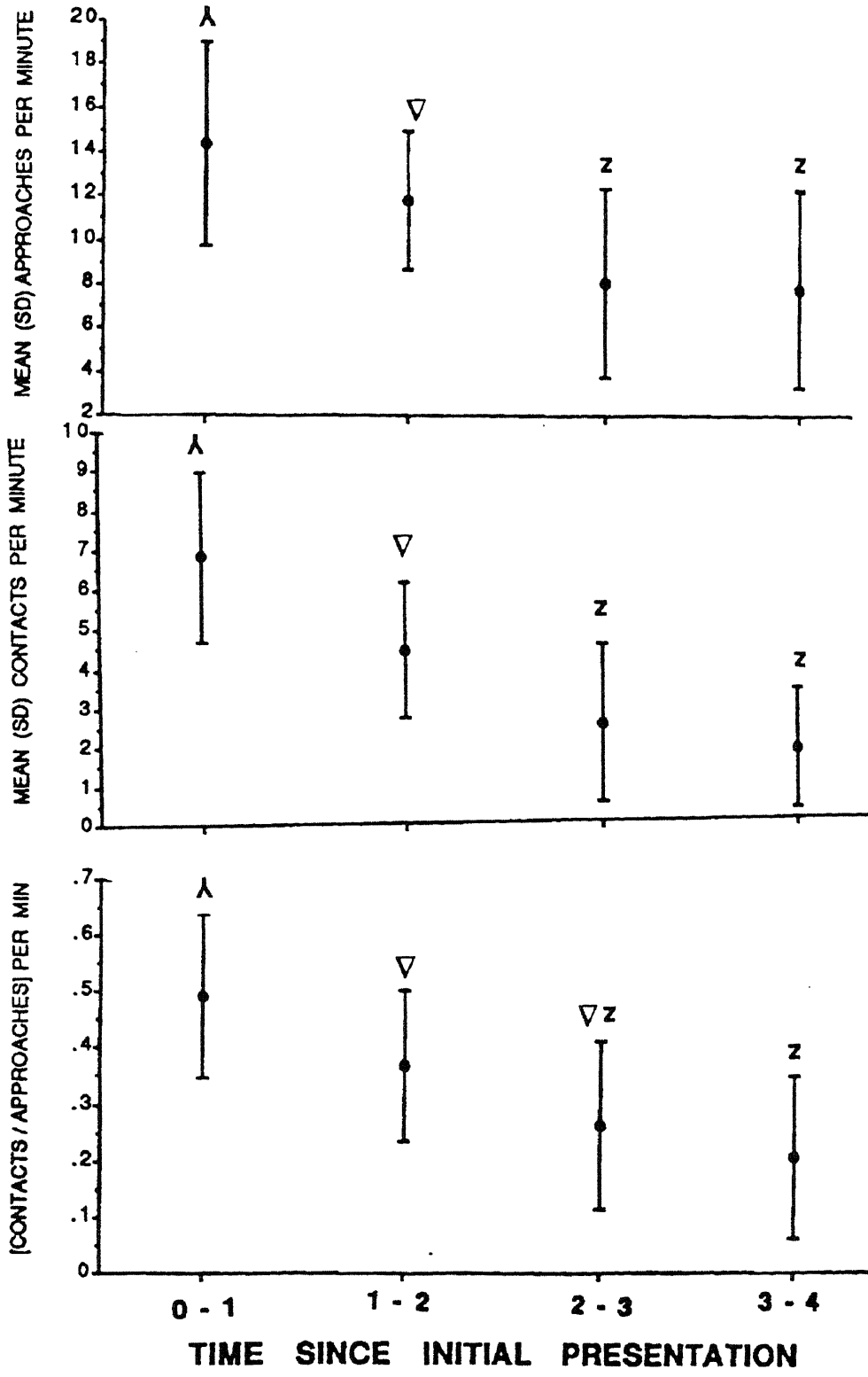


Figure 4.6. Line graphs showing the contacts/approaches by males towards individual unextracted females Lasioglossum figueresi.

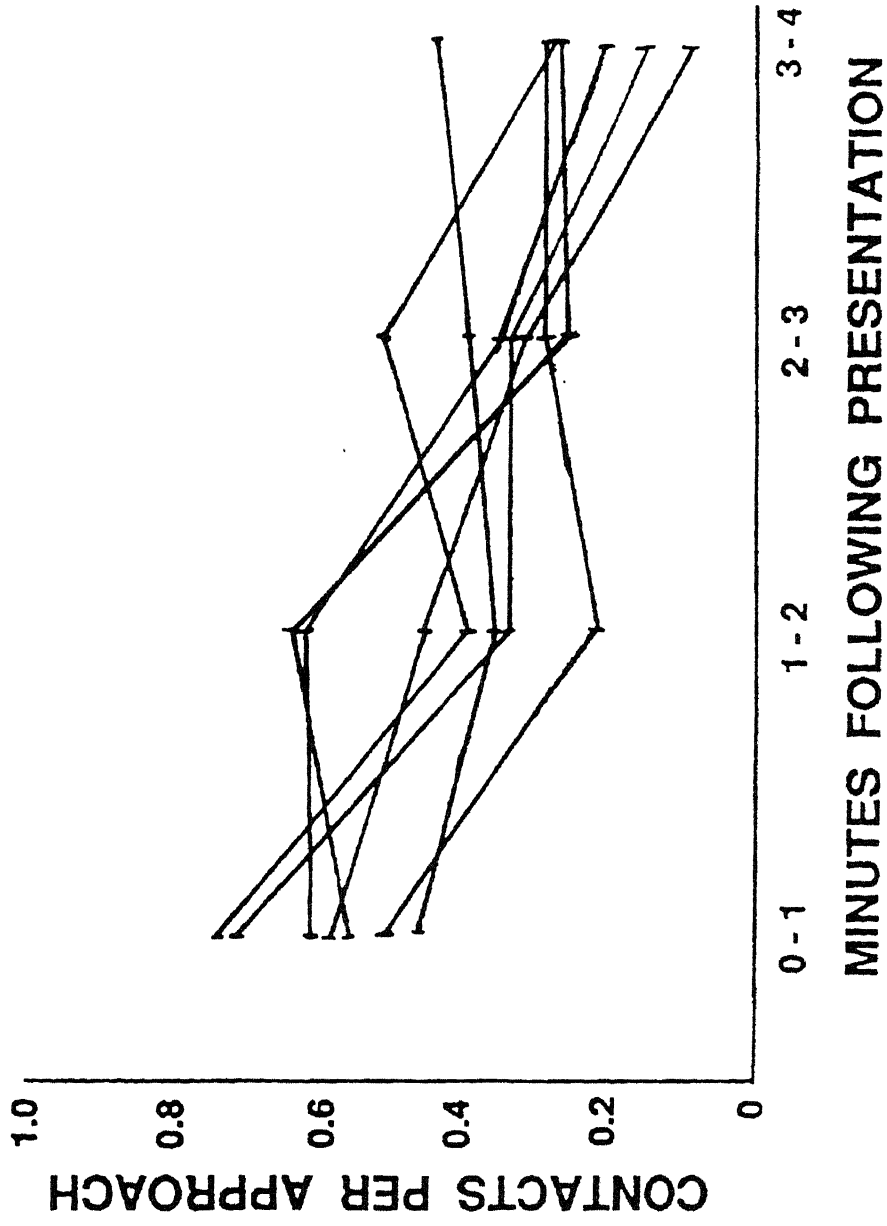


Figure 4.7. Histogram of the numbers of male (black) and female (hatched) Nomia triangulifera captured in emergence traps covering 2.5 m² throughout the active season for 1989 and 1990.

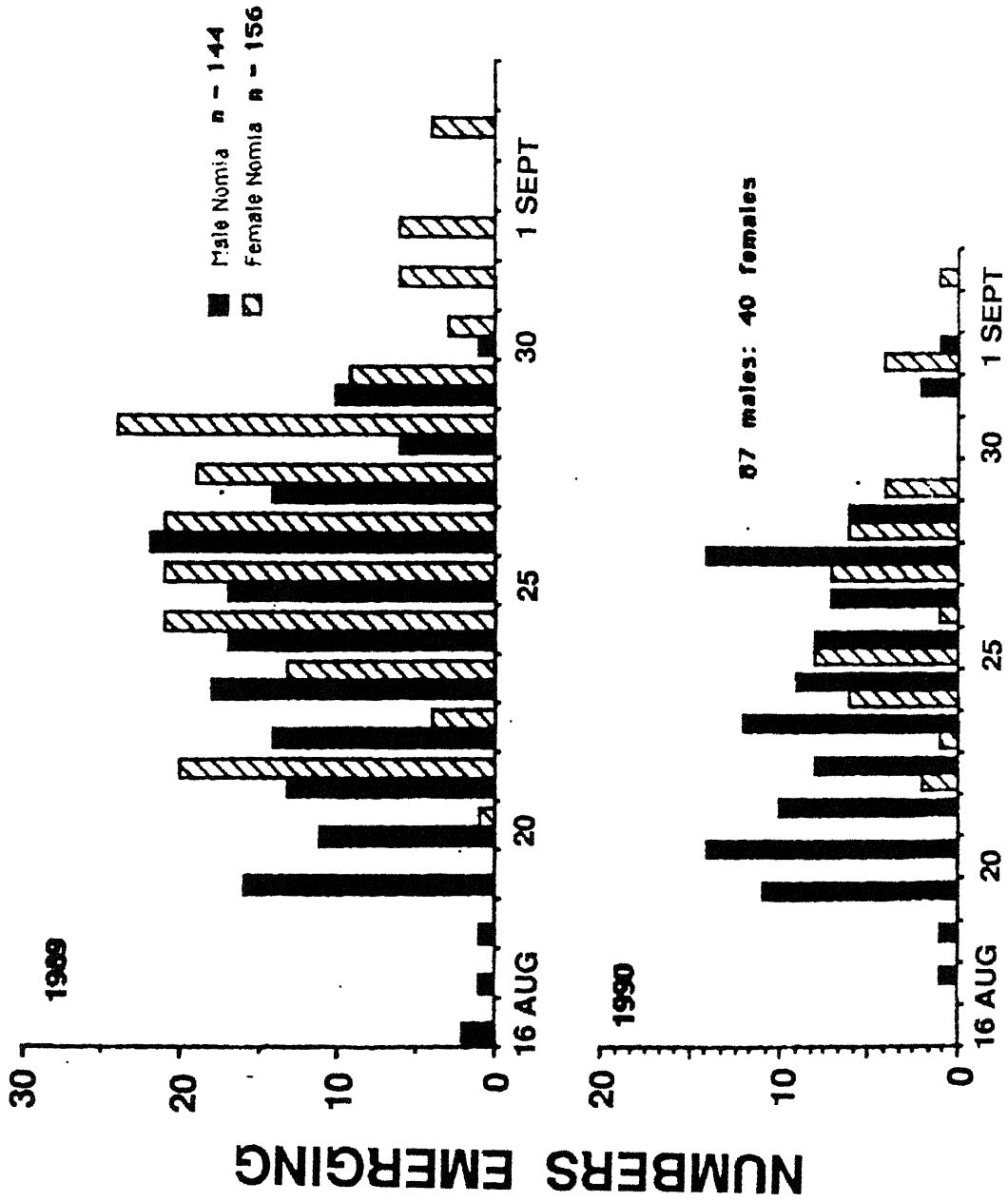


Figure 4.8. Daily operational sex ratio for Nomia triangulifera for 1989 and 1990.

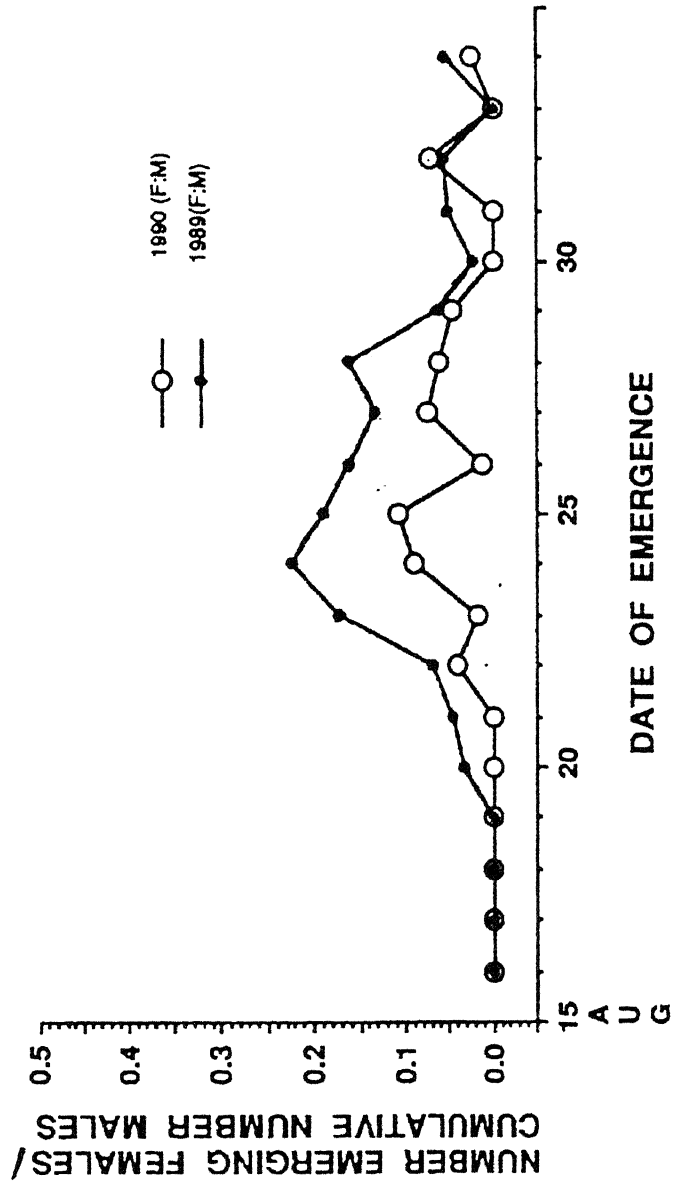


Figure 4.9. Histograms of the inter-tegular distance (mm) for males and females of Nomia triangulifera.

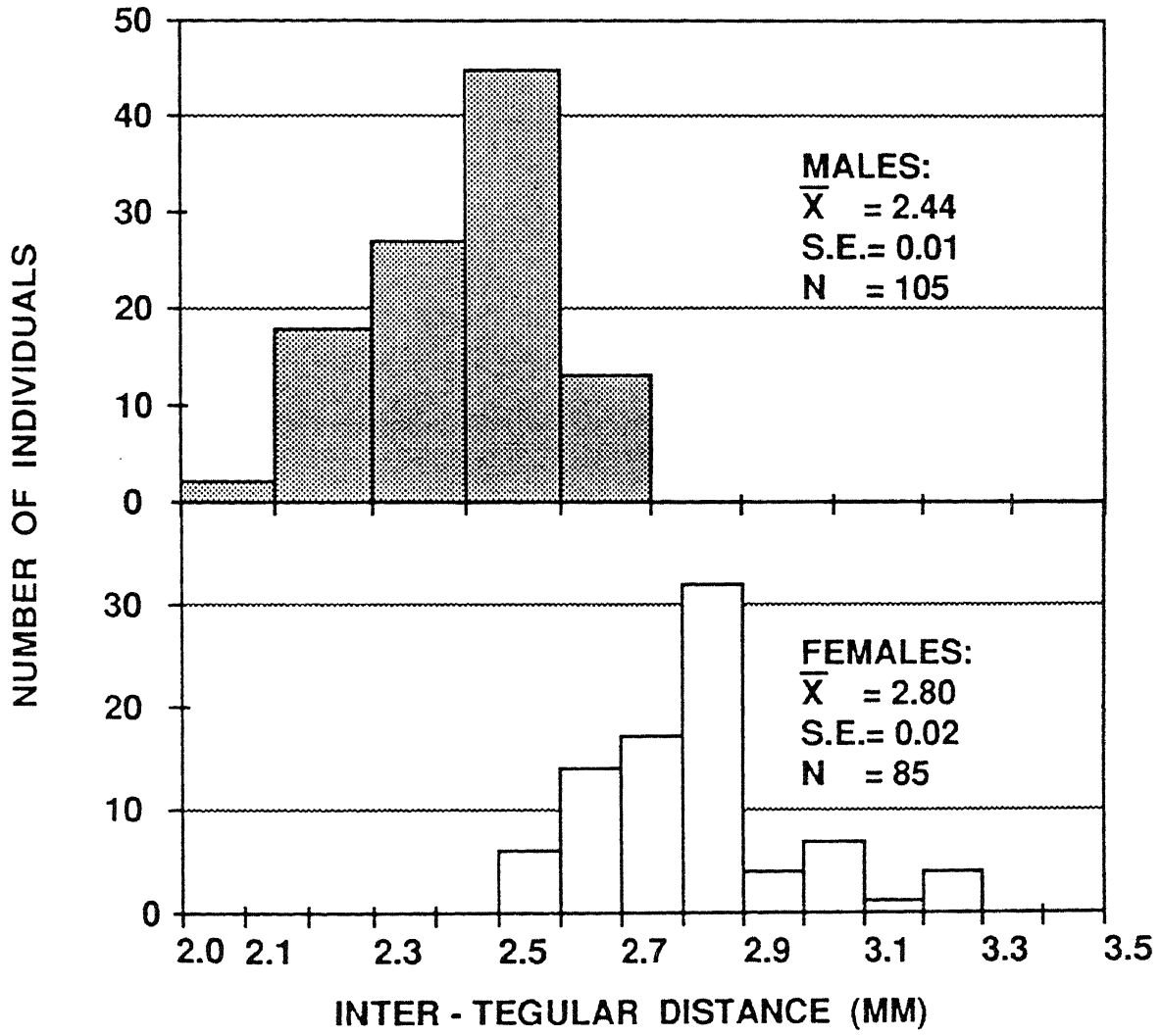


Figure 4.10. Histograms of the inter-tegular distance (mm) for males of Nomia triangulifera patrolling at sunflowers, patrolling at the emergence site, or mating. Triangles indicate arithmetic means.

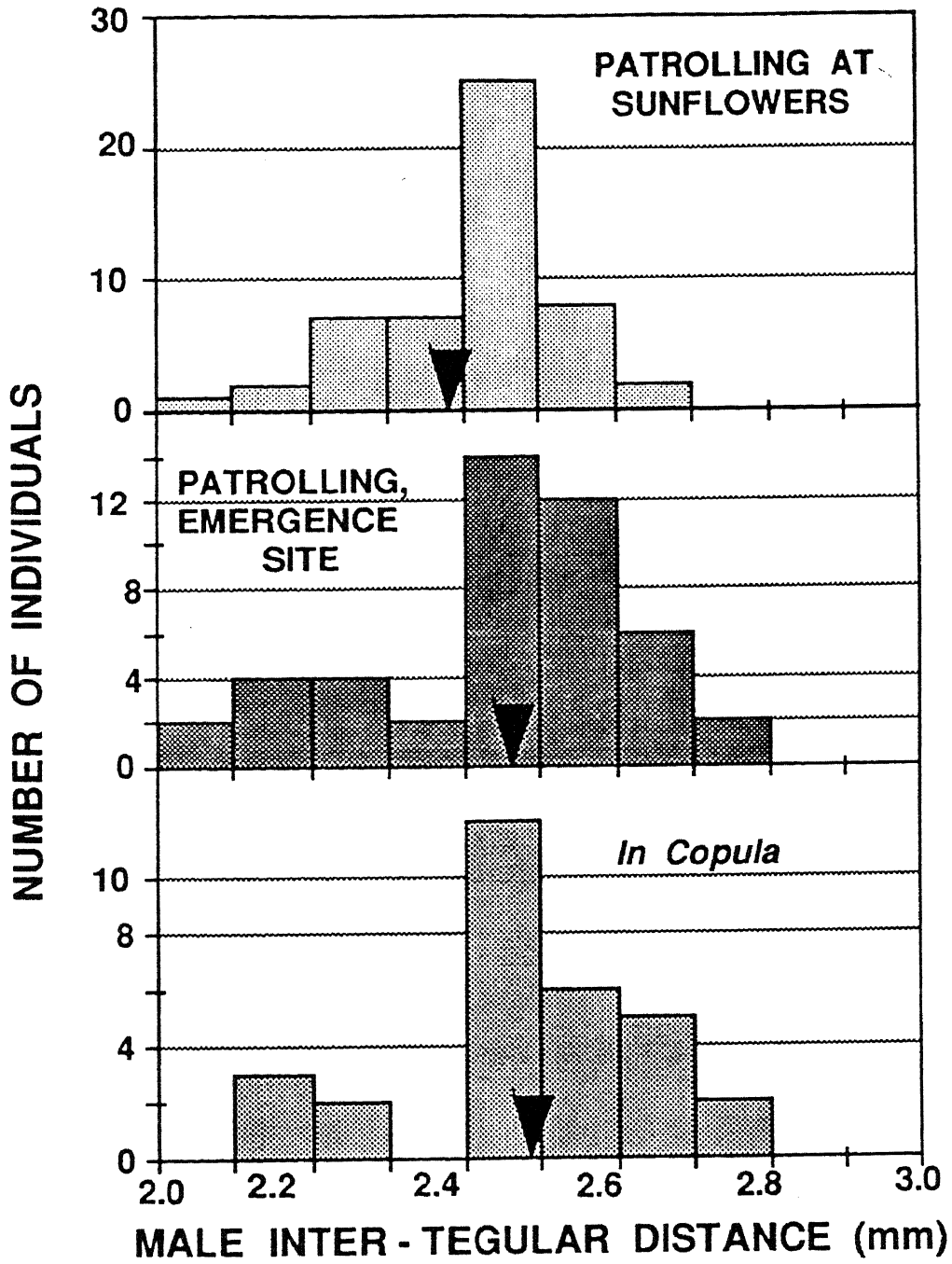
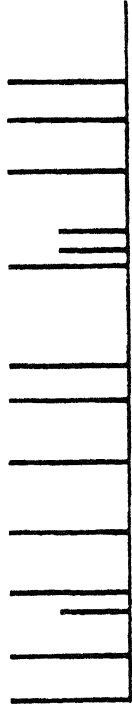
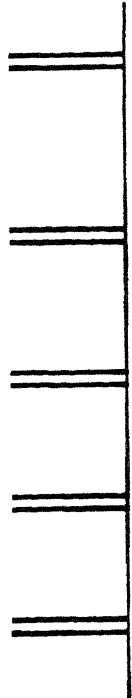


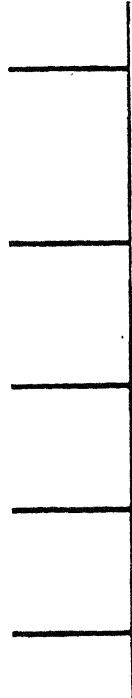
Figure 4.11. Schematic diagram of the pre-copulatory behavior of male Nomia triangulifera based on analyses of videotape.



ANTENNA MOVEMENT
(UP --> DOWN)



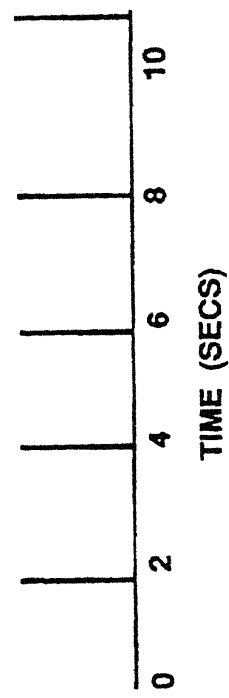
FORE - LEG TAPS
PRONOTUM &
EPISTERNUM



MID - LEG STROKES
PROPODEAL &
PLEURAL REGIONS



ABDOMINAL STERNA
TAP TERGA



"BUZZ" FROM
FLIGHT MUSCLES

TIME (SECS)

Figure 4.12. Representative sonagram of the pre-copulatory vibrations of male Nomia triangulifera.

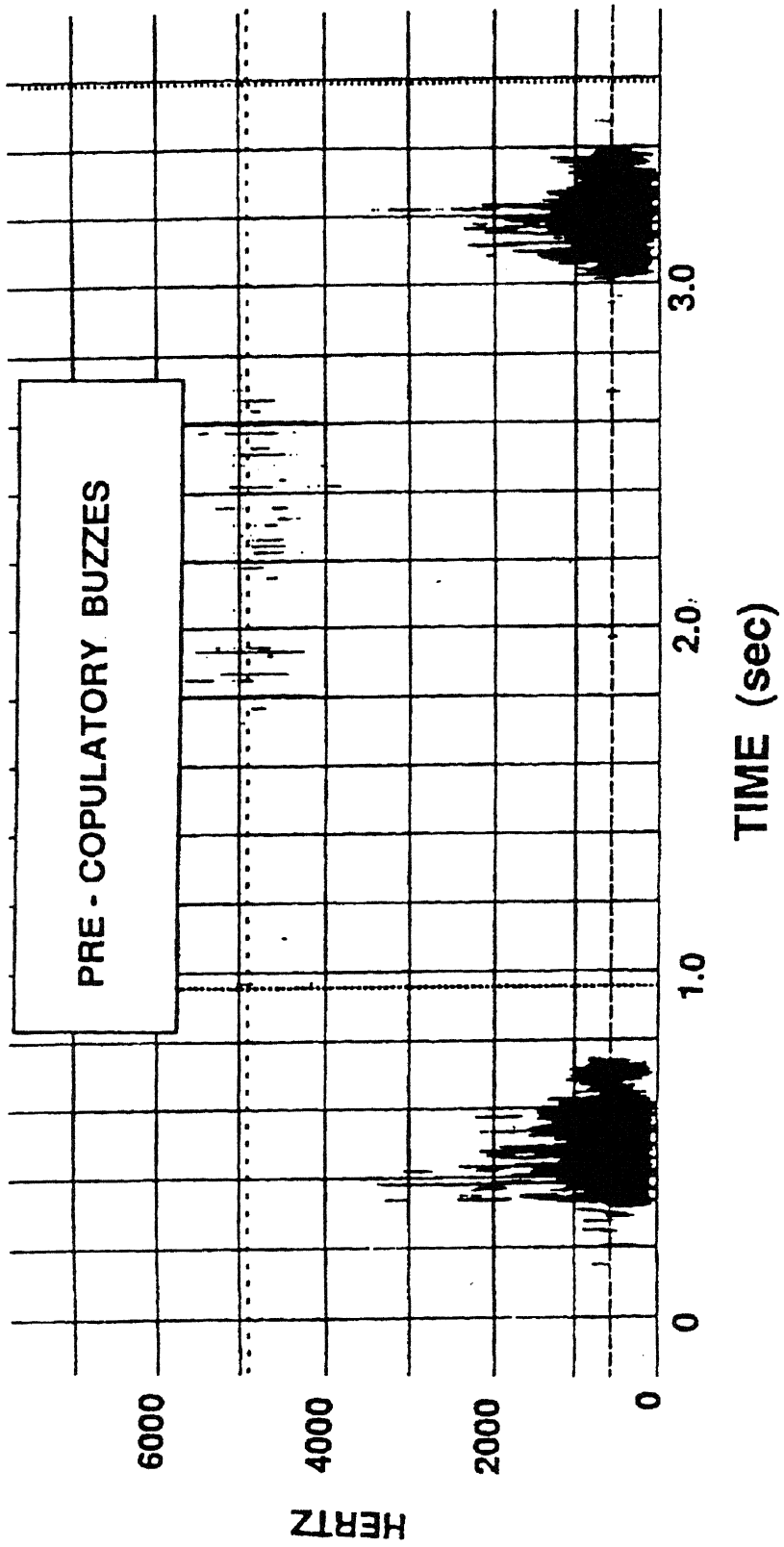


Figure 4.13. Representative sonagram of the copulatory vibrations of male Nomia triangulifera.

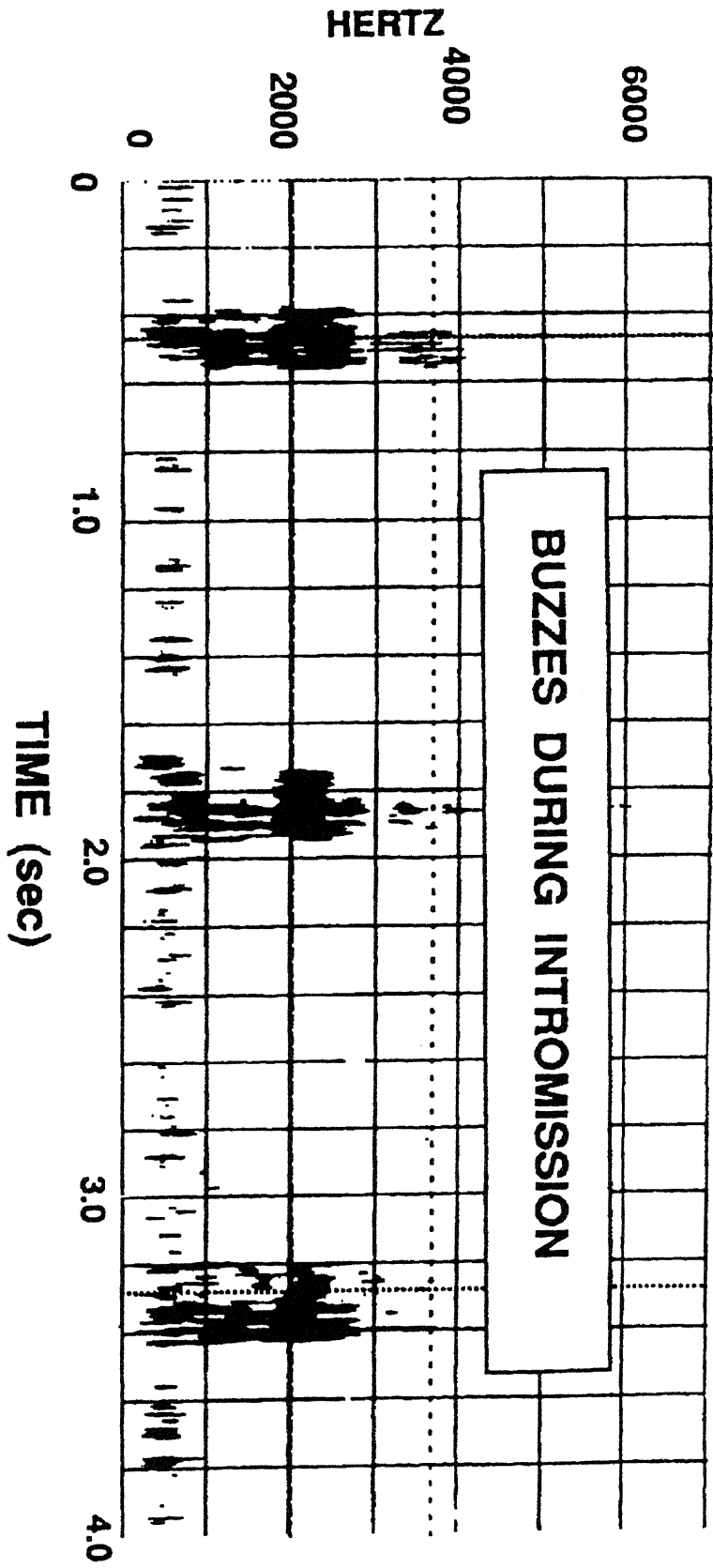
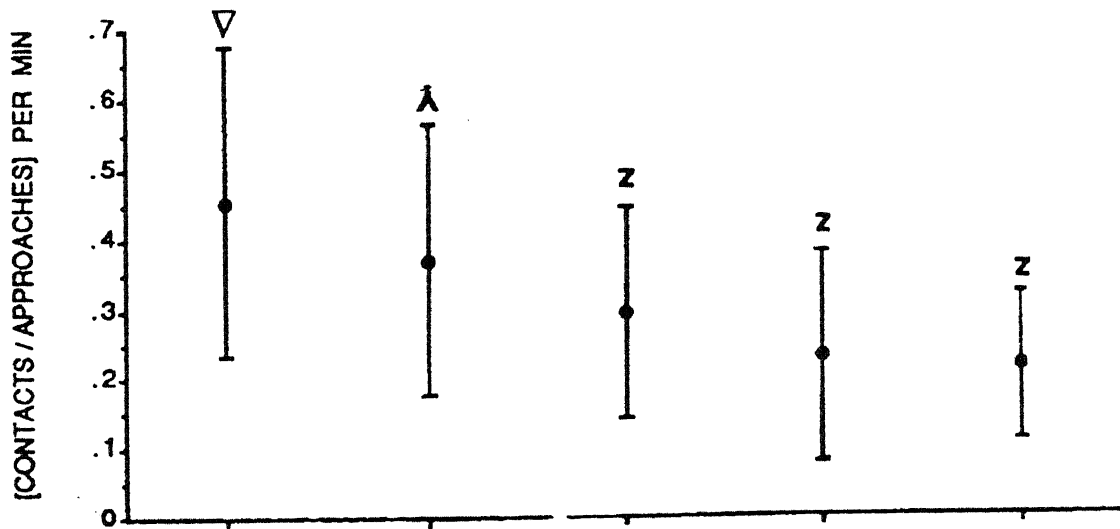
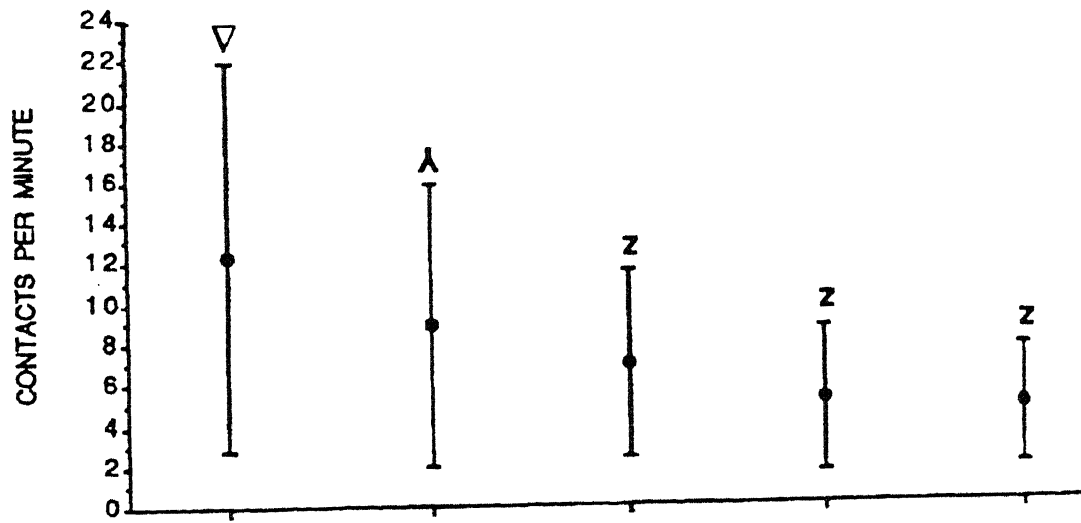
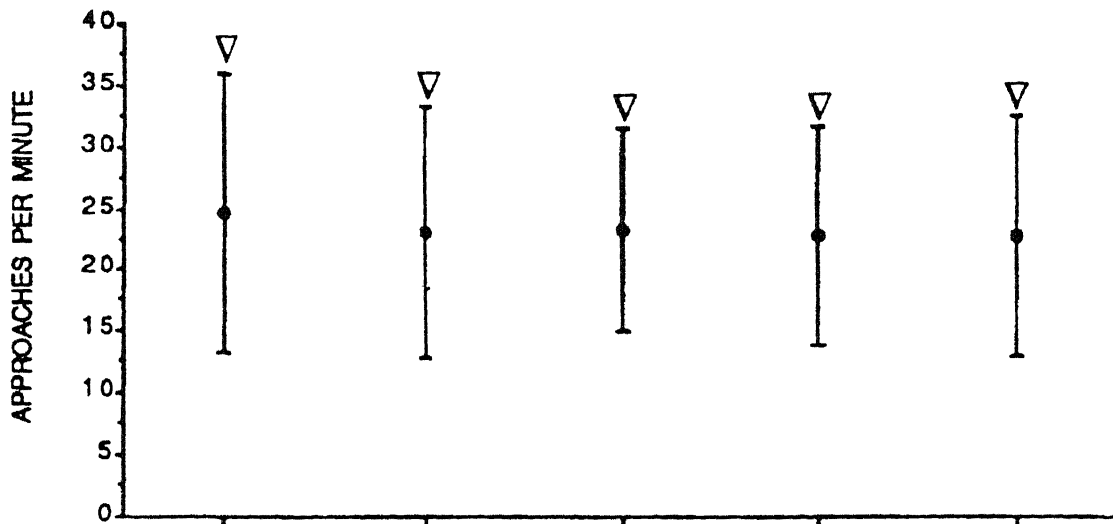


Figure 4.14. The mean (\pm standard deviation) number of approaches (top), contacts (middle), and contacts/approach (bottom) by male Nomia triangulifera presented with the unextracted females. Within each graph, values not sharing symbols are significantly different at $p < 0.05$. Data are based on analyses of videotape.



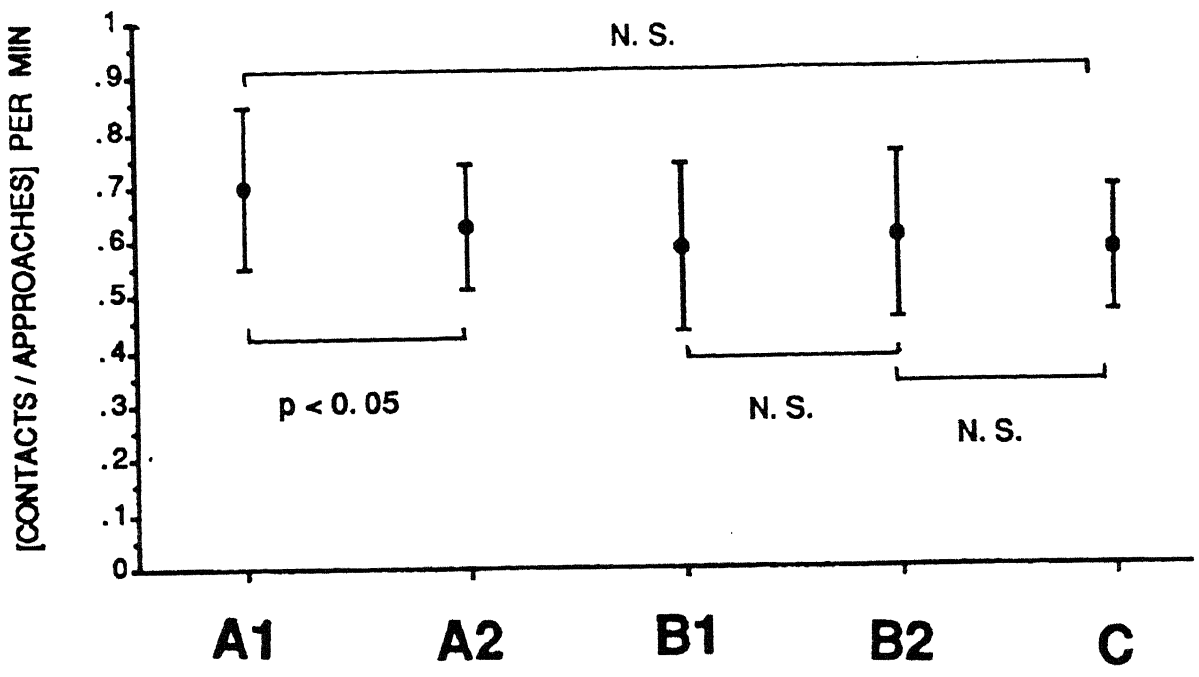
0 - 1 1 - 2 2 - 3 3 - 4 4 - 5

TIME SINCE INITIAL PRESENTATION

Figure 4.15. The mean number of contacts per approach for male Nomia triangulifera in response to the odors of frozen unextracted females at different sites and times. Each female was presented once at site A1 and B1, then again at both A and B (A2, B2), and then at C.

Figure 4.16. Line graphs showing the contacts/approaches by males towards individual frozen unextracted female Nomia triangulifera.

4.15



4.16

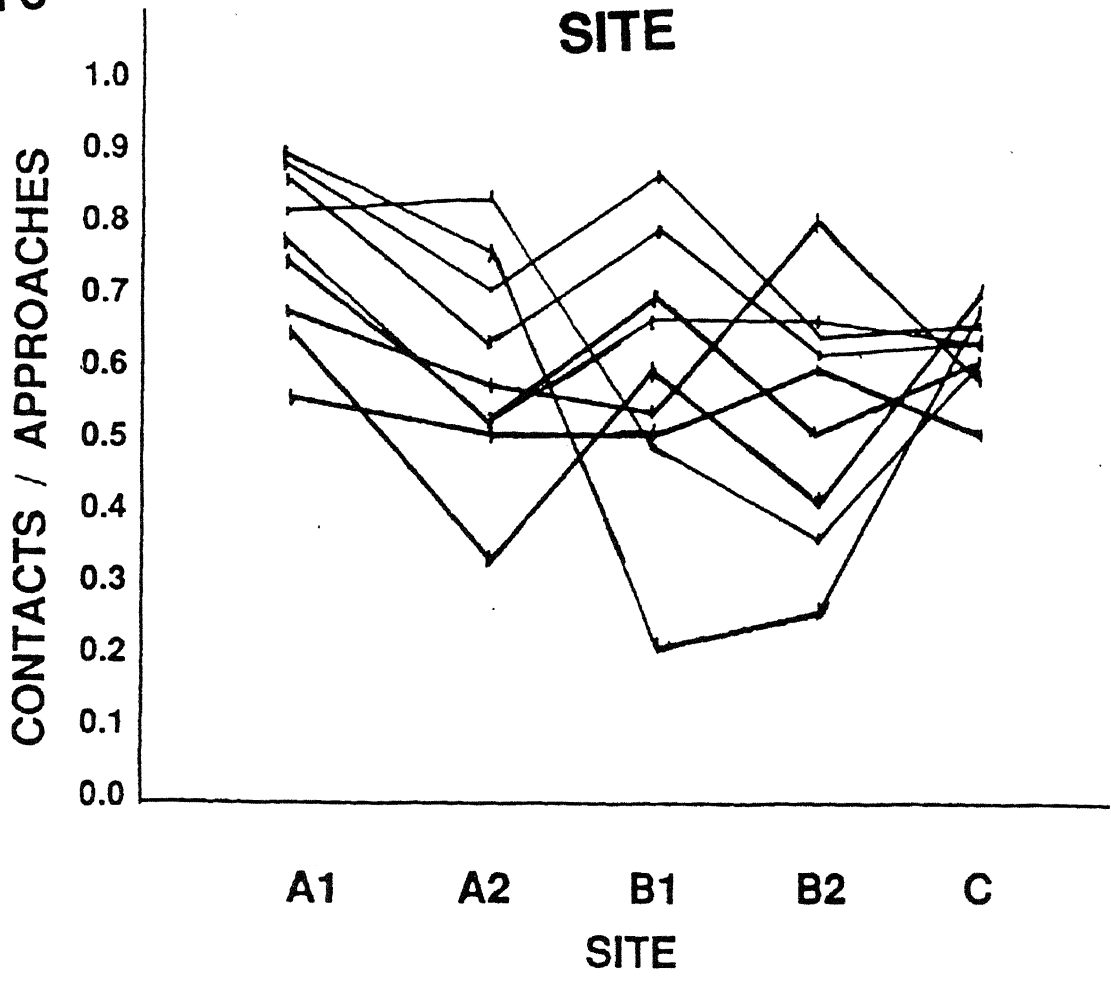
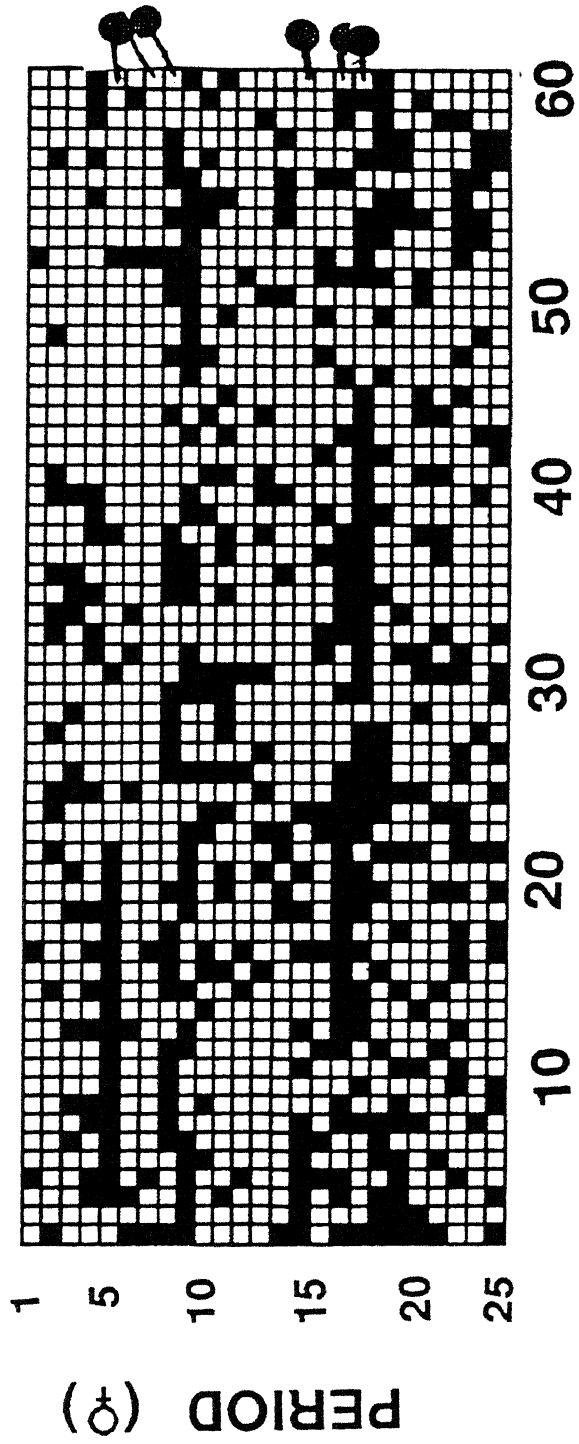


Figure 4.17. Results for 25 one-minute periods in which each second was treated as an event with two outcomes: a male approaches (black box) or does not approach (open box) a pinned, frozen unextracted female Nomia triangulifera. Males that remained on a model for more than one second were counted only once. An overall runs test gives a significant negative value ($t_s = -7.9$), showing that male approaches are clumped in time. Tested individually, those time periods with significantly non-random male "approaches" are indicated by a shaded circle.



- ♂ APPROACH TO UNEXTRACTED ♀
- NO ♂ APPROACH TO UNEXTRACTED ♀

Overall Runs test, $t_s = -7.6$, $p < 0.05$

● = $p < 0.05$, Runs test within periods

TABLE 4.1. Responses of caged male Lasioglossum figueres to unextracted or extracted frozen conspecific females.

	FEMALE CONTACTED?	
	YES	NO
UNEXTRACTED ♀	17	2
EXTRACTED ♀	1	10

($p < 0.0001$, Fisher's exact test, and Pearson's Phi)

Table 4. 2. Number of marked, and recaptured males of Nomia triangulifera.

AREA	MARKED	RECAPTURED
1	173	14
2	92	7
3	147	37
4	161	21
A	39	3 (14 unmarked)
B	62	6 (12 unmarked)

Table 4.3. The relationship between the receptivity of female *Nomia triangulifera* and prior sexual behavior.

SEXUAL EXPERIENCE	FEMALE MATES WITH	
WITH FIRST ♂:	SECOND	♂ ?
	YES	NO
MATED WITH 1 st ♂	4	30
UNRECEPTIVE TO 1 st ♂	3	15
RECEPTIVE TO 1 st ♂; SEPARATED BEFORE INTROMISSION	22	4

CHAPTER 5

EPILOGUE

A major goal of this research program is to understand general principles of social evolution, mainly by studying bees and wasps. The previous chapters present findings from studies on several aspects of social behavior in solitary bees. Taken individually, each chapter may seem remarkably pedestrian, but together they are intended to represent a few first steps toward an understanding of behavior as both a facilitator and inhibitor of evolutionary change. This important idea points to the special role of behavioral studies in producing a general synthesis of phenotypic evolution.

One of the more conspicuous patterns involving insect sociality concerns its biased phyletic distribution. Social and cuckoo behavior is most frequent in the order Hymenoptera, and within this group, it is exclusively found in the sub-order Aculeata. In turn, within Aculeata social behavior has evolved most often in Apoidea by comparison with other aculeates. As noted in the Introduction (Chapter 1), within the Apoidea complex social organizations have evolved repeatedly among bees (Apiformes), yet rarely in the wasps (Spheciformes).

To understand these evolutionary patterns it seemed useful to examine patterns involving the phyletic distribution of various social recognition mechanisms. Previous workers postulated that mating and

nest-finding behavior were relevant contexts in which to study such patterns. On the mating side, I began with male behavior for practical reasons*, despite the theoretical expectations that results would not be novel**. In the species studied, social conditions arising from the males' patrolling behavior create strong competition; there would be little opportunity for strong selection for refined discriminating abilities.

A female bee, no matter how busy, cannot fully provision a cell in one foraging trip. Consequently, there are conditions for selection for improved performance on spatial orientation tasks, as well as for refined abilities to discriminate among similar places. Studies on one species showed that females use visual cues to locate their nests, and then use olfactory cues to identify their nest and discriminate it from others. Similar multimodal orientation is known for other bees and a wasp, while others apparently rely exclusively on visual cues.

*I have not yet been able to develop a bioassay for female bees which would allow me to distinguish between females that are not receptive because they do not want to be ("female choice") and those that are not receptive because their reproductivity is suppressed ("worker-sterility").

**An unlikely hypothesis related to male learning and keen discriminating abilities has been repeatedly suggested; it is especially important to address the idea because it has crept into popular literature [e.g., Djerassi (1989) Cantor's Dilemma: it should not be surprising that one of the "fathers" (!) of the oral contraceptive pill is taken with the idea of responsible male behavior *viz-à-viz* sex].

The use of chemicals for architectural purposes could leave olfactory "signatures" at nests, due to individual variability in biosynthetic pathways. This increase in environmental complexity enables alternative modalities for recognition. Bees can learn to associate odors with places for more precise nest orientation abilities. These perceptual abilities might then be transferred to other contexts and used for identifying and discriminating among the signatures worn as chemical "badges" by individuals belonging to a group, thereby accepting nestmates but preventing an alien from parasitizing the group's labors.

Painters such as Monet sometimes returned again and again to the same "scene," yet produced strikingly different paintings when "environmental" conditions were changed. Biologists are familiar with analogous situations, yet have still largely refused to recognize that it is the form of the interaction between organisms and environments that evolves, and that it is not reducible to one or the other. This 'cybernetic' relationship means that the collective activities of organisms have evolutionary consequences, as proposed long ago. Darwin's Citadel is haunted by Lamarck's ghost!

Finally, I believe that we can never reduce our principles to any few simple terms. Existence is always too various and too complicated. We must supplement principles with faith. And the only faith that is both concrete and comprehensive is life, its abundance and its progress. My final belief is in life.

-- J.S. Huxley, "Life can be worth living"

LITERATURE CITED

- Abrams, J. and Eickwort, G.C. 1980. Biology of the communal sweat bee Agapostemon virescens (Hymenoptera: Halictidae) in New York. Search: Agriculture 1: 1-20.
- Alcock, J., Barrows, E.M., Gordh, G., et al. 1978. The ecology and evolution of male reproductive behaviour in the bees and wasps. Zool. Journ. Linn. Soc. 64: 293-326.
- _____ and Buchmann, S.L. 1985. The significance of post-insemination display by male Centris pallida (Hymenoptera: Anthophoridae). Z. Tierpsychol. 68: 231-243.
- _____ and Houston, T.F. 1987. Resource defense and alternative mating tactics in the Banksia bee, Hylaeus alcyoneus (Erichson). Ethology 76: 177-188.
- _____, Jones, C.E., Buchmann, S.L. 1976. Location before emergence of the female bee, Centris pallida, by its male (Hymenoptera: Anthophoridae). J. Zool., Lond. 179: 189-199.
- Alexander, R.D. 1974. The evolution of social behavior. Annu. Rev. Ecol. Syst. 5:325-383.
- Anonymous. 1965. Anuario meterologico, año 1965. Instituto Meterologico Nacional, Ministerio de Agricultura y Ganaderia, San José, Costa Rica.
- Anonymous. 1982. Anuario meterologico, año 1982. Instituto Meterologico Nacional, Ministerio de Agricultura y Ganaderia, San José, Costa Rica.
- Anzenberger, G. 1986. How do carpenter bees recognize the entrance of their nests? An experimental investigation in a natural habitat. Ethology 71: 54-62.
- Ayasse, M. 1990. Odor based interindividual and nest recognition in the sweat bee Lasioglossum malachurum, pp. 511-512. IN Veeresh, G.K., Mallik, B., and Viraktamath, C.A. (eds.). Social insects and the environment (Proc. 11th Internatl. Congr. IUSI). New Delhi: Oxford & IBH Publishing Co.

- Baerends, G.P. 1941. Fortpflanzungsverhalten und orientierung der Grabwespe Ammophila campestris Jur. Tijdschrift voor Entomol. Deel. 84: 68-275.
- Barrows, E.M. 1975 a. Individually distinctive odors in an invertebrate. Behav. Biol. 15: 57-64.
- _____. 1975 b. Mating behavior in halictine bees (Hymenoptera: Halictidae): III. Copulatory behavior and olfactory communication. Insectes Soc. 22: 307-322.
- Batra, S.W.T. 1966. The life cycle and behavior of the primitively social bee, Lasioglossum zephyrum (Halictidae). Univ. Kansas Sci. Bull. 64: 359-423.
- _____. 1987. Ethology of the vernal eusocial bee, Dialictus laevisimus (Hymenoptera: Halictidae). J. Kansas Entomol. Soc. 60:100-108.
- Bell, W.J. 1974. Recognition of resident and non-resident individuals in intraspecific nest defense of a primitively eusocial halictine bee. J. Comp. Physiol. 93:195-202.
- _____. 1990. Searching behavior patterns in insects. Annu. Rev. Entomol. 35: 447-467.
- _____ and Carde, R. (eds). 1984. Chemical Ecology of Insects. Sunderland: Sinauer Assoc.
- _____ and Hawkins, W.A. 1974. Patterns of intraspecific agonistic interactions in nest defense of a primitively eusocial halictine bee. J. comp. Physiol. 93:183-193.
- Bergmark, L., Bork-Karlson, A.-K., and Tengö, J. 1984. Female characteristics and odour cues in mate recognition in Dasygaster altercator (Hym., Melittidae). Nov. Act. Reg. Soc. Sci. Upsaliensis (Ser. V), C: 137-143.
- Bitterman, M.E. 1988. Vertebrate-invertebrate comparisons, pp. 251-276. IN Jerison, H.J. and Jerison, I. (eds.). Intelligence and Evolutionary Biology. NY: Springer-Verlag.
- Bogdany, F.J. 1978. Linking of learning signals in honeybees. Behav. Ecol. Sociobiol. 3: 323-336.

- Breed, M.D. 1975. Life cycle and behavior of a primitively social bee, Lasioglossum rohweri (Hymenoptera: Halictidae). J. Kansas Ent. Soc. 48:64-80.
- _____, Silverman, J.M., and Bell, W.J. 1978. Agonistic behavior, social interactions, and behavioral specialization in a primitively eusocial bee. Insectes Soc. 25:351-364.
- _____, Williams, K.R., and Fewell, J.H. 1989. Comb wax mediates the acquisition of nest-mate recognition cues in honey bees. Proc. Natl. Acad. Sci. (USA) 85:8766-8769.
- Brockmann, H.J. and Dawkins, R. 1979. Joint nesting in digger wasps as an evolutionarily stable preadaptation to social life. Behaviour 71:203-245.
- Brooks, R.W. and Cane, J.H. Origin and chemistry of the secreted nest entrance lining of Halictus hesperus (Hymenoptera: Apoidea). Journ. Kansas Entomol. Soc. 7: 161-165.
- Brothers, D.J. and Michener, C.D. 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.
- Butler, C.G. 1965. Sex attraction in Andrena flavipes Panzer (Hymenoptera: Apoidea), with some observations on nest-site restriction. Proc. R. Entomol. Soc. Lond. (A) 40:77-80.
- _____, Fletcher, D.J.C., and Watler, D. 1969. Nest-entrance marking with pheromones by the honeybee Apis mellifera L., and a wasp, Vespula vulgaris L. Animal Behavior 17: 142-147.
- _____, _____, & _____. 1970. Hive entrance finding by honeybee (Apis mellifera) foragers. Animal Behavior 18: 78-91.
- Carthy, J.D. 1956. Animal Navigation. How Animals Find Their Way About. London. Allen & Unwin, 151 pp.
- Coen, E. 1982. Climate, pp. 35-45, IN Janzen, D. (ed.). Costa Rican Natural History. Chicago: University of Chicago Press.
- Cowan, D.P. 1986. Sexual behavior of eumenid wasps. Proc. Entomol. Soc. Wash. 88:531-541.

- Cross, E.A. 1958. A revision of the bees of the subgenus Epinomia in the New World (Hymenoptera: Halictidae). Univ. Kansas Sci. Bull. 38: 1261-1301.
- _____ and Bohart, C.G. 1960. The biology of Nomia (Epinomia) triangulifera with comparative notes on other species of Nomia. Univ. Kansas Sci. Bull. 41: 761-792.
- Danks, H.V. 1970. Biology of some stem-nesting aculeate Hymenoptera. Trans. R. Entomol. Soc. Lond. 122: 323-399.
- Danforth, B.N. 1990. Provisioning behavior and the estimation of investment ratios in a solitary bee, Calliopsis (Hypomacrotera) persimilis (Cockerell) (Hymenoptera: Andrenidae). Behav. Ecol. Sociobiol. 27: 159-168.
- Darchen, R. and Delage-Darchen, B. 1986. Societies of spiders compared to the societies of insects. J. Arachnol. 14: 227-238.
- Darwin, C. 1859. On the Origin of Species by Means of Natural Selection (facsimile of the 1st edition). Cambridge: Harvard University Press.
- Dewsbury, D.A. 1988. Copulatory behavior as courtship communication. Ethology 79: 218-234.
- Dukas, R. 1987. Foraging behavior of three bee species in a natural mimicry system: female flowers which mimic male flowers in Ecballium elaterium (Cucurbitaceae). Oecologia 74:256-263.
- Eberhard, W.G. 1974. The natural history and behaviour of the wasp Trigonopsis cameronii Kohl (Sphecidae). Trans. Roy. Entomol. Soc. London 125: 295-328.
- _____. 1985. Sexual Selection and Animal Genitalia. Cambridge: Harvard University Press.
- _____. 1990a. Copulatory courtship in the wasp Eumenes consobrinus (Hymenoptera, Vespidae). Journ. Kansas Ent. Soc. 63:342-343.
- _____. 1990b. Imprecision in the behavior of Leptomorphus sp. (Diptera, Mycetophilidae) and the evolutionary origin of new behavior patterns. Journ. Insect Behav. 3: 327-357.

- Eickwort, G.C. 1986. First steps into eusociality: the sweat bee Dialictus lineatulus. Fla. Entomol. 69:742-754.
- _____ and Ginsberg, H.S. 1980. Foraging and mating behavior in Apoidea. Annu. Rev. Entomol. 25:421-446.
- Espelie, K.E., Wenzel, J.W., and Chang, G. 1990. Surface lipids of social wasp Polistes metricus Say and its nest and nest pedicel and their relation to nestmate recognition. Journ. Chem. Ecol. 16: 2229-2241.
- Evans, H.E. 1966. The behavior patterns of solitary wasps. Annu. Rev. Entomol. 11: 123-154.
- _____. 1977. Extrinsic versus intrinsic factors in the evolution of insect sociality. Bioscience 27:613-617.
- _____ and Hook, A.W. 1986. Nesting behavior of Australian Cerceris digger wasps, with special reference to nest re-utilization and nest sharing. Sociobiology 11:275-302.
- _____ and O'Neill, K.M. 1986. Reproductive and nesting biology of Bembecinus nasus strenuus (Mickel) (Hymenoptera, Sphecidae). Proc. Entomol. Soc. Wash. 88:628-633.
- _____ and West Eberhard, M.J. 1970. The Wasps. Ann Arbor: The University of Michigan Press.
- Ezhikov, T. 1934. Individual variability and dimorphism of social insects. Am. Nat. 68: 333-344.
- Fabre, J.H. 1914. The Mason-bees (transl.). New York: Dodd, Mead & Co. 315 pp.
- Ferguson, C.S. and Hunt, J.H. 1989. Near-nest behavior of a solitary mud-daubing wasp, Sceliphron caementarium (Hymenoptera: Sphecidae). Journ. Insect Behav. 2:315-324.
- Ferton, Ch. 1905. Sur l'instinct des hyménoptères mellifères et ravisseurs. Ann. Soc. Entomol. France 74: 56-104.
- Fletcher, D.J.C., and Michener, C.D. (eds.). 1987. Kin Recognition in Animals. London: John Wiley & Sons.

- Foster, R.L. and Gamboa, G.J. 1989. Nest entrance marking with colony specific odors in the bumblebee Bombus occidentalis (Hymenoptera: Apidae). *Ethology* 81:273-278.
- Free, J.B. 1987. Pheromones of Social Bees. Ithaca: Cornell University Press.
- Frisch, K. von. 1967. The Dance Language and Orientation in Bees. Cambridge: Harvard University Press.
- Frohlich, D.R. and Parker, F.D. 1985. Observations on the nest-building and reproductive behavior of a resin-gathering bee: Dianthidium ulkei (Hymenoptera: Megachilidae). *Ann. Entomol. Soc. Amer.* 78: 804-810.
- Gadagakar, R. 1990a. Origin and evolution of eusociality: a perspective from studying primitively eusocial wasps. *J. Genetics* 69:113-125.
- _____. 1990b. Evolution of eusociality: the advantage of assured fitness returns. *Phil. Trans. R. Soc. Lond.* 329:17-25.
- _____. 1990c. The haplodiploidy threshold and social evolution. *Curr. Sci.* 59:374-376.
- _____, Bhagavan, S., Malpe, R., and Vinutha, C. 1990. On reconfirming the evidence for pre-imaginal caste bias in a primitively eusocial wasp. *Proc. Indian Acad. Sci. (Animal Sci.)*. 99:141-150.
- Graenicher, S. 1906. A contribution to our knowledge of the visual memory of bees. *Bull. Wisconsin Nat. Hist. Soc.* 4: 135-142.
- Greenberg, L. 1988. Kin recognition in the sweat bee Lasioglossum zephyrum. *Behav. Genet.* 18:425-438.
- Haldane, J.B.S., and Spurway, 1954. A statistical analysis of communication in "Apis mellifera" and a comparison with communication in other animals. *Insectes Soc.* 1: 247-283.
- Hamilton. W.D. 1964. The genetical evolution of social behaviour, I and II. *Journ. Theor. Biol.* 7: 1-52.
- Hearst, E. and Wolff, W.T. 1989. Addition versus deletion as a signal. *Animal Learn. Behav.* 17: 120-133.

- Hefetz, A. 1987. The role of Dufour's gland secretions in bees. *Physiol. Entomol.* 12: 243-253.
- _____, Bergstrom, G., and Tengö, J. 1986. Species, individual and kin specific blends in Dufour's gland secretions of Halictine bees. Chemical evidence. *Journ. Chem. Ecol.* 12: 197-208.
- _____, Eickwort, G.C., Blum, M.S., Cane, J., and Bohart, G.C. 1982. A comparative study of the exocrine products of cleptoparasitic bees (Holcopasites) and their hosts (Calliopsis) (Hymenoptera: Anthophoridae, Andreninae). *J. Chem. Ecol.* 8: 1389-1397.
- _____, and Graur, D. 1988. The significance of multicomponent pheromones in denoting specific compositions. *Biochem. Syst. Ecol.* 16: 557-566.
- _____, Mevoreh, D., and Gerling, D. 1990. Nest recognition by scent in the carpenter bee Xylocopa pubescens, pp. 515-516. IN Veeresh, G.K., Mallik, B., and Viraktamath, C.A. (eds.). Social Insects and the Environment (Proc. 11th Internatl. Congr. IUSI). New Delhi: Oxford & IBH Publishing Co.
- Hirsch, J. and Holliday, M. 1988. A fundamental distinction in the analysis and interpretation of behavior. *J. Comp. Psychol.* 102:372-377.
- Hoffmann, G. 1985. The influence of landmarks on the systematic search behaviour of the desert isopod Hemilepistus reaumuri. I. The role of the landmark made by the animal; II. Problems with similar landmarks and their solution. *Behav. Ecol. Sociobiol.* 17: 325-334; 335-348.
- Hölldobler, B. and Carlin, N.F. 1987. Anonymity and specificity in the chemical communication signals of social insects. *J. Comp. Physiol.* A 161: 567-581.
- _____, and Michener, C.D. 1980. Mechanisms of identification and discrimination in social Hymenoptera, pp. 35-58. IN Markl, H. (ed.) Evolution of Social Behavior: Hypotheses and Empirical Tests. Weinheim: Verlag Chemie GmbH.
- _____, and Wilson, E.O. 1990. The Ants. Cambridge: Harvard University Press.

- Jacobs, W. 1924. Das Duftorgan von *Apis mellifera* und ähnliche Hautdrüsenorgane sozialer und solitärer Apiden. *Z. Morph. Okol. Tiere* 3: 1-80.
- Jacobs-Jessen, U.F. 1959. Zur Orientierung der Hummeln und einiger anderer Hymenopteren. *Zeitschr. vergl. Physiol.* 41: 597-641.
- Jaisson, P. 1985. Social behaviour, pp. 673-694. IN Kerkut, G.A. and Gilbert, L.I. (eds.). Comprehensive Insect Physiology Biochemistry and Pharmacology, Oxford: Pergamon Press.
- Jander, R. 1975. Ecological aspects of spatial orientation. *Annu. Rev. Ecol. Syst.* 6: 171-188.
- Kamm, D.R. 1974. Effects of temperature, day length, and number of adults on the sizes of cells and offspring in a primitively social bee (Hymenoptera: Halictidae). *J. Kansas Entomol. Soc.* 47:8-18.
- Keeping, M.G., Lipschitz, D., and Crewe, R.M. 1986. Chemical mate recognition and release of male sexual behavior in polybiine wasp, *Belanogaster petiolata* (Degeer) (Hymenoptera: Vespidae). *J. Chem. Ecol.* 12:773-779.
- Kennedy, C.H. 1927. Some non-nervous factors that condition the sensitivity of insects to moisture, temperature, light and odors. *Ann. Entomol. Soc. Amer.* 20:87-106.
- Knerer, G. 1981. Biologie von vier kleinen *Evyllaesus*-Arten im Mittelmeergebiet (Hymenoptera; Halictinae). *Zool. Anz.* 206:1-10.
- Koeniger, G. 1990. The role of the mating sign in honey bees, *Apis mellifera* L.: does it hinder or promote multiple mating? *Anim. Behav.* 39:444-449.
- Krombein, K.V. et al. 1979. Catalog of Hymenoptera North of Mexico.
- Kukuk, P. 1985. Evidence for an antiaphrodisiac in the sweat bee *Lasioglossum* (*Dialictus*) *zephyrum*. *Science* 227:656-657.
- _____. 1989. Evolutionary genetics of a primitively eusocial halictine bee, *Dialictus zephyrus*, pp. 183-202. In Page, R.E. and Breed, M.D. (eds.). Genetics of Social Evolution. Boulder: Westview Press.

- _____, Breed, M.D., Sobti, A., and Bell, W.J. 1977. The contributions of kinship and conditioning to nest recognition and colony member recognition in a primitively eusocial bee, Lasioglossum zephyrum (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* 2:319-327.
- _____ and Decelles, P.C. 1986. Behavioral evidence for population structure in Lasioglossum (Dialictus) zephyrum female dispersion patterns. *Behav. Ecol. Sociobiol.* 19:233-239.
- Kullenberg, B. 1973. Field experiments with chemical sexual attractants on aculeate Hymenoptera males. II. *Zoon (suppl.)* 1:32-44.
- Larsson, F. 1989 a. Insect mating patterns explained by microclimatic variables. *J. Therm. Biol.* 14:155-157.
- _____. 1989b. Mating patterns in six insect species: effects of weather and population density. *Acta Univ. Upsaliensis* 234:1-31.
- Larsen, O., Gleffe, G., and Tengö, J. 1986. Vibration and sound communication in solitary bees and wasps. *Physiol. Entomol.* 11:287-296.
- Lin, N. 1964. Increased parasitic pressure as a major factor in the evolution of social behavior in halictine bees. *Insectes Soc.* 11: 187-192.
- _____ and Michener, C.D. 1972. Evolution of sociality in insects. *Quart. Rev. Biol.* 47: 131-159.
- Linsenmair, K.E. 1987. Kin recognition in subsocial arthropods, in particular in the desert isopod Hemilepistus reaumuri, pp. 121-208. IN Fletcher, D.J.C. and Michener, C.D. (eds.). Kin Recognition in Animals. Chichester: John Wiley and Sons.
- Linsley, E.G. 1958. The ecology of solitary bees. *Hilgardia* 27: 453-599.
- Longair, R.W., Cane, J.H., and Elliott, L. 1987. Male competition and mating behavior within mating aggregations of Glenostictia satan Gillaspay (Hymenoptera: Sphecidae).
- Lubbock, J. 1882. Ants, Bees and Wasps (1929 ed.). NY: E.P. Dutton & Co.
- Malyshev, S.I. Genesis of the Hymenoptera. London: Methuen & Co.

- Markl, H. 1980. Introduction, pp. 1-10. IN Markl, H. (ed.) Evolution of Social Behavior: Hypotheses and Empirical Tests. Berlin: Verlag Chemie.
- _____. 1977. Mating behavior and sound production in harvester ants (Pogonomyrmex, Formicidae). *Insectes Soc.* 24:191-212.
- Matthews, R.W. 1968. Microstigmus comes: sociality in a sphecid wasp. *Science* 160:787-788.
- _____ and Naumann, I.D. 1988. Nesting biology and taxonomy of Arpactophilus mimi, a new species of social sphecid (Hymenoptera: Sphecidae). *Austral. Journ. Zool.* 36: 585-597.
- McCorquodale, D.B. and Naumann, I.D. 1988. A new Australian species of communal ground-nesting wasp in the genus Spilomena Shuckard (Hymenoptera: Sphecidae: Pemphredoninae). *J. Aust. Ent. Soc.* 27:221-231.
- McDaniel, C.A., Howard, R.W. 1987. Chemistry of male mandibular gland secretions of Philanthus basilaris Cresson and Philanthus bicinctus (Mickel) (Hymenoptera). *J. Chem. Ecol.* 13:227-235.
- Menzel, R., Steinmann, E., de Souza, J., and Backhaus, W. 1988. Spectral sensitivity of photoreceptors and colour vision in the solitary bee, Osmia rufa. *J. Exp. Biol.* 136: 35-52.
- Michener, C.D. 1964. Evolution of the nests of bees. *Amer. Zool.* 4:227-239.
- _____. 1974. The Social Behavior of the Bees. Cambridge: Harvard University Press.
- _____. 1982. Early stages in insect social evolution: individual and family odor differences and their functions. *Bull. entomol. Soc. Amer.* 28:7-11.
- _____. 1985. From solitary to eusocial: need there be a series of intervening species? pp. 293-305. IN Hölldobler, B. and Lindauer, M. (eds.). Experimental Behavioral Ecology and Sociobiology. Stuttgart: G. Fischer.
- _____. 1990. Reproduction and caste in social halictine bees. IN Engels, W. (ed.), Social Insects: An Evolutionary Approach to Castes and Reproduction. Berlin: Springer-Verlag.

- _____ and Bennett, F.D. 1977. Geographical variation in nesting biology and social organization of Halictus ligatus. Univ. Kansas Sci. Bull. 51: 233-260.
- _____ and Brothers, D.J. 1974. Were workers of eusocial Hymenoptera initially altruistic or oppressed? Proc. Natl. Acad. Sci. USA 71: 671-674.
- _____ and Lange, R.B. 1958a. Observations on the behavior of Brazilian halictid bees, III. Univ. Kansas Sci. Bull. 39:473-505.
- _____ & _____. 1958b. Observations on the behavior of Brazilian halictid bees (Hymenoptera, Apoidea). I. Pseudagapostemon. Ann. Entomol. Soc. Amer. 51:155-164.
- _____ & _____. Observations on the behavior of Brazilian halictid bees. V, Chloralictus. Insectes Soc. 5:28-379-407.
- _____ and Seabra, C.A.C. 1959. Observations on the behavior of Brazilian halictid bees, VI. Tropical species. J. Kansas Ent. Soc. 32:19-28.
- _____ and Smith, B.H. 1987. Kin recognition in primitively eusocial insects, pp. 209-242. IN Fletcher, D.J.C. and Michener, C.D. (eds.). Kin Recognition in Animals. Chichester: John Wiley & Sons.
- _____ and Wille, A. 1961. The bionomics of a primitively social bee, Lasioglossum inconspicuum. Univ. Kansas Sci. Bull. 42:1123-1202.
- Minckley, R.L., Buchmann, S.L., and Wcislo, W.T. 1991. Bioassay evidence for a sex attractant pheromone in the large carpenter bee, Xylocopa varipuncta (Anthophoridae: Hymenoptera). J. Zool., Lond. 224 (in press).
- Meyer-Holzapfel, M. 1984. Zur ethologie des männchens der Trugbiene (Panurgus banksianus Kirby) (Hymenoptera, Apidae). Z. Tierpsychol. 64:221-252.
- Muralidharan, K. Shaila, M.S., and Gadagkar, R. 1986. Evidence for multiple mating in the primitively eusocial wasp Ropalidia marginata (Lep.) (Hymenoptera: Vespidae). J. Genetics 65:153-158.
- Nielsen, E.T. 1945. Moeurs des Bembex. Spolia Zool. Mus. (Kobehavn) Hauniensis 7:1-174.

- O'Neill, K.M. and Bjostad, L. 1987. The male mating strategy of the bee Nomia nevadensis (Hymenoptera: Halictidae): leg structure and mate guarding. *Pan.-Pac. Entomol.* 63:207-217.
- Ono, M. and Sasaki, M. 1987. Sex pheromones and their cross-activities in six Japanese sympatric species of the genus Vespa. *Insectes Soc.* 34:252-260.
- Packer, L. 1986. The social organisation of Halictus ligatus (Hymenoptera: Halictidae) in southern Ontario. *Can. J. Zool.* 64: 2317-2324.
- _____. 1990. Solitary and eusocial nests in a population of Augochlorella striata (Provancher) (Hymenoptera; Halictidae) at the northern edge of its range. *Behav. Ecol. Sociobiol.* 27:339-344.
- _____ and Knerer, G. 1985. Social evolution and its correlates in bees of the subgenus Evylaeus (Hymenoptera; Halictidae). *Behav. Ecol. Sociobiol.* 17: 143-149.
- _____ and Knerer, G. 1986. The biology of a subtropical population of Halictus ligatus Say (Hymenoptera: Halictidae). I. Phenology and social organization. *Behav. Ecol. Sociobiol.* 18: 363-375.
- _____, Jessome, V., Lockerbie, C., and Sampson, B. 1989. The phenology and social biology of four sweat bees in a marginal environment: Cape Breton Island. *Can. J. Zool.* 67: 2871-2877.
- Papaj, D.R. and Vet, L.E.M. 1990. Odor learning and foraging success in the parasitoid, Leptopilina heterotoma. *J. Chem. Ecol.* 16:3137-3150.
- Peckham, G.W. and Peckham, E.G. 1898. Instincts and habits of solitary wasps. *Wisconsin Geol. & Nat. Hist. Bull.* 2: 1-245.
- Pedersen, A. and Blass, E.M. 1981. Olfactory control over suckling in albino rats, pp. 359-381. IN Aslin, R.N., Alberts, J.R., and Petersen, M.R. (eds). Development of Perception. New York: Academic Press.
- Pfennig, D.W. and Reeve, H.K. 1989. Neighbor recognition and context-dependent aggression in a solitary wasp, Sphecius speciosus (Hymenoptera: Sphecidae). *Ethology* 80: 1-18.

- Plateaux-Quénu, C. and Plateaux, L. 1985. La variatiion (sic) individuelle d'Evylaeus villosulus (K.), espece solitaire (Hym., Halictinae). Comparaison des fondatrices de printemps et de leurs files, appartenant a la premiere generation. Actes Coll. Insectes Soc. 2: 293-302.
- Rabaud, E. 1926. Acquisition des habitudes et reperes sensoriels chez les gûepes. Bull. Biol. France Belgique 60: 313-333.
- Rau, P. 1929. Experimental studies on the homing of carpenter and mining bees. J. Comp. Physiol. 9: 35-70.
- Richards, O.W. 1927. Sexual selection and allied problems in the insects. Biol. Rev., Cambridge Phil. Soc. 2:298-364.
- _____ 1961. An introduction to the study of polymorphism in insects, pp. 2-10. IN Kennedy, J.S. (ed.). Insect Polymorphism (Proc. Roy. Entomol. Soc. London).
- Roff, D. 1983. Phenological adaptation in a seasonal environment: a theoretical perspective, pp. 253-270. IN Brown, V.K., Hodek, I. (eds.). Diapause and Life Cycle Strategies in Insects. The Hague: Dr. W. Junk Publ.
- Rosenheim, J.A. 1987. Host location and exploitation by the cleptoparasitic wasp Argochrysis armilla: the role of learning. Behav. Ecol. Sociobiol. 21: 401-406.
- Ross, K.G. and Matthews, R.W. 1989. Population genetic structure and social evolution in the sphecid wasp Microstigmus comes. Amer. Nat. 134: 574-598.
- Sakagami, S.F. and Maeta, Y. 1987. Sociality, induced and/or natural, in the basically solitary small carpenter bees (Ceratina), pp. 1-16. In Itô, Y., Brown, J.L., and Kikkawa, J. (eds.). Animal Societies: Theories and Facts. Tokyo: Japan. Sci. Soc. Press.
- _____ and Michener, C.D. 1962. The Nest Architecture of the Sweat Bees. Lawrence: University of Kansas Press.
- _____ and Moure, J.S., CMF. 1967. Additional observations on the nesting habits of some Brazilian halictine bees. Mushi 40:119-138.

- _____ and Munukata, M. 1972. Distribution and bionomics of a transpalearctic eusocial halictine bee, Lasioglossum (Evylaeus) calceatum, in northern Japan, with reference to its life cycle at high altitude. J. Fac. Sci., Hokkaido Univ. Ser. VI, Zool. 18:411-439.
- Schöne, H. 1984. Spatial Orientation. Princeton: Princeton University Press.
- Serradilla, J.M. and Ayala, F.J. 1983. Alloproctict selection: a mode of natural selection promoting polymorphism. Proc. Natl. Acad. Sci. USA 80:2022-2025.
- Shimron, O. and Hefetz, A. 1985. Mating behavior and sex attraction of Eucera palestinae Friese (Hymenoptera: Anthophoridae). J. Kansas Entomol. Soc. 58:526-531.
- Shimron, O., Hefetz, A., and Tengo, J. 1985. Structural and communicative functions of Dufour's gland secretions in Eucera palestinae (Hymenoptera; Anthophoridae). Insect Biochem. 15: 635-638.
- Shinn, A.F. 1967. A revision of the bee genus Calliopsis, and the biology and ecology of C. andreniformis (Hymenoptera: Andrenidae). Univ. Kansas Sci. Bull. 46:753-936.
- Sivinski, J. and Webb, J.C. 1989. Acoustic signals produced during courtship in Diachasmimorpha (=Biosters) longicaudata (Hymenoptera: Braconidae) and other Braconidae. Ann. Entomol. Soc. Amer. 82:116-120.
- Skaife, S.H. 1952. The yellow-banded carpenter bee, Mesotrichia caffra Linn, and its symbiotic mite, Dinogamasus Braunsi Vitzthun. Journ. Entomol. Soc. S. Africa 15:63-76.
- Smith, B.H. 1983. Recognition of female kin by male bees through olfactory signals. Proc. Natl. Acad. Sci. USA 80:4551-4553.
- _____ and Ayasse, M. 1987. Kin-based male mating preferences in two species of halictine bee. Behav. Ecol. Sociobiol. 20:313-318.
- Sokal, R.R., and Rohlf, F.J. 1981. Biometry (2nd ed.). New York: W.H. Freeman & Co.
- _____ and Braumann, C.A. 1980. Significance tests for coefficients of variation and variability profiles. Syst. Zool. 29:50-66.

- Spangler, H.G. 1969. Suppression of honey bee flight activity with substrate vibration. *J. Econ. Entomol.* 62:1185-1186.
- Steiner, A.L. 1983. Predatory behavior of digger wasps (Hymenoptera, Sphecidae) VI. Cutworm hunting and stinging by the ammophiline wasp Podalonia luctuosa (Smith). *Melandria* 41: 1-16.
- Steinmann, E. 1973. Über die Nahorientierung der einsiedlerbienen Osmia bicornis L. und Osmia cornuta Latr. (Hymenoptera, Apoidea). *Mitt. Schweiz. Entomol. Ges.* 46: 119-122.
- _____. 1976. Über nahorientierung solitärer Hymenopteren: individuelle markierung der nesteingänge. *Bull. Soc. Entomol.Suisse* 49: 253-258.
- _____. 1985. Die wand-pelzbiene Anthophora plagiata (Illiger) (Hymenoptera: Apoidea). *J. Natf. Ges. Graubunden* 102: 137-142.
- _____. 1990. Zur nahorientierung der solitären sandbiene Andrena vaga, Panzer 1799 (Hymenoptera, Apoidea) am nesteingang. *Mitt. Schweiz. Entomol. Ges.* 63: 77-80.
- Tengö, J. and Bergström, G. 1977. Comparative analyses of complex secretions from heads of Andrena bees (Hym., Apoidea). *Comp. Biochem. Physiol.* 57:197-202.
- _____, Eriksson, J., Borg-Karlson, A.-K. et al. 1988. Mate-locating strategies and multimodal communication in male mating behavior of Panurgus banksianus and P. calcaratus (Apoidea, Andrenidae). *J. Kansas Entomol. Soc.* 61:388-395.
- Tepedino, V.J. , McDonald, L.L., and Rothwell, R. 1979. Defense against parasitization in mud-nesting Hymenoptera: can empty cells increase net reproductive output. *Behav. Ecol. Sociobiol.* 6:99-104.
- Tinbergen, N. 1958. Curious Naturalists. New York: Basic Books.
- _____. 1972. The Animal in its World, vol. 1. Cambridge: Harvard University Press.
- Toro, H. 1985. Ajuste mecanico para la copula de Callonychium chilense (Hymenoptera, Andrenidae). *Rev. Chil. Entomol.* 12: 153-158.

- Tripplett, D.C. and Gittins, A.R. 1988. Nesting, mating, and foraging habits of Melissodes (Melissodes) tepida tepida Cresson in Idaho (Hymenoptera: Anthophoridae). Proc. Entomol. Soc. Wash. 90: 462-470.
- Trivers, R.L. 1974. Parent-offspring conflict. Amer. Zool. 14:249-264.
- Tsuneki, K. 1961. Colour vision and figure discriminating capacity of the solitary diplopterous wasp, Odynerus frauenfeldi Saussure. Mem. Fac. Lib. Arts, Fukui Univ., Ser. II, Nat. Sci. 11: 103-160.
- Turner, C.H. 1908. The homing of the burrowing bees (Anthophoridae). Biol. Bull. 15: 247-258.
- _____, 1923. The homing of the Hymenoptera (posthumous publ.). Trans. Acad. Sci. St. Louis 24: 27-45.
- van Iersel, J.J.A. 1975. The extension of the orientation system of Bembix rostrata as used in the vicinity of its nest, pp. 142-168. IN Baerends, G., Beer, C., and Manning, A. (eds.). Function and Evolution in Behaviour. Oxford: Clarendon Press.
- Verlaine, L. 1924. L'instinct et l'intelligence chez les Hyménoptères. I. Le problème du retour au nid et de la reconnaissance du nid. Acad. Roy. Belgique, Classe Sci. Mem. 8: 1-72.
- _____. 1925. L'instinct et l'intelligence chez les Hyménoptères. III. La reconnaissance du nid et l'éducabilité de l'odorat chez la Vespa germanica Fab. Ann. Soc. roy. Zool. Belgique 55: 67-117.
- Wade, M.J. 1987. Measuring sexual selection, pp. 197-207. IN Bradbury, J.W. and Andersson, M.A. (eds.), Sexual Selection: Testing the Alternatives. Berlin: Springer-Verlag.
- Wcislo, W.T. 1986. Host nest recognition by a cleptoparasitic fly Metopia campestris (Fallén) (Diptera: Sarcophagidae: Miltogramminae). J. Kansas Entomol. Soc. 59:82-88.
- _____. 1987a. The role of learning in the mating biology of a sweat bee, Lasioglossum zephyrum (Hymenoptera: Halictidae). Behav. Ecol. Sociobiol. 20: 179-185.

- _____. 1987b. The roles of seasonality, host synchrony, and behaviour in the evolutions and distributions of nest parasites in Hymenoptera (Insecta), with special reference to bees (Apoidea). *Biol. Rev., Cambridge Phil. Soc.* 62: 515-543.
- _____. 1989. Behavioral environments and evolutionary change. *Annu. Rev. Ecol. Syst.* 20: 137-169.
- _____. 1990a. A new species of Lasioglossum from Costa Rica. *J. Kansas Entomol. Soc.* 63: 450-453.
- _____. 1990b. Olfactory cues in nest recognition by solitary bees (Lasioglossum figueresi; Halictidae) as a "pre-adaptation" for the evolution of kin associations, pp. 412-413. IN Veeresh, G.K., Mallik, B., and Viraktamath, C.A. (eds.) Social Insects and the Environment (Proc. 11th Internatl. Congr. IUSI). New Delhi: Oxford & IBH Publishing Co.
- _____. 1991. Parasitic and courtship behavior of Phalacrotophora halictorum (Diptera:Phoridae) at a nesting site of Lasioglossum figueresi (Hymenoptera: Halictidae) *Rev. Biol. Trop.* (in press).
- _____, B.S. Low, and C.J. Karr. 1985. Parasite pressure and repeated burrow use by different individuals of Crabro (Hymenoptera: Sphecidae). *Sociobiology* 11: 115-125.
- _____, West-Eberhard, M.J., and Eberhard, W.G. 1988. Natural history and behavior of a primitively social wasp, Auplopus semialatus, and its parasite, Irenangelus eberhardi (Hymenoptera: Pompilidae). *Journ. Insect Behav.* 1:247-260.
- Wehner, R. 1981. Spatial vision in arthropods, pp. 287-616. IN Autrum, H. (ed.) Handbook of Sensory Physiology, vol. 7, Vision in Invertebrates.
- Wenzel, J.W. 1987. Male reproductive behavior and mandibular glands in Polistes major (Hymenoptera: Vespidae). *Insectes Soc.* 34:44-57.
- _____, and Pickering, J. 1991. Cooperative foraging, productivity, and the central limit theorem. *Proc. Natl. Acad. Sci. (USA)* 88:36-38.
- West-Eberhard, M.J. 1969. The social biology of polistine wasps. *Misc. Publ. Mus. Zool., Univ. Mich.* 140:1-101.

- _____. 1978. Polygyny and the evolution of social behavior in wasps. *J. Kansas Entomol. Soc.* 51:832-856.
- _____. 1979. Sexual selection, social competition, and evolution. *Proc. Amer. Phil. Soc.* 123:222-234.
- _____. 1981. Intragroup selection and the evolution of insect societies, pp. 3-17. IN Alexander, R.D. and Tinkle, D.W. (eds.). Natural Selection and Social Behavior. New York: Chiron Press.
- _____. 1983. Sexual selection, social competition, and speciation. *Quart. Rev. Biol.* 58:155-183.
- _____. 1984. Sexual selection, competitive communication, and species-specific signals in insects, pp. 283-324. IN Lewis, T. (ed.). Insect Communication. NY: Academic Press.
- _____. 1986. Alternative adaptations, speciation, and phylogeny (A Review). *Proc. Natl. Acad. Sci. USA* 83:1388-1392.
- _____. 1987. Flexible strategy and social evolution, pp. 35-51. IN Itô, Y., Brown, J.L., and Kikkawa, J. (eds.). Animal Societies: Theories and Facts. Tokyo: Papan Sci. Soc. Press.
- _____. 1989. Kin recognition in animals (book review). *Evolution* 43:703-705.
- _____. in press. Sexual selection and social behavior. IN Tiger, L. and Robinson, M.H. (eds.). Man and Beast Revisited. Washington, D.C.: Smithsonian Institution Press.
- Wheeler, W.M. 1928. The Social Insects: Their Origin and Evolution. London: Kegan Paul.
- Wille, A. and Orozco, E. 1970. The life cycle and behavior of the social bee Lasioglossum (Dialictus) umbripenne (Hymenoptera: Halictidae). *Rev. Biol. Trop.* 17: 199-245.
- Wilson, E. O. 1971. The Insect Societies. Cambridge: Harvard University Press.
- Yanega, D. 1988. Social plasticity and early-diapausing females in a primitively social bee. *Proc. Natl. Acad. Sci., USA* 85: 4374-4377.

- _____. 1989. Caste determination and differential diapause within the first brood of Halictus rubicundus in New York (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* 24:97-107.
- _____. 1990. Philopatry and nest founding in a primitively social bee, Halictus rubicundus. *Behav. Ecol. Sociobiol.* 27:37-42.