

**AGGREGATION, COURTSHIP, AND BEHAVIORAL INTERACTIONS
IN EUROPEAN EARWIGS,
FORFICULA AURICULARIA L. (DERMAPTERA: FORFICULIDAE)**

by

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APPROVED:



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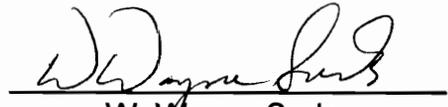
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AGGREGATION, COURTSHIP, AND BEHAVIORAL INTERACTIONS IN
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(ABSTRACT)

Due to its relatively cool, humid summers, southwestern Virginia provides an ideal climate for European earwigs, *Forficula auricularia*. In 1990 - 1992, nymphs were captured in wooden groove-board traps beginning in late May, adults were captured beginning in mid-June, and disappeared from sampling sites by September or October. Sex ratios were significantly female-biased most of the season, becoming more marked by the fall. The pest status of *F. auricularia* is exacerbated by its gregarious nature. Gas chromatography-mass spectroscopy and accompanying behavioral bioassays showed that aggregation occurred as a result of a pheromone located on the male cuticle, which is probably a minor component of the hydrocarbon profile. Approximately 88% of the detected volatiles on the cuticle were identified as a series of normal and branched alkanes. Fatty acids and hydrocarbons were also identified in nymphal and adult legs, but these extracts were not attractive. Frass, which also contained fatty acids and hydrocarbons, was attractive, but likely acquired its attractancy through the earwigs' proclivity for consuming carcasses and exuviae. The defensive quinones produced by *F. auricularia* repel conspecifics. A study of the behavioral repertoire of *F. auricularia* showed that, contrary to previous reports, only nymphs are nocturnal. Many differences in behavior were due to gender, age, and partner age. (e.g., females spent more time feeding than did males, adults fed more when paired with nymphs than when paired with adults). Social behaviors (communal feeding, aggression, contact, and dorsal palpation) comprised <10% of the insect's behavioral repertoire.

Since dorsal palpation, a previously undescribed behavior and a form of allogrooming, occurred more frequently during reproductive periods, it may have a sexual significance. Dorsal palpation also may augment the distribution of defensive quinones on the cuticle of *F. auricularia*. An analysis of nymphal group dynamics demonstrated that as group size increased, nymphs spent significantly less time

feeding alone and grooming, but more time resting. Antennal contact rates between group members increased significantly with group size. Detailed observations of the courtship and mating of *F. auricularia* revealed a complex of sexual behaviors for both males and females. Receptive females were behaviorally active during courtship. The significance of the male cerci was demonstrated by their use in early courtship with displays, and later use as a tactile stimulus for the female; and study of males from which the cerci had been removed, which showed no mating by amputated males. Male forcep length was bimodally distributed and positively allometric, while female forcep length was normally distributed. Males with longer forceps did not have a mating advantage. Further research is needed to identify the chemical composition of the aggregation pheromone, and to quantify any advantages of body and forcep size on mating success.

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INTRODUCTION

The European earwig, *Forficula auricularia* Linnaeus (Dermaptera: Forficulidae) was first reported in the United States in 1901 (Jones, 1917). It is a minor pest of ornamental and cultivated plants (Crumb et al., 1941), but is best known as a pervasive urban and suburban pest in some regions of the United States (Ebeling, 1978). The earwig is omnivorous and nocturnal (Crumb et al., 1941), and its population dynamics are synchronized with environmental factors such as temperature and rainfall (McLeod and Chant, 1952).

F. auricularia presents intriguing possibilities for behavioral research. It is regarded as a subsocial insect (Michener, 1969) because the female cares for the eggs and first instar nymphs (DeGeer, 1773; Lamb, 1976b), but there is no cooperative brood care or division of labor. Its cerci are sexually dimorphic (Hoffman, 1987), with the female having relatively straight forceps and the male having heavy, curved forceps resembling old-fashioned ice tongs. The basis for this dimorphism is unknown, but may be related to sexual behavior since divergences in morphology of structural features not related to survival are often related to adaptations for sexual use (Gadgil, 1972). Further, the male is reportedly represented by two morphs, one with short forceps, and the other with long forceps (Diakonov, 1925; Radesater and Halldorsdottir, 1993). Except for its maternal care, the earwig's behavior has not been well studied. The insect's behavioral repertoire and activity budget have not been described. Although the mechanics of copulation

have been described (Popham, 1965), courtship behaviors have not. Social interactions between conspecifics, if they exist, have also not been investigated. *F. auricularia* is defended by a mixture of quinones (Schildknecht and Weis, 1960). Late-instar nymphs and adults typically live in large aggregations (Lamb, 1975), yet the defensive and gregarious behaviors of the earwigs have not been studied.

Some aspects of the European earwig's behavior are the focus of the following research. The life history and population characteristics of *F. auricularia* in southwestern Virginia needed to be investigated first, in order to provide a framework for understanding of the insect's behavior (Chapter 1). The pheromonal basis for the earwig's aggregation behavior, and the effect of its defensive chemicals on behavior is discussed in Chapter 2. A quantitative analysis of the insect's behavioral repertoire and the effect of increasing group density on behavior is the subject of Chapter 3. Finally, Chapter 4 deals with the courtship and mating behavior of *F. auricularia*.

LITERATURE REVIEW

Taxonomy, Morphology and Geographical Distribution

Forficula auricularia Linnaeus, the European earwig, derives its curious name from an old European superstition that the insect crawls into the ears of sleeping humans and bores into the brain. The word "earwig" comes from the Anglo-Saxon "earwicga," literally meaning "ear creature" (Shetlar, 1982). This species is also sometimes known as the common earwig.

A member of the order Dermaptera and family Forficulidae, the European earwig is chiefly distinguished from other earwigs by the male's basally broadened, rounded forceps extending from the abdomen (Hoffman, 1987). The insect is dark reddish brown with yellowish-brown legs and completely developed wings folded beneath tegmina 2 mm in length (Weems and Skelley, 1989). Adults are 15-20 mm long (Hoffman, 1987) but female length depends on whether or not she is gravid (Crumb et al. 1941). Other morphological characters include a smooth cuticle, fourteen antennal segments in adults (Crumb et al., 1941), chewing mouthparts, and 3-segmented tarsi (Borror and White, 1986). The forceps are sexually dimorphic and can easily be used to sex adults: the male's forceps are curved, widely separated at the base, and have one or more prominent teeth on the inner margin. The female's forceps are relatively straight, close together at the base, with no teeth on the inner margin. The earwig's abdomen is also sexually dimorphic as the male

has 10 abdominal segments and the female has only 8, the eight and ninth segments being fused with the tenth (Hoffman, 1987).

Metamorphosis is gradual, with 5 to 6 nymphal instars. Besides the marked absence of the adult dimorphic cerci, nymphs can be recognized by their lighter color, and conspicuous cranial ecdysial lines. Each instar is progressively larger than the last (Hoffman, 1987).

Indigenous to Europe, western Asia and northern Africa (Lamb and Wellington, 1974), *F. auricularia* is distributed widely in the temperate regions of the world. It was first reported in the United States in Newport, Rhode Island in 1901. A small colony was also reported on the Pacific coast, in Seattle, Washington, in 1915 (Jones, 1917). It is unknown how the first individuals were introduced.

In North America, the European earwig's range extends from Canada to North Carolina, and westward to Arizona and California (Hoffman, 1987), and the Pacific Northwest (Langston and Powell, 1975). In Canada, *F. auricularia* is known in the provinces of British Columbia, Manitoba, Newfoundland, Nova Scotia, Ontario, Quebec and Saskatchewan. Hoffman (1987) also cited unpublished U.S. records for Kansas, Maryland, Michigan, New Hampshire, Nebraska, Ohio, Pennsylvania and Wisconsin.

Dispersal is mainly by humans. Since the European earwig reportedly flies very little and appears incapable of sustained flight, natural dispersal is limited (Weems and Skelley, 1989). Because the earwig prefers dark, inaccessible hiding

places and is commonly associated with humans, it has been easily transported to new regions (Lamb and Wellington, 1974) through such venues as crates of commercial products, lumber, cut flowers and ornamental shrubs, and bundles of newspapers. In addition, *F. auricularia* is especially well adapted to such dispersal since it can withstand a wide range of environmental stresses and because the female is apparently capable of ovipositing months after mating (Crumb et al., 1941).

Life Cycle

Details on the European earwig's life cycle are based on a limited number of studies. Crumb et al. (1941) examined *F. auricularia* populations in Puyallup, Washington. Lamb and Wellington (1975) studied a population of European earwigs in Vancouver, British Columbia. Maxwell (1988) studied earwig populations at two different sites in Quebec, Canada.

Emergence, duration of developmental period and hibernation are all highly synchronized with annual fluctuations in temperature and rainfall (Crumb et al., 1941). Therefore, the timing of life history events differs slightly with geographic region. In early to mid-spring, earwigs usually appear above ground, ending their hibernation. Adult males and females from the parental generation, as well as first-instar nymphs, were seen in Washington in the first sampling of the year (Crumb et al., 1941). In Vancouver, almost all the trapped earwigs in early spring were adult males (Lamb and Wellington, 1975). Only second-instar nymphs were caught in the first spring sampling in Quebec, but males and females from the parental generation

were collected somewhat later, in early summer (Maxwell, 1988). For immatures, development time to the following stadium was about 14 to 21 days. Nymphs reached maturity by early (Crumb et al., 1941) to late July (Maxwell, 1988). Males from the parental generation generally disappeared from sampling traps in spring, although some reentered the soil with parental females to remate at this time (Crumb et al., 1941). Females from the parental generation apparently died by midsummer (Crumb et al., 1941; Maxwell, 1988).

Mating was generally observed above ground in late summer to early fall, and in nests in late winter. In Canada, Lamb and Wellington (1975) and Maxwell (1988) reported mating pairs in traps from late August through late September. Adult male and female pairs burrowed underground to overwinter between late September and November, depending on the timing of cool weather (Crumb et al., 1941; Lamb and Wellington, 1975; Maxwell, 1988). Lamb and Wellington (1975) noted that while most earwigs overwintered in pairs in underground nests, some overwintered in aggregations on the surface. Oviposition occurred by the following January or February in Washington (Crumb et al., 1941) and in February or March in British Columbia (Lamb and Wellington, 1975).

Females stayed in the subterranean nests to guard the eggs for an average of 73 days, while males left the cells soon after mating (Crumb et al., 1941; Lamb and Wellington, 1975). Crumb et al. (1941) suggested that females may have forcibly ejected their mates, citing the fact that in enclosed laboratory nests where

males could not escape, males were frequently found dead and sometimes mangled during the period following mating.

Mean number of eggs per clutch in British Columbia varied significantly from year to year from 55 one year to 43 the next. The number of eggs per clutch was positively correlated with female weight (Lamb and Wellington, 1975).

Egg hatch occurred in May in British Columbia (Lamb and Wellington, 1975) and Washington (Crumb et al., 1941). Females and second-instar nymphs began leaving the nest the week following molt to the second instar (Lamb and Wellington, 1975). Crumb et al. (1941) reported that a small minority of females, approximately 15%, remated and reentered the soil with mates, in early May to early June. Incubation periods for the second brood were considerably shorter, about 20 days. These offspring were mature by mid-September. Lamb and Wellington (1975) found similar results with respect to second broods. Eggs of the second brood in their study hatched by the end of June, and these nymphs appeared above ground by early July. By late August, most of the nymphs of both broods were mature.

Lamb (1975) described two discrete phases of the life cycle, depending on degree of population dispersal: nesting and free-foraging. During the nesting stage, the female and her nymphs stayed close to their own nest, although the female, and later the nymphs, left the nest in the evening to forage. This phase ended when the nymphs failed to return to the nest, thus initiating the free-foraging period. This life stage was characterized by little attachment to a specific location, frequent

interchange of shelters, more extensive travel and dispersal during foraging, and mixing of unrelated individuals. Adult sex ratios in British Columbia varied significantly with season. In the spring, nearly all adults in shelters were male; the initial ratio of new adults was about 50:50, but had changed to predominantly females by early fall (Lamb and Wellington, 1975). Nymphs from second broods survived at greater rates than first-brood nymphs, but weighed less. Females and males were similar in weight when first mature, but females weighed more before overwintering. Populations living in densely vegetated areas developed somewhat faster than those in sparsely vegetated areas (Lamb and Wellington, 1975).

Ecology

The European earwig has some key ecological requirements for survival. Humidity level is crucial, with nearly saturated conditions necessary for egg hatch and high levels necessary for nymphal development. Very high temperatures are not well tolerated. As a result, the European earwig survives well in cool, moist regions but cannot live in warm, dry climates (Hoffman, 1987). Survivorship and population density are greatest in regions where the July mean temperature does not exceed 24° C and where yearly precipitation is at least 51 cm (Crumb et al., 1941).

Nymphal growth and development is directly related to fluctuations in temperature so that oviposition, incubation, and emergence vary geographically and yearly (Crumb et al., 1941). Abundance in any given year is positively correlated

with stable daily temperatures and wind velocity (Chant and McLeod, 1952). Atmospheric pressure is positively correlated with earwig abundance. Population density appears to be affected by degree of cloud cover, falling on days following evenings with little or no cloud cover (Crumb et al., 1941).

Overwintering adults are relatively cold tolerant, but soil type used for nest construction affects survival. In a series of experiments, Crumb et al. (1941) found that poorly drained soils yielded lower survival. Weems and Skelley (1989) reported that females in natural populations favored rich garden soil with a southern exposure for oviposition. Eggs are remarkably well adapted to resist both cold and heat damage (Chauvin et al., 1991).

The European earwig is omnivorous in its food habits. Under natural conditions, mosses, lichens, and green algae are preferred food items over higher plants, and aphids are preferred animal food items. Although earwigs eat live insects, including those larger than themselves, they probably act more often as scavengers than as predators. Adults eat a higher percentage of animal food than do nymphs (Crumb et al., 1941).

Under fairly adverse conditions, earwigs can still reach maturity, although adult body size may be reduced by as much as half the average for earwigs reaching maturity under more favorable conditions. In addition, adults shrink in dry conditions or if food supplies are insufficient (Crumb et al., 1941).

Earwigs are active at night, foraging and dispersing. They rest during the day in secluded hiding places. Natural shelter sites may include under rocks, loose logs, in cracks in the soil (Ebeling, 1978) or under trash and debris (Chant and McLeod, 1952). In addition, shelter sites appear to be selected partly for protection from the environment: occupancy is negatively correlated with temperature, and high relative humidity is important. In addition to providing resting spots, shelters may afford protection from avian predators and may be important as sites for social interaction (Lamb, 1975). Shelter sites are also apt to be more concentrated in areas providing access to foraging, as well as better protection from predators; trees frequently harbor more earwigs than grasses (McLeod and Chant, 1952; Maxwell, 1988).

Several natural pathogens can threaten earwig populations. The fungus *Entomophthora forficulae* attacks predominantly nymphs, and can result in high nymphal mortality. *Metarrhizium anisopliae* and *Oospora destructor* are other fungi attacking earwigs. Common digestive tract pathogens are gregarines and round worms (Crumb et al., 1941; Ball et al., 1986). Parasites include tyroglyphid mites (Crumb et al., 1941) and the larvae of tachinid flies, (McLeod and Chant, 1952; Morris, 1984).

Although earwigs are probably prey items for other organisms, it is unclear to what degree natural populations are threatened by predation. Evidence for specific predators is limited. In the Pacific Northwest, snake kills have reportedly resulted

from ingestion of earwigs poisoned by pesticides (Crumb et al., 1941). Body parts of *F. auricularia* have been found in fecal samples of various animals including hedgehogs (Obrtel and Holisova, 1981), toads, snakes and the Chinese pheasant (Crumb et al., 1941), implicating these animals as earwig predators. Lamb (1974) suggested that shelters may protect earwigs from birds, but reported no specific instances of bird predation. Crumb et al. (1941) conducted feeding experiments with potential predators and found that although chickens readily ate earwigs when presented with them, they had difficulty locating and retrieving them from their hiding places. Similarly, Crumb et al. (1941) reported that carabid and staphylinid beetles consumed earwigs in enclosed arenas, but not at rates sufficient to reduce earwig populations.

Economic Importance

Although the European earwig is capable of feeding on a wide variety of agricultural crops, ornamental plants, and stored products, its notoriety as a pest is largely due to its propensity for invading homes and business establishments in large numbers (Crumb et al., 1941; Ebeling, 1978). With nocturnal, gregarious habits like those of cockroaches, earwigs create a nuisance for homeowners by gathering in large groups in inaccessible places such as around windows and inside door jambs (Ebeling, 1978), under loose boards on buildings, in shrubbery, and at the base of trees (Weems and Skelley, 1989). Homeowners also frequently object to what they perceive as the repulsive appearance and distasteful odor of the insect.

Because earwigs frequently hide among the leaves and petals of cultivated plants outside the home, earwigs' potential to be brought inside the home is great (Weems and Skelley, 1989). Once inside the home, the earwig can also infest stored products such as flour, starches, and sugar (Tillyard, 1925, in Crumb et al., 1941).

Its reputation as a residential pest aside, *F. auricularia* is also considered to be the most economically destructive earwig. It can occasionally cause substantial economic injury to cereal, fruit, and vegetable crops, seedlings, flowers (Hoffman, 1987), ornamental shrubs and trees (Ebeling, 1978). However, it is usually considered only a minor pest of cultivated plants (Crumb et al., 1941). The earwig's impact on individual agricultural crops may be limited because of the wide scope of its diet (Shetlar, 1982) so that no one crop is economically threatened.

Secondary agricultural injury can be caused by interference with pollination of certain crops. Earwigs eat the silks of corn and pollen of flowers such as dahlias, pinks, carnations, and zinnias (Crumb et al., 1941). Earwigs are also frequent residents of beehives, where they consume honey (Ebeling, 1978; Kaczmarek, 1991). *F. auricularia* may also be a vector of some crop diseases including corn smut, *Ustilago zea* (Crumb et al., 1941).

Crumb et al. (1941) reported that *F. auricularia* may have the potential to carry and transmit human disease pathogens, but no documented cases have been found and there is no recent mention of this vector ability in the literature. Ebeling

(1978) did, however, note a few reports of some dermapteran species pinching humans with their forceps, drawing blood.

In regions where the European earwig is considered a pest, recommended control is generally a combination of cultural and chemical control. Homeowners are directed to clean up debris around the outside of the house and other structures, including mulch and unessential plant debris. The objective is to establish a warm, dry zone of soil or concrete around the house to discourage earwig invasion into the area. These measures can be supplemented by applications of pesticides such as bendiocarb, chlorpyrifos, diazinon, and propetamphos in a 0.9 to 1.8 m band around the house. Some residual control can also be achieved with exterior baits of granular chlorpyrifos, carbaryl, or diazinon (Shetlar, 1982). Earlier research (e.g., Morris, 1965) suggested control by means of trapping, but clearly, this requires much manpower to set out traps, empty the traps, and destroy the insects.

Biological control programs for *F. auricularia* have been executed using nematodes (W. Wilson, 1971) and the tachinid flies *Bigonichaeta setipennis*, *Ocytata pallipes* (Ebeling, 1978; Langston and Powell, 1975), *Rhacodineria pallipes*, and *Digonochaeta spinipennis* (Phillips, 1983). The larvae of *B. setipennis* and *O. pallipes* were first introduced into Oregon in 1924. They were later mass-reared and released into the field as a full-scale biological control program (Langston and Powell, 1975). *B. setipennis* has also successfully reduced earwig numbers to manageable levels in Newfoundland, Canada (Morris, 1984).

Conversely, *F. auricularia* is viewed as a beneficial arthropod in The Netherlands (Mueller et al., 1988) and in the Pacific Northwest (Carroll and Hoyt, 1984), where it is used to control aphids on apple. In Washington state, *F. auricularia* is used to augment chemical control of *Aphis pomi*, the apple aphid, in orchards (Carroll and Hoyt, 1984). In The Netherlands, *F. auricularia* is released to help control the woolly apple aphid, *Eriosoma lanigerum* (Mueller et al., 1988). The European earwig appears to have a prodigious appetite for aphids. Buxton (1974, in Mueller et al., 1988) reported that a single female ate as many as 134 damson-hop aphids, *Phorodon humuli*, in one night.

Aggregation Behavior

One of the most striking aspects of the behavior of *F. auricularia* is its formation of aggregations numbering from a few to several hundred insects. Observations of *F. auricularia* invariably yield a clumped distribution of individuals (Lamb, 1975).

Gregarious behavior may have several biological benefits, including enhancement of juvenile growth and development (Fuchs et al., 1985), facilitation of mate selection (Antony et al., 1985), efficient harvesting of clumped resources (Brown, 1975), and predator defense (Hamilton, 1971). The significance of aggregation in *F. auricularia* is currently unknown, but may include some or all of these factors.

Insect aggregations may have a wide variety of causes, including spatial, visual, tactile, and auditory cues or chemical stimuli such as pheromones (Nagel and Cade, 1983), as well as environmental factors. Social factors, such as gender and reproductive condition, can also influence group formation and composition (Bret et al., 1983). In addition, when pheromones mediate insect aggregation, the chemicals may do double duty as sex pheromones by promoting encounters between males and females (Aller and Caldwell, 1979).

Pheromonal initiation of insect aggregation has been well researched in a variety of species. Several different classes of chemical compounds have been implicated as components of aggregation pheromones for insects, including esters, fatty acids, alcohols, hydrocarbons, and terpenes (Francke et al., 1989). Some aggregation pheromones work in multiple steps: one component attracts, and a second component acts as an arrestant, as in *Blattella germanica* (Fuchs et al., 1985).

Insect pheromones are frequently contained in the feces. Frass mediates aggregation in several insects, including *Blaberus discoidalis*, *Acheta domestica*, *Blattella germanica* (Ishii, 1970; McFarlane and Alli, 1985), *Periplaneta americana* (Bell et al., 1973) and *Phlyctinus callosus* (Barnes and Capatos, 1989).

In other insect species, hydrocarbons on the insect cuticle have been implicated as aggregants (Howard and Blomquist, 1982). Cuticular hydrocarbons fall into three general classes: n-alkanes, methyl-branched alkanes, and n-alkenes.

Branched alkenes and internally branched, internal alkenes are rare (Brown et al., 1990). Low volatility, long-chain hydrocarbons are not generally used for long-range attraction (Antony and Jallon, 1982). As a chemical class, cuticular hydrocarbons appear to be species-specific, and may serve as taxonomic characters (Grunshaw et al., 1990; Page et al., 1990). They may also vary in proportion from colony to colony and from caste to caste in social insects as in dampwood termites, *Zootermopsis* (Haverty et al., 1988) and in *Reticulitermes virginicus* (Howard et al., 1982), and different populations of the same species such as *Coptotermes formosanus* (Haverty et al., 1990) and *Drosophila melanogaster* (Jallon and David, 1987). There is also sexual dimorphism in proportion and types of cuticular hydrocarbons in some insects, as in *Drosophila melanogaster* (Jallon and David, 1987), suggesting a gender difference in cuticular function. Lifestyle may also influence hydrocarbon profile among closely related species. The cuticular hydrocarbons of solitary locusts are more condensed than those of gregarious species (Genin et al., 1986). Cuticular hydrocarbons are probably produced in the oenocytes or epidermal cells (Wigglesworth, 1977). N-alkanes are not synthesized de novo, but derived from the diet (Blomquist and Jackson, 1973). Diet affects the type and variety of hydrocarbons an insect can synthesize (Lockey, 1976).

Limited research on the causal factors for group formation in *F. auricularia* exists. Crumb et al. (1941) tested 590 different compounds for attractivity to earwigs. They reported that oils were the best attractants, but that earwigs were

also attracted to their own odor because increasing numbers of earwigs were found in traps the longer traps had been used. Legner (1962) found that peanut butter was a better attractant than fish oil in pitfall traps. Morris (1965) compared the attractivity of Newfoundland earwigs to groove-board traps and pitfall traps containing one of several compounds, including cod oil, sugar, molasses, honey, peanut butter, and macerated earwigs. Honey was the most effective attractant in the pitfall traps, but the groove-board traps were 4-1/2 times more effective than the most effective baited pitfall traps, those with honey.

More recently, Sauphanor (1992) suggested that compounds contained within the tibial glands (Brousse-Gaury, 1983) of *F. auricularia* are responsible for its gregarious behavior on the basis that extracts of amputated legs and of filter paper "trails" caused aggregation. Other observations associated with aggregations are that nymphal weight increases with decreasing group size, and earwigs in aggregations groom each other (Lamb, 1975).

Chemical Defenses

The chemical defenses of *F. auricularia* are some of the earliest elucidated in insects, consisting of 2-methyl-1,4-benzoquinone and 2-ethyl-1,4-benzoquinone. These compounds are produced and stored in a pair of abdominal glands which open dorsally on the posterior margins of the third and fourth abdominal tergites. The quinones are readily released when the insects are handled (Schildknecht and Weis, 1960).

Benzoquinones are the most widely distributed defense secretions in arthropods, occurring in 6 orders within the Insecta, Diplopoda and Acari (Ikan et al., 1970). In addition to *F.auricularia*, 2-methyl-1,4-benzoquinone (toluquinone) is produced by the carabid, staphylinid, and tenebrionid beetles and blaberids, termitids, and mastotermitids. 2-Ethyl-1,4-benzoquinone is also produced by blaberids, tenebrionids, carabids, and staphylinids (Blum, 1981).

In general, the quantity and quality of defensive secretions produced by any given insect are probably dependent on many factors. The defensive glands of both immature and adult arthropods are thought to function at suboptimal levels until the insect has spent several days at a given age class. Gender, physiological state and season may also affect production level (Blum, 1981).

Quinones act primarily as repellents, but also have some toxic effects (Ikan et al., 1970). In both vapor and liquid form, quinones are particularly irritating to sensitive tissue such as mucous membranes (Eisner and Meinwald, 1966) and tan the skin of humans (Wood et al., 1975). The compounds affect the predator's olfactory receptor sites by interacting with amino acids of the receptor proteins and changing the membrane potential of sensory dendrites, thereby resulting in a protracted loss of sensory capability for the predator (Norris, 1976, and Kittredge, 1974, in Brossut, 1983). Defense efficacy may be improved by additional strategies such as that employed by the tenebrionid beetle *Argoporis alutacea*, which deliberately spreads the quinones it emits over its body, and that of its attacker.

Social Behavior and Organization

Except for analysis of aggressive encounters, debate over forcep function, and its maternal care, the social behavior of *F. auricularia* has received very little attention. The areas that have been noted are almost completely based on anecdote and limited observation rather than rigorous, detailed examination.

Aggression

The European earwig appears to be aggressive toward conspecifics as well as potential predators, and use of the forceps figures prominently in agonistic encounters. Fulton (1924) noted aggressive contests between two females confined to the same experimental cage with their respective clutches of eggs. He noted, but did not describe in detail, that females directed their forceps to approaching males, but no actual combat occurred between the sexes. Both sexes threatened each other over access to food. Earwigs also threatened potential predators with their forceps. Another early report (Morgan, 1923) did not specify the species of earwig observed, but stated that males were aggressive, sometimes killing conspecifics with their forceps, or lifting the opponent off the substrate by grasping the opponent's body with its forceps. In general, earwigs raised their forceps any time they were disturbed, and frequently rested in hiding places with only their forceps protruding and raised (Morgan, 1923). Crumb et al. (1941) observed that both sexes threatened potential predators with raised forceps, and described instances in which females escaped from entrapment in spider webs by seizing the spider with their

forceps and then cutting the silk with her mandibles. Forcep use was also observed in interfemale fighting.

Forceps Function

The function of the forceps of earwigs has been a subject of fascination for many researchers. Because insect cerci are sensitive to air movement and sometimes act in sound reception, they usually have a sensory function (Chapman, 1982), but may have other uses as well.

Indeed, the above discussion of earwig aggression demonstrates that one of the functions of forceps is defense. Morgan (1923) suggested that the forceps, when raised to threaten, protect the thoracic area of the insect. Fulton (1924) believed that the forceps are used chiefly for defense from rear attacks because the insect lives primarily in holes and crevices. Crumb et al. (1941) also declared that the forceps' function was defensive.

Klostermeyer (1942, in Ebeling, 1978) reported that earwigs may use forceps in order to grasp food while eating. Ebeling (1978) thought the cerci were appendages with several functions, including defense, prey capture, probing inside narrow crevices, and for folding and unfolding wings.

The sexual dimorphism of the forceps poses an additional question. When cercus shape differs between the sexes, it suggests that the cerci play a role in copulation (Chapman, 1982). However, Morgan (1923), Fulton (1924, 1927), Crumb et al. (1941), and Ebeling (1978) believed that the male forceps were not used as

claspers in mating. The only disputing report in the literature is by Goe (1925), who observed forceps use in earwigs, but did not specify the species. He noted that the male of this earwig species uses his cerci in mating by backing up to female and grasping her between his forceps, which are held wide open. Crumb et al. (1941) attempted to account for the difference in forcep shape by suggesting that it was due to differing cutting actions performed by the sexes: piercing for males, and shearing for females.

Use of forceps in courtship has been reported for some other earwig species, including the African earwig, *Euborellia annulipes* (Bharadwaj, 1966), the seaside earwig, *Anisolabis maritima* (Bennett, 1904), the striped earwig, *Labidura riparia* (Caussanel, 1975), and the toothed earwig, *Vostox apicedentatus* (Moore and Wilson, 1993).

In addition to bearing sexually dimorphic forceps, the European earwig is characterized by male cercus length that is reportedly bimodal in distribution: the majority of males have either short or long forceps, with few having forceps of intermediate length. Short forceps were described by Crumb et al. (1941) as about 3.5 mm in length, and long forceps as about 7.0 mm in length, with longer-forceped males generally having bigger bodies as well. Like the debate on forcep function, researchers have disputed each other's contentions. Diakonov (1925) compiled statistics to show that forcep length was bimodally distributed while body length (minus forcep length) was normally distributed. He suggested that the two morphs

were likely due to environmental rather than genetics or to habitat. Crumb et al. (1941) reported that short-forceped males were much more common, and that forcep length was probably inherited. However, Kuhl (1928, in Van Heerdt, 1953) and Van Heerdt (1953) questioned the validity of a bimodal distribution for forcep length on the basis that Diakonov (1925) obtained his population samples from hiding places with metal tweezers, a practice which could prejudice samples in favor of long-forceped males. Recent reports are equivocal. Eberhard and Gutierrez (1991) suggested that the overlap between the small and large morphs is too broad to constitute a dimorphism, but their analysis is based on measurements made by Diakonov (1925) rather than on new data. More recently, Radesater and Halldorsdottir (1993) measured 143 male earwigs in Sweden, and concluded that forcep length is bimodally distributed.

Within the Dermaptera, male forcep length is positively allometric, that is, that larger males have proportionately larger forceps. This relationship is not valid for *F. auricularia*, however, unless large- and small-forceped males are analyzed separately. In that case, body and forcep size for small-forceped males are isometric, whereas large-forceped males are positively allometric (Simmons and Tomkins, 1996).

For any given earwig, length of each individual cercus may differ to some extent. Radesater and Halldorsdottir (1992) recently suggested that degree of asymmetry between length of each cercus may adversely affect mating success in

males. A small minority of earwigs in population samples have also been found to have one morphologically female and one male forcep; most of these have been described as physiological males (Crumb et al., 1941).

Courtship and Mating

Although the sequence of courtship behaviors has not been previously described, the mechanical features of copulation were reported by Popham (1965). Copulation occurs in the apposed position, with the male twisting his posterior abdominal segments in an anticlockwise position from the front part of the body so that the left side is moved over the right. This movement brings the ventral side of the male's abdomen beneath the ventral side of the female. The male then everts the aedeagus, and inserts it into the female's vagina. Fulton (1924, 1927) also reported that the male locates the female with his antennae, and then turns around and tries to slip his forceps under the tip of the female's abdomen. He observed that if left undisturbed, earwig pairs might remain in copula for several hours.

Males with larger forceps and larger overall body size have greater mating success, according to reports by Radesater and Halldorsdottir (1993), but the bases for this (e.g., male-male interactions, female choice, etc.) have not been fully explored. Inheritance of forcep and body size has not been evaluated.

Parental Care

Female care of the eggs and first-instar larvae was first reported in 1773 by DeGeer. While *F. auricularia* does care for its offspring in the early stages, it is

considered to be subsocial rather than eusocial because there are no reproductive castes or cooperative brood care (Michener, 1969). All the earwig species studied thus far exhibit parental care, but few have been well studied because the order is largely tropical and of little economic importance, and the insects are secretive and hard to observe (Lamb, 1976b). Those in which maternal care has been observed include *Anisolabis maritima*, the seaside earwig (Bennet, 1904), and *Labidura riparia*, the striped earwig (Shepard et al., 1973; Ammar and Farrag, 1974).

Although only females have been observed building nests, males may play an as yet unidentified role. Crumb et al. (1941) reported that females confined in field enclosures with a male survived better and constructed better galleries than females confined alone. Evidence suggests that males are forcibly driven from nests by females just after oviposition (Crumb et al., 1941; Lamb and Wellington, 1974). Nests are usually made in the soil (Lamb, 1976b) and females have been observed excavating nests by moving particles of soil with their mouthparts or forelegs, and carrying them to the surface (Fulton, 1924). Alternatively, nests have been associated with natural cavities (Fulton, 1924), half-buried stones, pieces of wood, or plant roots (Lamb, 1976b). Nest design and construction vary greatly, from a short, blind tube uniform in diameter to a maze of tunnels and chambers with several entrances (Lamb, 1976b). Nest depth is about 3 to 5 cm (Crumb et al., 1941; Lamb, 1976b).

During the incubation period, the female moves the eggs about the nest frequently, repositioning them, especially if there is a disturbance to the nest, such as a threat from a potential predator (Fulton, 1924; Lamb, 1976b). Changes in humidity may also promote egg-gathering and repositioning (Lamb, 1976b). The female manipulates the eggs by opening her mandibles and carrying them with her palpi (Fulton, 1924). Based on observations of female manipulation of the eggs, Lamb (1976b) and Good (1982) suggested that in nests built under stones, the female may employ the stone as a heat source to regulate egg temperature and accelerate hatching by moving eggs nearer to the surface or against the stone as the surface of the stone warms. Emergence is probably facilitated by the female's act of arranging the eggs in a single layer shortly before hatching (Lamb, 1976b).

Egg-cleaning also appears to be an important part of maternal care (Lamb, 1976b), and is probably performed in order to remove foreign material (Shepard et al., 1973) such as mold. In experiments in which females have been removed from their eggs, the eggs were soon inundated by mold (Lamb, 1976b). In *Labidura riparia*, the striped earwig, the female's secretions have been implicated as beneficial to the eggs (Shepard et al., 1973). The female cleans the eggs by rotating them with her palps (Lamb, 1976b).

The female feeds very little, if at all, during egg incubation. She maintains a characteristic posture with her head and thorax positioned over the eggs (Lamb,

1976b). She also defends the eggs and nymphs from intruders in the nest (Fulton, 1924; Lamb, 1976b).

Crumb et al. (1941) reported that newly hatched nymphs sometimes have difficulty extracting themselves from the membrane surrounding the egg, but that the female never helps them. Following egg hatch, the female also moves the nymphs about the nest, retrieving them when they wander away (Fulton, 1924; Lamb, 1976b). She moves them by grasping them in her mouth with her palpi (Fulton, 1924) and continues to protect the nymphs by positioning herself over them in the same manner as she did over the eggs (Lamb, 1976b). The female provisions the nest with food and may also feed the nymphs by regurgitating into their mouths. Nymphs have been observed approaching the female and prodding her mouthparts with theirs, suggesting the existence of trophallactic feeding (Fulton, 1924; Lamb, 1976b).

Females may incubate eggs other than their own. In experimental settings where multiple females and their clutches were maintained, Fulton (1924) observed that one female attempted to gather all of the eggs in the cage, which led to fighting between the females. The larger female eventually gathered all the eggs and intimidated the smaller one into avoiding her and the eggs. Good (1982) found natural nests in which one female had taken over the eggs of a female from an adjoining nest.

Late in the first-instar, nymphs aggregate near the nest entrance, but do not leave. After a short period of time, nymphs also leave the nest to forage in the evening. However, they depart the nest later in the day than the female, and return to it before she does (Lamb, 1974).

The phase of parental care is at an end when the nymphs disperse from the nest and do not return; there is no evidence that the female shows any particular reactions to her young after the nesting period (Lamb, 1974). Behaviors of nymphs ready to separate from the nest differed from those still in the nesting phase; those deserting the nest were more active than those continuing to use the nest, and could not be made to reenter the nest even when directed toward it (Lamb, 1976b). There has been no research on whether siblings tend to stay close together once leaving the nest.

A small percentage of females lay second and, rarely, third clutches of eggs.

Remating may take place prior to second and third ovipositions, but is not necessary (Crumb et al., 1941). Lamb (1976a) compared the behavior of females that produced one, two, and occasionally three broods per year. Those that produced second and third broods abandoned the first nest sooner than did females producing only one brood. Female behavioral patterns differed according to whether the female was in a nesting or dispersing phase: dispersing females remained active throughout the foraging period, feeding and moving about, but not reentering the nest or interacting with young. Nesting females foraged, but returned

to the nest with food and spent most of their time sitting near the entrance of the nest, grooming or interacting with the young. Females producing only one brood had lower fecundity, but longer lasting parental care. Females that brood twice may disperse between broods in order to reduce competition for food.

Clutch order may affect numbers and viability of eggs, and behavior of nymphs. In one study (Tourneur and Gingras, 1992), only laboratory females produced a second clutch of eggs while those in a nearby natural population brooded once. First clutches contained significantly more eggs than did second clutches (Tourneur and Gingras, 1992). Eggs in second clutches in another study (Lamb, 1976b) hatched at a slower rate than did first-clutch eggs, or were moribund. Second-brood nymphs dispersed earlier in life (Lamb, 1976b).

Parental behavior in earwigs appears to be controlled by a complex of behavioral and physiological factors. In *Labidura riparia*, the parental cycle is triggered by declining ovarian function, reduction in size of the corpus allatum, and reduction in intercerebralis neurosecretion (Vancassel and Caussanel, 1968). Copulation and the presence of seminal fluid in the spermatheca stimulate maternal care in *L. riparia* (Vancassel, 1973). Vancassel and Foraste (1980) studied mother-nymph contacts in *F. auricularia* and *L. riparia* and concluded that females producing more than one brood interrupt contact with the first group of offspring earlier than do females producing only one clutch of eggs. In experiments where females were deprived of their first clutch, the majority produced a second brood. When females

are left in contact with their offspring, vitellogenesis seems to be blocked or retarded.

CHAPTER 1: LIFE HISTORY, POPULATION CHARACTERISTICS AND SEX RATIO

Introduction

The life history of *F. auricularia* had been explored in only a limited number of studies, based in Canada and the northwestern United States. Typically, earwigs emerged in mid-spring, reached maturity by midsummer, and burrowed underground in autumn (Crumb et al., 1941; Lamb and Wellington, 1975; Maxwell, 1988). According to records of citizen calls maintained by the Virginia Tech Cooperative Extension Service, outbreaks of earwigs in Blacksburg, Virginia had become increasingly common in the early 1980s. However, other than judging from the timing and frequency of the calls and comments, little was known about the population dynamics of *F. auricularia* in southwestern Virginia.

Data on insect emergence and population characteristics are useful in designing sampling programs (Resh, 1979) and toxicity studies (Buibema and Benfield, 1970). Variables such as photoperiod, temperature, or diet can affect life history (Stearns, 1977; Rankin et al., 1995). Sex ratio data can provide information to help interpret reproductive behaviors. Although parental fitness is generally maximized by a 1:1 sex ratio of offspring, greater investment in one sex may be adaptive if that sex is cheaper to produce (Fisher, 1958). This might be the case if that sex had a shorter development time, required fewer nutritional expenditures from the parent to develop, or if it had lower mortality during the parental care period

than the other sex Thornhill and Alcock, 1983). Parents might skew sex ratio if mating is nonrandom, with one sex having greater variance in reproductive success than the other (Fisher, 1958). In a sexually dimorphic animal such as the European earwig, one might predict, for example, that males with the largest forceps obtain most of the copulations, thereby making it advantageous for healthy parents to produce males, with less fit parents playing it safer and investing preferentially in daughters. In addition, there is frequently seasonal variation in sex ratios of insect populations (e.g., Bailey et al., 1984; Regniere, 1981; Fleming, 1972). These variations may be caused by factors such as differential emigration behavior (Regniere et al., 1981), differential mortality rates, or behavioral differences which may lead to sampling bias, (e.g., females may be ovipositing later in the season, and are not caught in monitoring traps) (Thornhill and Alcock, 1983). Therefore, observation of incremental changes in sex ratio, if present, can be valuable to augment life history data on little studied insects such as *F. auricularia*, as well as provide the basis for a future examination of why sex ratio changes seasonally.

Previous earwig studies have employed groove-board traps to sample earwig populations (Legner and Davis, 1962; Morris, 1965; Lamb and Wellington, 1974). Some of these studies modified the general design of Crumb et al. (1941). In an evaluation of the efficacy of traps baited with several different foods and potential attractants, Legner and Davis (1962) found that traps baited with attractants worked better than those without, and that peanut butter worked better than earwig "scent"

or fish oil. Morris (1965) tested the efficacy of traps baited with sugar, molasses, peanut butter, cod oil, and honey, the last of which was most effective. Morris (1965) also tested attractivity of macerated earwigs, but found the results less promising than those of honey-baited traps. Lamb and Wellington (1974) improved trap catches by utilizing strips of tar paper taped to the outside of the trap to form a moveable flap, and by shading traps with white painted masonite shields.

The objective of Chapter 1 was to gather information on the life history of *F. auricularia* in its natural setting in southwestern Virginia, in order to provide a background for the interpretation of later behavioral studies, and to provide a preliminary report of the pest status of the insect.

Materials and Methods

Earwig Collection

Sites

Earwigs were collected primarily in Blacksburg and Christiansburg, Virginia, and other areas in Giles and Montgomery Counties, Virginia, from 1989 - 1992. In 1992, a small number of earwigs also were collected from privately owned beehives on a property in McLean (Fairfax County) Virginia, and from a house in Gettysburg, Pennsylvania. Most sites were sampled only once or twice while some sites were censused on a regular basis, in multiple years, in order to reflect population and sex ratio changes.

Collection sites were located in a variety of ways. Some areas were identified by reviewing logs of telephone calls made by local homeowners to the Virginia Tech Cooperative Extension Office asking for assistance with control of earwigs. In 1990 and 1991, I arranged for the Extension Office to place articles and advertisements in newspapers in Blacksburg, Christiansburg, and surrounding areas in the New River Valley requesting homeowners with earwig infestations to contact the Department of Entomology at Virginia Tech. These articles and ads generated over 100 telephone calls. Preference was given to visiting sites that were relatively close to the university and which also appeared to have large numbers of earwigs. Several dozen sites were visited and sampled at least once. However, most of the sites sampled regularly and over two or three of the sampling years were identified by personal communication with students, faculty, and staff at Virginia Tech. Many homeowners responding to the newspaper ads and articles were primarily interested in short-term removal or control of the insects, but were generally not interested in maintaining long-term traps on their property.

Individual numbers assigned to sites indicate that earwigs were counted and sexed following collection. Collections were made from groove-board traps (Crumb et al., 1941) at some sites (on occasion, manually or by vacuum aspiration), on a regular basis (Table 1.1) and by vacuum aspiration at other sites, on an irregular basis (Table 1.1). In 1990 and 1991, regular collections were made from the end of

Table 1.1. Virginia sites where *F. auricularia* were collected primarily by groove-board traps, from 1989-1992, and by vacuum aspiration from 1989-1990.

Groove-Board Traps

Site #	Location	Description	Years Sampled	Trap # and location
1	NW Blacksburg	SFH	1989-92	1: next to bee hive 2: under apple tree
2	NW Blacksburg	SFH	1989-92	1 and 2: in wood pile 3 and 4: in wood pile with metal scraps
3	SE Blacksburg	Apartment in SFH	1989-91	1: under crabapple tree 2: near bird bath
4	SW Blacksburg	SFH	1990-91	1 and 2: in crotches of deciduous trees
5	NE Blacksburg	Apartment complex	1990-91	1: behind scrap lumber 2: on wooden deck

Vacuum Aspiration

Site #	Location	Description	Years Sampled	Location
6	Christiansburg	SFH	1990	wooden shed and under debris
7	Christiansburg	SFH	1990	wooden treehouse
8	NE Blacksburg	SFH	1990	in grooves of split rail fence
9	NW Blacksburg	SFH	1990	in tube of plastic sheeting
10	NW Blacksburg	SFH	1990	in wooden sand box
11	NW Blacksburg	Apartment complex	1990	under plywood sheets on grass
12	NW Blacksburg	Church	1989	at base of tree, in grass

Note: SFH=Single family home

May through early October. Earwigs were collected on an irregular basis in 1989 and 1992.

Sites differed in residence type from apartment dwelling to single-family homes. Most of the sites were in Blacksburg or the nearby area. Specific locations of traps varied from site to site but included a variety of habitats (Table 1.1).

Trap Design

Trap design was based on Crumb et al. (1941), and consisted of two pieces of pine board in which grooves had been cut out the length of both pieces, placed with the grooves facing together. Two trap sizes were used: large, measuring 30.5 cm x 20.3 cm, and 1.3 cm thick, with grooves 0.6 cm wide cut every 1.3 cm and 0.6 cm deep; and small, measuring 20.0 cm x 15.0 cm, with grooves 0.6 cm wide, placed every 1.3 cm and 0.6 cm deep.

Traps were initially baited in 1990 with peanut butter, placed together with the grooves facing each other, and secured with rubber bands. However, preliminary tests showed that unbaited traps were as effective in capturing earwigs as baited traps. Therefore, use of bait was discontinued in the summer of 1990, as was the use of rubber bands since they tended to deteriorate quickly when left outside, and it was not necessary to secure or tie the trap halves together.

Additional Collection Methods

A modified portable car vacuum cleaner was used frequently to collect earwigs from non-trap sites. The vacuum cleaner was modified by attaching cables to a 12-v car battery by battery clamps. The front vent of the vacuum cleaner was cut off and fitted with a sheet of Plexiglas made into a tube 15.0 cm-long and 4.5 cm in diameter, with a fiberglass mesh screen glued in place in the back of the tube to prevent the insects from entering the motor. A detachable Plexiglas nozzle (1.3 cm in diameter) was attached to the distal end of the tube, with a 4.7 cm-diameter apron 6.0 cm from the top of the nozzle that fit over the end of the tube. The nozzle was secured to the tube by a rubber band looped around the apron of the nozzle and attached to small anchors glued to the sides of the tube. The tube was emptied by removing it from the cleaner, and removing the nozzle from the tube. It was believed that the groove-board trap and suction collection methods were unbiased with regard to sex or age class.

Collection Schedule and Protocol

Collections of earwigs were made on four occasions between early July and late September in 1989. At regularly established sites, samples were taken every 1 to 8 days ($\bar{X}=4$) in 1990 and every 1 to 10 days ($\bar{X}=6$) in 1991, between May and August. In 1990, sampling continued every 7 to 10 days through the beginning of October. In 1991, however, insects were collected only every 3 to 4 weeks

beginning in August, and continuing until the end of September. No collections were made the last 2 weeks of August 1991. Earwigs were collected on only two dates in 1992. Sampling at some sites was discontinued as the season progressed, if no earwigs were collected for a few weeks.

Collections at regular sites were usually made between 0800 h and 1000 h. Collections at sites identified by homeowner phone calls to the Department of Entomology were sometimes made in the afternoon or evening, especially if the homeowner wished to be present, or if entry into the home was necessary to collect the insects.

Traps were emptied by separating the halves and shaking them over a funnel placed over a 400 ml glass Mason jar. Early in the season when trap catch was expected to be large, a thin film of Vaseline was applied around the mouth of the jar to prevent earwig escape. After the traps had been completely emptied, they were replaced in their original locations. Jars were labeled with permanent marking ink according to site number.

After collection, the jars were placed in a cooler with ice packs, and transported back to the laboratory. Earwigs were counted, and the adults were sexed in the laboratory; no external characters can be used to sex nymphs (Lamb, 1974). In general, the earwigs were relatively easy to retrieve from the collecting jars and to sex, without the use of anesthesia.

Because data on emergence were of secondary importance to this study, nymphal instar data were not recorded. Categorization of instar would have required counting antennal segments (Behura, 1956), and anesthetization for examination under a dissecting microscope. Although some previous researchers (e.g., Chant and McLeod, 1952) immobilized earwigs with carbon dioxide before handling, anesthetization was avoided because it might have short- or long-term effects on behavior.

In 1990 and 1991, collection totals and sex ratios were computed on a biweekly basis for each site, from the end of May through late October in 1990 and late September in 1991. In both years, collection data from sites were also lumped and sex ratios computed biweekly. In 1990, data from Sites 1-3 were used to compile sex ratios and age distribution. In 1991, data from an additional two sites were also used; since Sites 4 and 5 were close to Sites 1-3, all data probably reflected the same population. Total nymph counts were also computed every 5 days for both years.

Weather Data

Temperature and precipitation records for Blacksburg, Virginia for 1989 - 1991 were obtained from the Virginia State Climatology Office at the University of Virginia. Data were derived from weather station 440766, Blacksburg 3 SE, located 4.8 km from the center of the town and compiled by the National Climatic Data Center in South Carolina. Record averages reflect mean values from November

1952 through 1992. Weather data for July 1989 are missing from the data base; the reason is unknown.

Adult Development

In 1991 and 1992, a small number of nymphs were sequestered and allowed to develop into adults to provide virgins for mating experiments (Chapt. 4). Sample sizes were small in both years, primarily because the insects were being isolated for the primary purpose of providing virgins for mating studies, rather than assessing emergence rates on the basis of sex. These nymphs also provided limited data on whether development rates differed for males and females.

Nymphs were set up in three separate groups in 1991, one week apart, and two separate groups in 1992, one week apart. Nymphs from a given weekly cohort came from the same site, and were assumed to be about the same age. Although instar was not recorded prior to sequestration, most nymphs from a given site appeared morphologically to be at about the same developmental stage and size. Nymphs were randomly selected from the insects collected, and individually sequestered in 30 ml glass vials stoppered with cotton wool, and provisioned with a small wedge of carrot. Fresh pieces of carrot were placed in the vials every week. Development into male or female adults was recorded at least every week. Mortality rate was also recorded, as was the number of insects that escaped.

Pest Status

In the process of locating collection sites, talking with homeowners and citizens, and maintaining sampling sites, a preliminary view of the earwig's pest status in southwestern Virginia was obtained. This included anecdotal information about homeowner attitudes, time and patterns of earwig infestation, and history of control efforts.

Results

Population Dynamics

General Population Patterns

Since earwigs were only collected on a few occasions in 1989 and 1992, little can be learned about population levels and characteristics from those data. In 1990 and 1991, Sites 1, 2, and 3 were the sampling locations used most regularly. Groove-board traps were monitored for earwig appearance beginning in late spring, but only nymphs were found on the first day traps contained earwigs, in both years, May 31. In general, at regularly established sites, nymphs predominated from late May until mid- to late June. Nymphs were not found in trap catches after mid-July. Adults were collected beginning in early June, peaking in mid- to late July, and ending when no further earwigs could be found in late September or October.

Nymphal Patterns

Although nymphs were found at Sites 1 and 2 in both 1990 and 1991 on May 31, nymph levels peaked about 5 days later in 1991 than in 1990 (Figure 1.1).

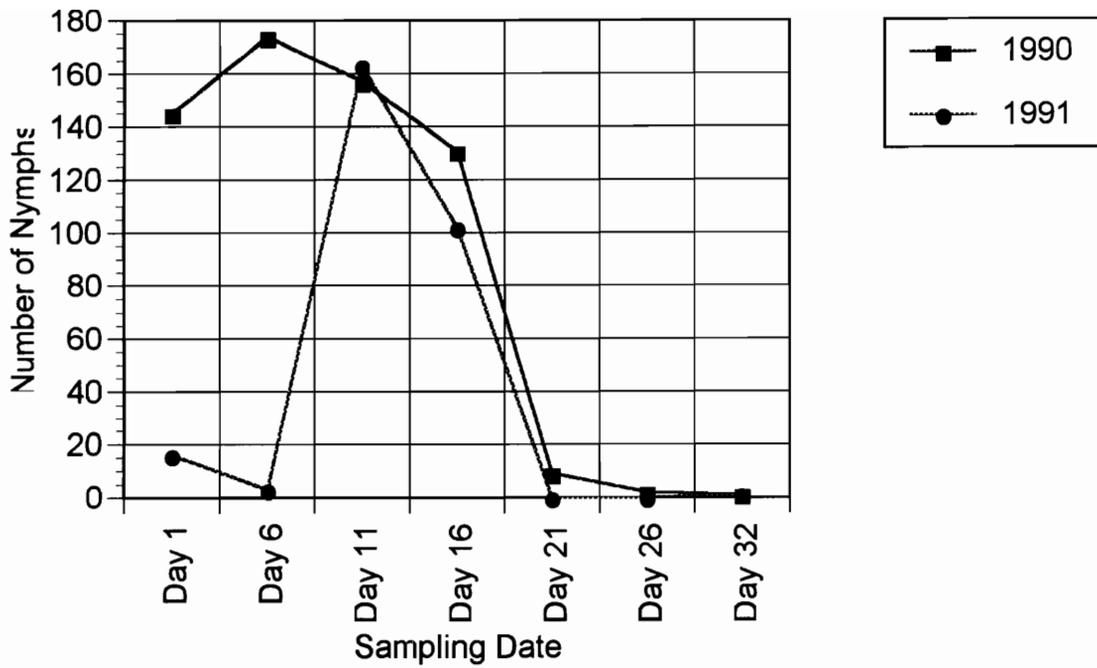


Figure 1.1. Mean number of *F. auricularia* nymphs collected at Sites 1 and 2 in Blacksburg, Virginia, in 1990 and 1991.

Nymphs were also collected for about 10 days longer in 1990 than in 1991. About 2 to 3 weeks into the season, most earwigs had reached maturity, and few nymphs were found. As with the general pattern of greater abundance in 1990 compared with 1991, about twice as many nymphs were collected in 1990 as in 1991. The number of nymphs that emerged and were caught in traps in 1990 significantly declined over time as the sampling period progressed (least-squares regression, $F=20.92$, $df=6$, $P<0.006$). This relationship was not significant ($P>0.05$) for 1991. The regression of number of trapped adults on time was not significant ($P>0.05$) for either year.

Local Weather Patterns

In 1990, mean maximum temperatures for April through July were about average (Figure 1.2). August and September 1990 were only slightly warmer than average. In 1991, June was average, but the months from June through September were all warmer than average. The spring of 1990 was drier than average but, except for June, the summer was wetter than normal (Figure 1.3). In contrast, March 1991 was wetter than the average March, but the summer was drier than average. In 1990, total spring and summer precipitation was significantly correlated with combined nymph and adult trap captures (Pearson product-moment correlation, $r=0.976$, $df=3$, $P<0.01$).

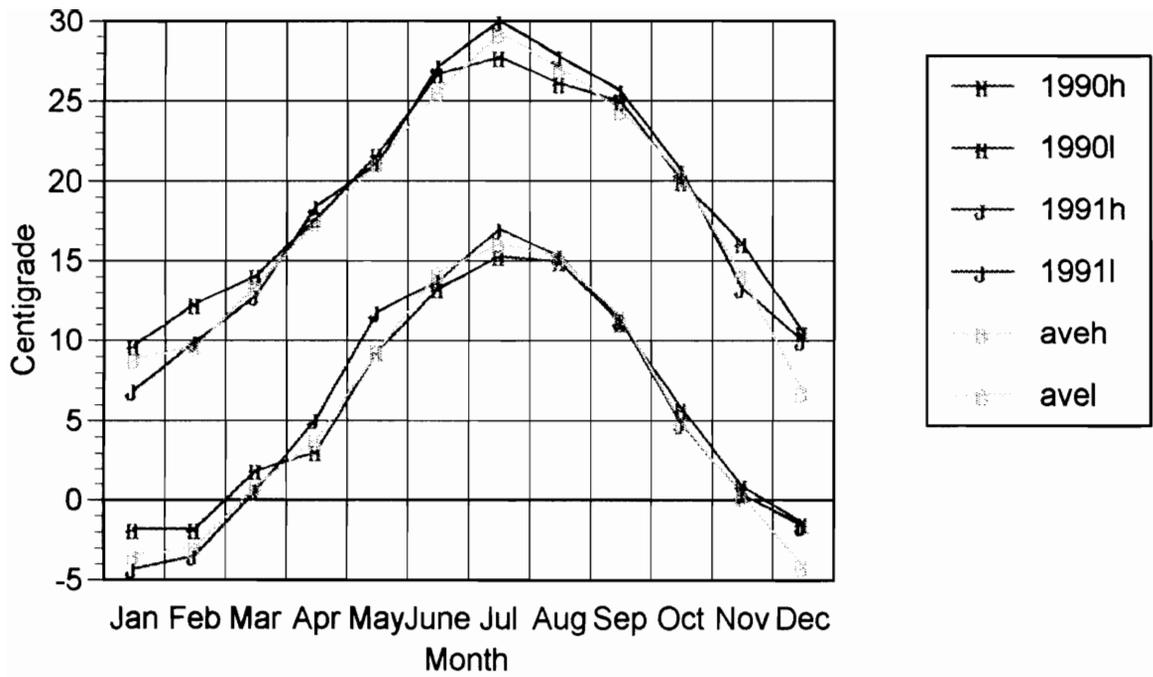


Figure 1.2. Monthly mean minimum and maximum temperatures recorded at a meteorological station in Blacksburg, Virginia during 1990 and 1991. High (h), low (l), average from 1952-1992 (ave).

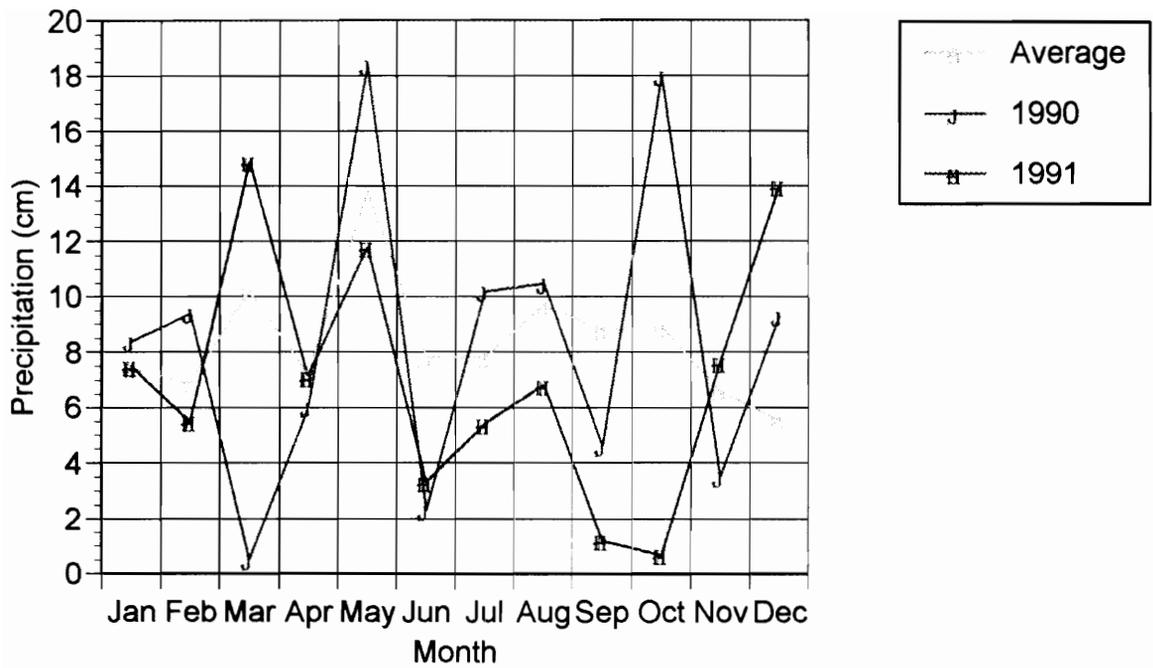


Figure 1.3. Total monthly and average (from 1952-1992) precipitation recorded at a meteorological station in Blacksburg, Virginia during 1990 and 1991.

Age Distribution

Nymphs comprised more than 96% of the insects collected from late May to mid-June in 1990 (Figure 1.4) and 84% of the insects collected during the same time period in 1991 (Figure 1.5). Similarly, a greater proportion of earwigs collected in the following two weeks were immatures in 1990 (14%) than in 1991 (2%).

Sites 6 and 7 were sampled only on June 15, 1990 (Figure 1.6). Nymphs predominated in the catch at Site 6 (about 67%), but made up only about 36% of the collection at Site 7, only a few blocks away.

Sites 8 through 11 were sampled two or three different times between July 12 and 27, 1990 (Figure 1.6). No nymphs were collected.

Sex Ratios

1989

Since earwigs were collected only sporadically in 1989, site data were not pooled. Site 1 was female-biased in early July (37.7% males to 62.3% females, N=69, $\chi^2=4.2$, $P<0.05$), and became even more female-biased by late September (32.8% males to 67.2% females, N=137, $\chi^2=16.1$, $P<0.001$).

At Site 2, the ratio of females to males in late August was not significantly different from 1:1 (N=63, $P>0.05$). A week later, in early September, females predominated, 71.4% to 28.6% (N=14).

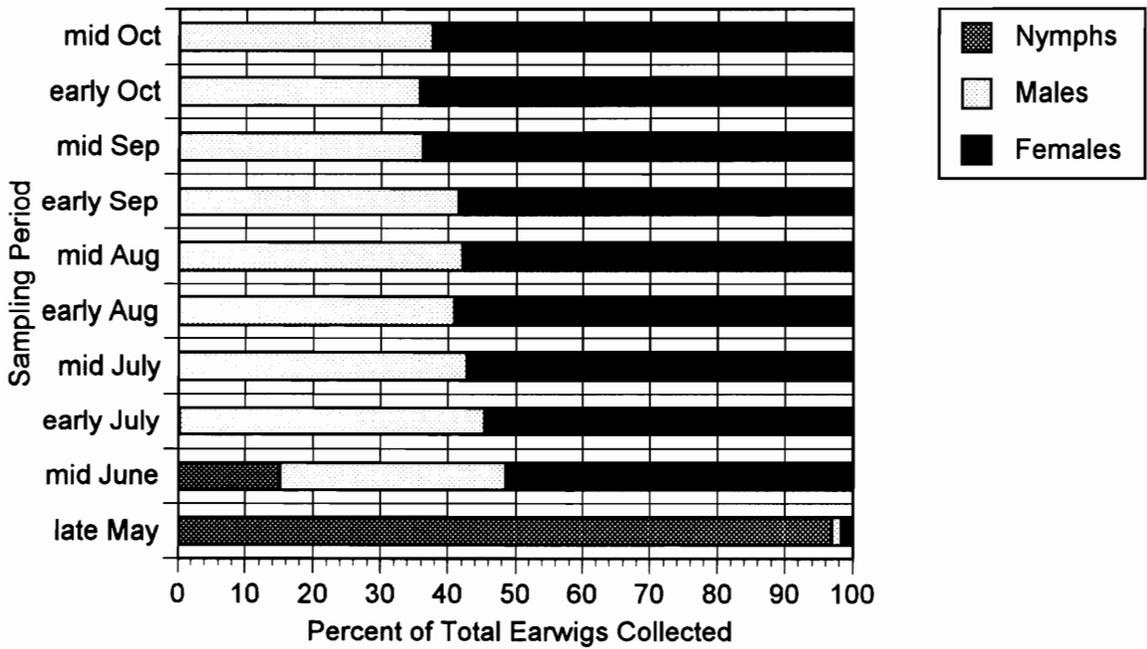


Figure 1.4. Age and sexual distribution of *F. auricularia* at Sites 1, 2 and 3 in Blacksburg, Virginia in 1990. (N=1,731; N=683; N=416, $\chi^2=25.7$, df=1, P<0.05; N=741, $\chi^2=15.5$, df=1, P<0.05; N=569, $\chi^2=18.6$, df=1, P<0.05; N=266, $\chi^2=6.6$, df=1, P<0.05; N=573, $\chi^2=16.4$, df=1, P<0.05; N=549, $\chi^2=42.3$, df=1, P<0.05; N=207, $\chi^2=16.8$, df=1, P<0.05; N=16 from late May through mid-October, respectively).

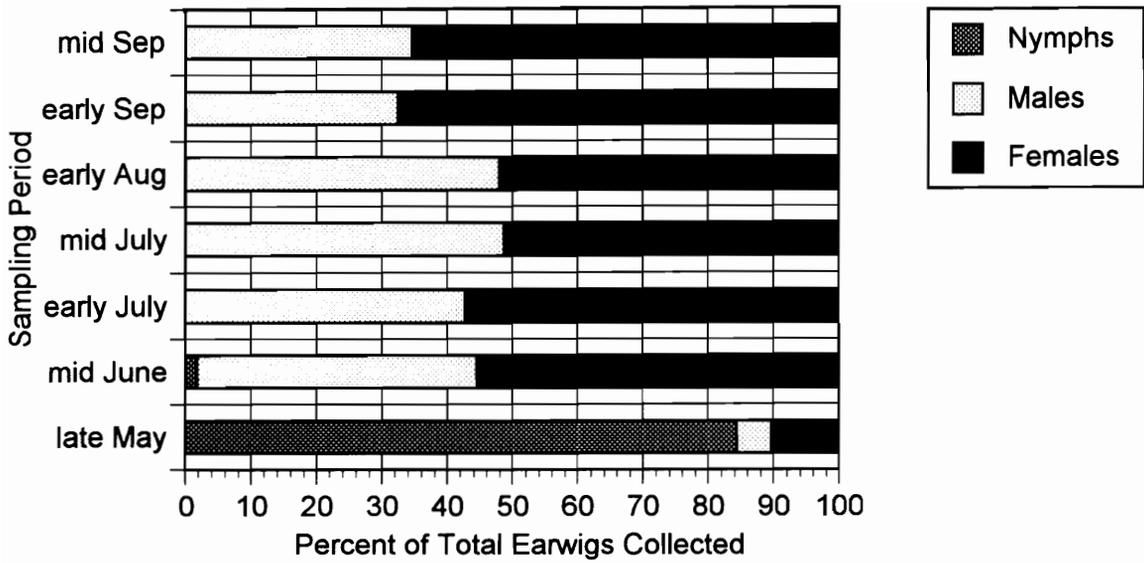


Figure 1.5. Age and sexual distribution of *F. auricularia* at Sites 1-5 in Blacksburg, Virginia in 1991. (N=690, $\chi^2=10.7$, $P<0.05$, $df=1$; N=534; N=889, $\chi^2=8.7$, $P<0.05$, $df=1$; N=298, $\chi^2=18.7$, $P<0.05$, $df=1$; N=127; N=202, $\chi^2=24.5$, $P<0.05$, $df=1$; N=144, $\chi^2=13.4$, $P<0.05$, $df=1$; from late May through mid-September, respectively).

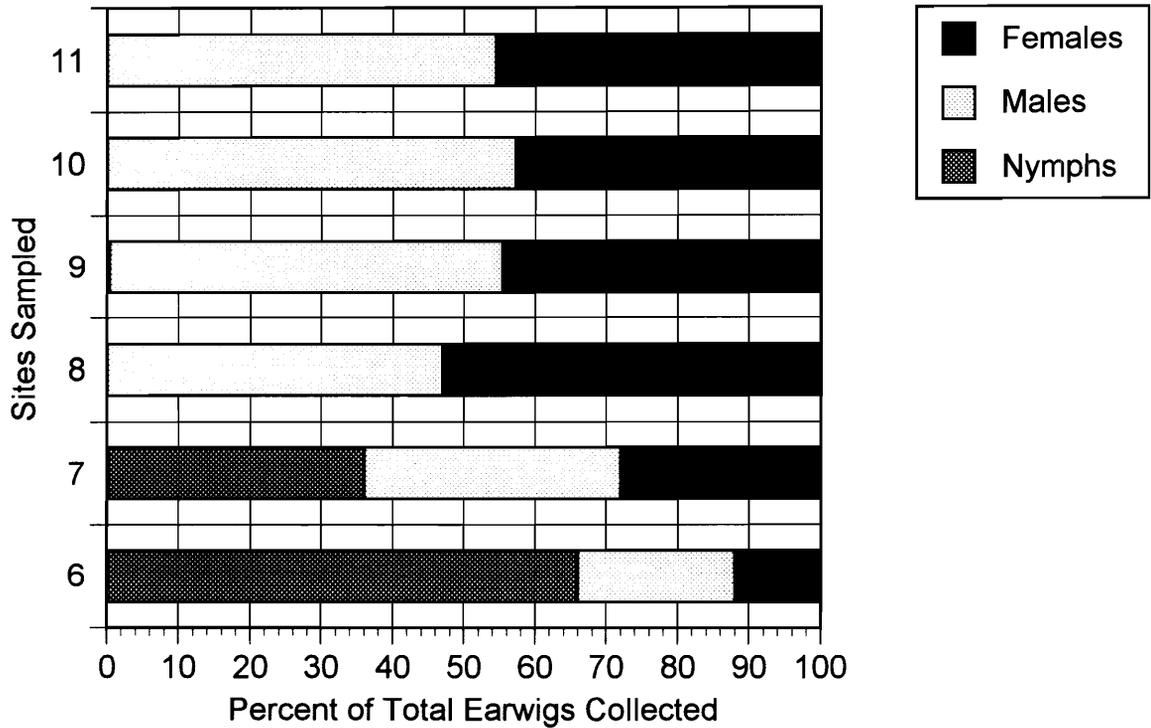


Figure 1.6. Age and sexual distribution of *F. auricularia* at Sites 6 (N=242, $\chi^2=6.3$, df=1, P<0.05) and 7 (N=157) in Christiansburg, Virginia in mid-June 1990, and Sites 8 (N=66), 9 (N=249), 10 (N=246, $\chi^2=5.3$, df=1, P<0.05), and 11 (N=242) in Blacksburg, Virginia in July 1990.

At Site 12, censused only in late September 1989, the sex ratio was 42.9% males to 57.1% females (N=42), not significantly different from 50:50 ($P>0.05$).

1990

In 1990, the overall sex ratio of earwig catches at Sites 1-3 was significantly ($P<0.05$) female-biased most of the season (Figure 1.4), with the exception of early July, and two periods in which either few adults were collected (the first two weeks of collection, when most earwigs were immature) or few insects were found (the last two weeks of collection). Females comprised about 60% of the trap catches throughout the season.

Sites 6 through 11 were sampled with the modified car vacuum cleaner. Sites 6 and 7 were sampled only on June 15, 1990. At Site 6 (Figure 1.6), the sex ratio of the adults was significantly ($P<0.05$) male-biased (N=242). Similarly, at Site 7, sampled the same day, the sex ratio was male-biased, but not significantly (N=157, $P>0.05$). Sites 8-11 were sampled only in July 1990 (Figure 1.6). The sex ratio was not significantly ($P>0.05$) different from 50:50 except at Site 10, which was also male-biased.

1991

The 1991 collection totals were significantly ($P<0.05$) female-biased for all periods except mid-July through mid-August (Figure 1.5), averaging about 60% female, as in 1990.

Adult Development

In both 1991 and 1992, slightly more males emerged per week. However, the difference was not significant ($P>0.05$) except for the week of July 5, 1992, (Table 1.2).

Qualitative Observations on Pest Status

From 1989 - 1992, consumer calls to the Virginia Tech Extension Office concerning earwig infestations began in late May, increased in frequency until mid-June, and dropped off about the beginning of July. This pattern was probably related to the emergence of large numbers of earwigs in late May and then gradual dispersal as the summer continued. Since the European earwig is only a relatively recent summer resident of southwestern Virginia, most homeowners knew little or nothing about the earwig, and many did not even know its name. Most callers were bothered primarily by two factors related to the infestation: the insects invaded their living space and the insect's odor, which was usually described as "disagreeable." A smaller, but substantial, number of homeowners were worried that the insect could cause structural damage to their homes. Others were concerned that the insect's forceps could draw blood.

Earwigs were observed more frequently outside the house. Outdoor infestations were most common in moist, dark, protected areas. These included inside storm doors, window frames, drain pipes from rain gutters, woodpiles,

Table 1.2. Emergence of adult *F. auricularia* from nymphs in the laboratory on a weekly basis in 1991 and 1992.

	Males	Females	χ^2	Escaped	Died
1991					
Jun 8	21	17	NS	5	7
Jun 15	24	22	NS	5	9
Jun 23	18	19	NS	11	11
Jun 29	6	4	NS	5	2
Jul 7	1	0	NS	0	5
Total	70	62	NS	26	34
1992					
Jun 27	9	6	NS	0	14
Jul 5	1	10	7.3	0	8
Jul 12	3	5	NS	0	0
Total	13	21	NS	0	22

between the slats of wooden and metal lawn furniture, mulches, sandboxes, fencing postholes, under birdbaths, landscaping stones, rugs and doormats, compost piles, piles of debris, cracks in concrete steps and walkways, between the bricks and siding of houses, among seed in bird feeders and in birdhouses, commercial beehives, and under loose flooring in outdoor structures such as porches, garages, sheds and playhouses. Inside the house, earwigs could frequently be found in humid spaces such as the bathroom and kitchen. However, even though insects were less frequently found inside the house, homeowners were more repelled by these invasions than by outdoor infestations

Some homeowners observed that earwigs attacked garden plants and ornamental shrubs and flowers. Earwigs were also found in such nonresidential locales as an old field of annual weeds in Blacksburg, and among the bark of trees on a shady, wooded hillside near a parking lot on the campus of Virginia Tech. Trees were a favorite resting spot, especially under the bark of deciduous species. At one site, hundreds of earwigs were collected from the deep grooves of a chestnut tree, many of them embedded in frass.

In 1989, several homeowners mentioned that they noticed earwigs around their homes shortly after receiving a truckload of bark mulch. Records in the Virginia Tech Cooperative Extension Office in Blacksburg indicated several similar complaints from homeowners over the previous two or three years, possibly

suggesting bark mulch as a method of dispersal. However, this problem was not investigated, since it was outside the scope of the study.

Discussion

Population Characteristics

Earwigs thrive in geographic regions where the July mean temperature does not exceed 23.9° C, and where annual precipitation is at least 50.8 cm (Crumb et al., 1941). Blacksburg has a suitable climate for earwigs, with annual precipitation averaging 97.1 cm and July mean temperatures of 22.7° C (Virginia State Climatology Office, 1994).

Population levels were much lower in 1991 than in 1990. This was likely due in part to the warmer and drier than average summer of 1991, although conclusions cannot be made without more detailed weather data, such as daily temperatures and precipitation. It is possible that not only were populations smaller in 1991 than in 1990, but that numbers of trapped earwigs declined rapidly in 1991 because of earlier than normal dispersal of the population, due to the hot, dry weather. Indeed, earwigs were scarce in collection traps on mornings following hot, dry days. Homeowner complaints also fell off during these periods. Crumb et al. (1941) observed that when environmental conditions were favorable, earwig populations tended to remain in a small area, but if unfavorable, the insects frequently dispersed widely. Higher than average precipitation in 1990 was significantly ($P < 0.05$) correlated with population levels during that period; since earwigs prefer moist

environments (Crumb et al., 1941), it would follow that ample rainfall would favor increased population levels.

Life history events were similar to those in some other earwig studies, with the exception that no adults could be readily discerned as belonging to the parental generation. No adult males or females were collected in traps in the first collection in May, as found by Maxwell (1988). However, Lamb and Wellington (1975) and Crumb et al. (1941) found adults, especially males, from the previous year's generation, in their spring monitoring. These results may differ primarily because earwigs were not found in traps in Blacksburg until late May, although adults from the parental generation may have still been present in the population earlier in the spring, but were simply not attracted to the traps. Since most nymphs were fairly large when collected in late May or early June, and the majority of them developed into adults within about two weeks of the beginning of sampling, second- or third-instar nymphs were likely above ground earlier than the end of May. Traps were left out at Sites 1, 2 and 3 all winter in order to provide data on initial emergence times; why nymphs were not attracted to traps until later in May was unknown, but was probably related to nymphal and maternal female attachment to the nest (Lamb 1976a) rather than to other available shelters such as traps. Although there is no evidence that siblings maintain a cohesive aggregation within the nest due to attraction to each other, that possibility also exists.

Since the adult fraction of collected earwigs increased over time, it was apparent that most, if not all, of the collected adults were from the current year's generation. Crumb et al. (1941) noted that parental adults die by midsummer, but it is unclear how these adults were identified as parental rather than newly mature.

Mating pairs were never found in traps in the 3 years that insects were collected by trapping, in contrast to Lamb and Wellington (1975) and Maxwell (1988). This might be explained by temporal variations in mating behavior in geographically disparate populations. European earwigs in Virginia were not observed to begin mating until late September or early October, a time when few earwigs were collected in the field, and the probability, therefore, of finding mating pairs in traps was low.

Since no nymphs were collected at any site in any year later than mid-July, there was no direct evidence for multiple broods as found by Crumb et al. (1941) and Lamb and Wellington (1975). This fact suggests that either rebrooding in southern populations of *F. auricularia* is unusual, or that rebrooding occurred at about the time of the first collections of insects, so that discriminating between the two broods would have been difficult. In many collections, nymphs of appreciably different body sizes were observed. However, without noting instar, it is difficult to say if bigger nymphs were older, or bigger due to genetics or better nutrition. If nymphal instar data had been recorded, these data may have shown the emergence

of a small, but substantial, minority of younger nymphs collected at a time when most nymphs were nearly mature.

Lamb (1975) observed that the earwig spends the first portion of its life cycle close to the natal area, and the second portion dispersing and foraging. As in previous studies, earwigs were no longer found in late fall.

Sex Ratios

Earwig populations in 1990 and 1991 were significantly ($P < 0.05$) female-biased most of the season. Lamb and Wellington (1974) found marked seasonal variations in sex ratio in Vancouver, British Columbia populations: in spring, nearly all adults in shelters were male, the initial sex ratio of first brood adults was about 50:50, and females predominated by early fall. They hypothesized that the spring males were those from the parental generation which had survived the winter, and that females from the parental generation were not caught in traps because they were still in their underground burrows. In Quebec, Maxwell (1988) found male-biased sex ratios. The results of the present study are not consistent with Lamb and Wellington's (1974) initial brood ratio, but are consistent with their fall ratios. No adults were found in spring in Virginia, which may explain the discrepancy between these spring results and those of Lamb and Wellington (1974). Differences between climate and geography between British Columbia, Quebec, and Virginia are also probably important in emergence times and mortality, reflected in sex ratios.

Both Sites 6 and 7, located in Christiansburg, were male-biased in mid-June 1990, when the Blacksburg population was significantly ($P < 0.05$) female-biased. This difference could reflect a true difference between the two populations. However, since the Christiansburg sites were sampled only once, it would be imprudent to ignore the possibility that differences reflect only natural variability.

In the present study, sex ratios were about 65% females to 35% males by the end of sampling in September or October. Lamb (1974) explained the pattern of fall predominance of females by suggesting equal mortality rates for both sexes during the nymphal period with a slight but steady increased male mortality once insects reach maturity, but he did not offer any evidence for these possibilities. Sex ratios may vary due to differential emergence times, mortality, or emigration (Wiener, 1974; Werren and Charnov, 1978). Male earwigs may emerge earlier in the season than females, leading to a predominance in spring traps, and, although they have similar longevities, die sooner. Earlier male emergence is productive in many insects because males can gather near female emergence sites to mate with newly eclosed females, thereby increasing the chance of obtaining as many mates as possible (Price, 1984). However, since *F. auricularia* does not mate prior to mid-summer, and more usually in late summer to early fall (Chapt. 4), it would not be energetically advantageous for male earwigs to precede females in eclosion. Indeed, no significant differences were found in developmental schedules for males and females in the present study, although these results might have been different if

it were possible to define with greater accuracy the age of nymphs before sequestration. Because there are no reported methods available for sexing nymphs, it cannot be determined if male nymphs die at a rate different than that of female nymphs. Sampling removed individuals from the population, which may have also affected sex ratios.

Sex ratios may also be female-biased if males have a shorter lifespan than females, because they are more vulnerable to predation, or are more visible to predators because of their bigger forceps. Males may disperse more widely than females, making them more apparent to predators. Males of many insects, such as *Drosophila melanogaster*, have shorter lifespans than females (Partridge and Farquhar, 1981).

Another possible reason for the unbalanced sex ratios which may be due to shorter male longevity is that males may not be necessary to rear offspring (Crumb et al., 1941). Since males apparently contribute little toward parental care (Lamb, 1976b), there may be no purpose for males to survive beyond mating in the fall and early winter. However, the mating scenario described for earwigs in which male and female pair up and construct an underground cell (Crumb et al., 1941) would seem to argue for 50:50 sex ratios, usual for monogamous species (Alexander, 1974). Otherwise, some females will be left without mates, which would not make good evolutionary sense. Females reportedly eject males from the nest soon after its construction (Lamb and Wellington, 1974), which would theoretically give males

time enough to find other females and mate with them. But hibernation and nest-building is probably environmentally-mediated by cooler temperatures and shorter day-lengths, so that if mating is associated with these activities, it is probably synchronized. Few females would be left for mating opportunities if males tried to optimize reproductive success by looking for additional mates after being ejected from the nest of the first female mate. Since most of the work on the earwig's nest-building and parental behavior has been done in the laboratory (e.g., Lamb, 1976b), female-skewed sex ratios late in the season may in fact suggest that mating may take place prior to nest construction. However, since sex ratios are female-biased beginning relatively early in the season, it would not appear that reproductive roles are entirely responsible for the observed ratios.

Earwigs also disperse as the season progresses (Lamb, 1975), but it is unknown whether there are sexual differences in the rate of dispersal. It is possible that males disperse at a greater rate than females for some reason, leading to skewed sex ratios.

Pest Status

The European earwig is clearly a pest in suburban and urban areas of southwestern Virginia. Large outbreaks can occur in years with favorable weather patterns. However, the earwig's pest status derives primarily from its early summer invasions of homes and apartments, and psychological aversion of homeowners rather than economic damage to crops or ornamental plants. Aside from largely

psychological concerns or fears due to ignorance about the insect's habits, earwig infestations were actually not very severe. Residents' complaints of infestations were primarily confined to a 2-3 week period in the beginning of the season. Although many people mentioned wanting to use pesticides to control the insects, it appeared that not many did so. In a few cases of severe infestations, homeowners mentioned that they had contracted with local pest control companies to treat their homes and yards; it was interesting to note that these residents later complained that treatment did not help. In later sampling years, as people became more knowledgeable about the insect, it appeared that their attitudes shifted more toward grudging acceptance of the earwig as a nuisance for a few weeks in early summer, rather than emphasis on immediate control with insecticides. These anecdotal data suggest a tentative conclusion that the European earwig, while a nuisance pest, is not a very serious problem in southwestern Virginia and that more effective education through extension activities or newspaper articles would increase tolerance. However, a more systematic investigation of homeowner attitudes and a comprehensive, detailed examination of areas of infestation would be needed to definitively depict the earwig's pest status.

CHAPTER 2: AGGREGATION BEHAVIOR

Introduction

Observations of natural populations of European earwigs indicate that these insects frequently aggregate in large numbers. Aggregation behavior has also been observed in laboratory cultures where earwigs congregate in discrete areas, such as corners of aquaria or the depressions in cardboard egg crates.

Earwig aggregation behavior is poorly understood. Previous research in this area primarily focused on the efficacy of various potential attractants for the purpose of control (e.g., Crumb et al., 1941; Legner, 1962). In his study of the population dynamics of *F. auricularia*, Lamb (1975) noted that European earwigs usually had a clumped distribution, and that while earwigs tend to disperse from natal areas as they mature, gregariousness is, for the most part, a distinctive behavior.

In attempting to assess aggregation behavior in *F. auricularia*, a number of factors have been considered, such as whether aggregation was due to attraction to conspecifics (Taylor, 1978) or due to selection pressure to maximize use of available resources where they are most abundant (Taylor and Taylor, 1977), or to a combination of these factors. Resources may include food, refugia, cover, protection from sunlight or excessive heat, and mates. If groups form due to attraction to other earwigs, aggregation could be chemically mediated via pheromones contained within the feces or cuticle, or exuded or emitted from glandular sources at appropriate times (Blum, 1985). Aggregation pheromones

have been well documented in a wide variety of insect species (Blum, 1985), including cockroaches (e.g., Roth and Cohen, 1973; Rust and Appel, 1985), fruitflies (e.g., Schaner and Jackson, 1992) and crickets (e.g., McFarlane et al., 1983; Nagel and Cade, 1983). European earwigs are associated with a distinctive oily, sweet odor, which might indicate presence of a pheromone or pheromonal blend; indeed, Crumb et al. (1941) reported that oily, greasy, or sweet attractants were the most effective baits. Chemical mediation also seemed likely since preliminary observations indicated that aggregation is a pervasive behavioral trait throughout the life cycle. The possible chemical basis for aggregation was explored in this study, including specific compounds that might mediate gregariousness.

Materials and Methods

In order to evaluate the potential pheromonal basis for the aggregation behavior of *F. auricularia*, preliminary experiments were performed to more fully understand this behavior, and to gather data to design further experiments. Later, detailed analyses and comparative bioassays of extracts from the frass, cuticle and legs of the insect were conducted. The attractivity of various chemicals found to be components of the frass or cuticle was also tested.

Laboratory Conditions

Field-collected insects (Chapt. 1) were used in aggregation bioassays. Immediately following collection, insects were placed in containers in the laboratory. Three different types of containers were used for population maintenance in the lab:

- 1) 0.4 l glass Mason jars fitted with screen or mesh tops;
- 2) 12.5 x 6.5 x 4.0 cm plastic boxes fitted with lids which had two 3.0 cm-diameter holes drilled in them and pieces of fiber mesh glued in place for ventilation;
- 3) 39.0- and 76.0-l aquaria with Plexiglas lids.

Number of insects per container varied with size of the container, from 50-100 in Mason jars to several hundred in aquaria.

Since earwigs can easily climb vertical surfaces and negotiate small cracks and crevices, escape was possible, even with lids. Lamb and Wellington (1974) took measures to prevent escape by painting interior surfaces of rearing containers with fluon. In this study, use of Vaseline was effective to prevent escape. In all three types of containers, a thin film of Vaseline was applied about 1.0-2.0 cm inside the lip of the container. Vaseline was also frequently applied to the interior corners of aquaria since corners provided the most frequently used route of escape.

Artificial shelters were placed in containers to approximate natural refugia. Several types were employed:

- 1) The upper or lower lid of a 1-dozen cardboard egg carton, inverted and placed on the bottom of aquaria. Most earwigs preferred resting in the interior or exterior hollows of the carton to other areas of the tanks, although a minority of insects oriented along the inside corners of the tanks. The number of insects aggregating in the corners

increased with population density of the tank, but was always less than the number of insects aggregated on the egg carton.

2) A small (12.0 cm x 15.0 cm) piece of window screen folded lengthwise about every 2.0 cm and fanned out, inserted vertically into the glass jars and horizontally into the plastic boxes. This shelter design provided opportunities for earwigs to spread out in perching positions within the container, instead of aggregating along the sides of the jars.

3) Pieces of moistened, loosely rolled paper toweling (Lamb and Wellington, 1974) or corrugated cardboard. As with the egg cartons, earwigs preferred resting underneath the toweling or cardboard. These shelters were used primarily in the plastic boxes. The toweling or cardboard was moistened on an irregular basis; as with all shelters, their use appeared to be more attractive over time, regardless of whether they were moist or not. In addition, mold frequently developed if the containers were kept closed and the shelters kept too wet.

4) Split halves of firewood, placed bark side up on the bottom of aquaria. One large group of earwigs was also collected in a half-decayed log. The log was then placed directly into an aquarium and used as a shelter.

5) In 1989 only, sand or potting soil was placed in the bottom of glass aquaria at a depth of 6.0-7.0 cm, and kept moistened as necessary. This substrate was selected in order to attempt to observe gallery construction. However, it proved untenable since earwigs generally burrowed into the sand or soil in areas away from the glass, so that the galleries could not be observed, and because the high humidity which developed as a result of keeping moist sand or soil in a glass aquarium caused invasions of mold and mites. Therefore, the use of sand or soil was discontinued after the summer of 1989.

Containers were kept in a room illuminated by natural light, and temperature was maintained 20-25° C. Although temperatures were generally lower than ambient outdoor temperatures in the summer, they were higher than ambient temperatures in the fall and winter. Lamb (1974) kept earwigs in a similar setting, in an unheated room with natural lighting where average temperatures were higher than ambient in British Columbia, about 15-20° C.

Artificial lighting was not used except when behavioral tests were conducted in the evening. In that case, red light was utilized. Because earwigs cannot visually discriminate light in the red wavelength, 650 Å (Chant and McLeod, 1952), it was believed that the use of such lights would not disrupt normal behavioral patterns. McLeod and Chant (1952) observed that the use of fluorescent or incandescent bulbs disturbed normal nocturnal activity of earwigs.

Food and water supplies were checked at least weekly, and frequently more often in larger containers housing larger numbers of insects. Water was supplied in small (5.0 ml) to medium (20.0 ml) glass vials stoppered with moistened cotton balls.

Because of the earwig's omnivorous feeding behavior, insects were easy to maintain on artificial diets in laboratory colonies. Previous laboratory studies have utilized a variety of foods: carrots (McLeod and Chant, 1952; Lamb and Wellington, 1974), lettuce (McLeod and Chant, 1952), broad beans (Lamb and Wellington, 1974), live and decaying mosses, lichens and algae (Ebeling, 1978), dahlia blooms and lecanum (McLeod and Chant, 1952), commercial bee pollen (Lamb and Wellington, 1974), meat meal (McLeod and Chant, 1952), rat chow (Lamb and Wellington, 1974), and live or dead insects (Ebeling, 1978), especially aphids (McLeod and Chant, 1952; Lamb and Wellington, 1974). In this study, insects were also fed a variety of foods, including bee pollen, lettuce, apples, and live aphids, but the staples of the diet were premoistened cat chow and slices of carrot. Food type did not appear to be a problem for survival: earwigs survived well regardless of whether they were fed mainly carrots or cat chow.

Preliminary Aggregation Experiments

Experiments 1-7

Since so little was known about the factors promoting aggregation in *F. auricularia*, a number of simple, preliminary experiments were initially conducted in order to obtain information about the aggregation process, and to gather data to

design further bioassays (Table 2.1). Observations made during field collections and inspections of homeowners' properties showed that earwigs tended to aggregate in localized areas, which became noticeably spotted with frass over time. While frass might merely be incidental to the aggregation process, occurring as the insects stayed in one spot, it was tested to determine if frass plays a role in mediating and reinforcing the aggregation process. Frass was manually collected from earwig shelters at field collection sites as well as from laboratory stocks, and tested while fresh. Attraction to frass was also evaluated in some experiments by conditioning Whatman filter paper (7.0 cm-diameter) or 2.5- x 6.25-cm strips of Whatman chromatographic paper (McFarlane and Alli, 1986) by placing in a laboratory culture of earwigs for 24-48 h. The filter paper, which was then spotted with frass, was removed and placed opposite an untreated control piece of filter paper in one of three types of arenas: a small plastic shoe box; a large glass cylinder, placed on a 645-cm² piece of glass, to which a thin film of Vaseline was applied to the inside top and bottom rims of the jar to prevent insect escape.; and an 11.4-cm plastic Petri dish. Twenty test insects were randomly, without regard to age class, body size, or sex, withdrawn from lab cultures and sequestered for 1 h in a 30.0 ml glass vial, stoppered with cotton balls. The insects were then introduced into the arenas, and their positions were recorded 1 h later, as either on or touching the experimental paper or on or touching the control paper..

Table 2.1. Protocol for preliminary experiments to examine aggregation in *F. auricularia*.

Experiment	Arena type	No. earwigs / replicate	No. replicates
1. Conditioned filter paper disk	Plastic box	6	1
2. Conditioned filter paper strip	Plastic Petri dish	1	7
3. Conditioned filter paper strip	Glass cylinder	20	7
4. Frass (2.0 g)	Glass cylinder	20	17
5. Earwig corpses (N=15)	Wooden honey bee cage	15	10
6. Earwigs	Plastic Petri dish	2	20
7. Earwigs + conditioned filter paperstrips	Plastic Petri dish	2	30

The behavioral response of earwigs to the corpses of earwigs was tested since Morris (1965) noted that earwigs are attracted to macerated conspecifics. Fifteen earwigs that had been dead at least 24 h were placed in a 1.8 x 3.0 x 8.0-cm wooden honeybee queen cage, covered with a 2.6 x 7.6 cm piece of rigid fiber mesh screen. The edges of the screening were firmly secured to the box with masking tape to prevent direct access to the corpses, and possible consumption. Test insects were, however, able to smell and antennate the corpses. The objective was to test whether insects were attracted to chemicals present on the bodies of the dead earwigs, rather than to see if they were attracted to dead earwigs as potential food items. Indeed, earwigs were frequently observed to consume corpses in laboratory stocks, and, on occasion, to attack and devour molting or teneral individuals. It is not known whether cannibalism in *F. auricularia* occurs in the wild, or if it is a laboratory artifact. The experimental cage was placed opposite an empty control cage in the glass cylinder arena.

If aggregation is mediated by pheromones on the body of conspecifics rather than in the frass, shelter selection by earwigs might be influenced by prior occupancy by other earwigs. Experiments 6 and 7 examined attraction of earwigs to individual conspecifics. In Experiment 6, one test insect was introduced into arenas containing two untreated filter paper strips. After 1 h, paper selection was recorded, and a second insect was introduced into the arena. After the second h, paper selection was recorded for both insects. Experiment 7 was conducted in the same

way as Experiment 6, except a conditioned piece of filter paper was used with an untreated piece of filter paper before introduction of the first insect into the arena.

Experiment 8. Field tests of old vs. new traps.

Crumb et al. (1941) found that the longer pine field traps were in use, the greater the number of earwigs that were trapped. This observation suggested that a pheromone or pheromones are present which may become increasingly concentrated within the porous surfaces of the pine traps as more earwigs congregate within them. To investigate this hypothesis, an experiment was conducted utilizing a pair of identical traps, one which had previously trapped earwigs (designated as "old"), and one which had never been used (designated as "new").

Two small (20.0 cm x 15.0 cm) wood groove-board traps were placed adjacent to each other at one location at Site 1, and at 2 locations at Site 2. Site 1 traps were placed next to each other under an apple tree; at Site 2, two traps were placed next to each other in a pile of wood and metal scraps. Later tests utilized two sets of traps in two locations at Site 2: the pile of wood and metal scraps, and at a second woodpile. Traps were set up on one day, and emptied every few days thereafter. Trapped earwigs were removed from the site; therefore, collection totals over time represent recruitment of new individuals for every collection day ("new" traps continued to be designated as "new" even though they were reused for the length of time of the experiment).

Natural Extracts

Extracts of frass, whole cuticles, legs only and defensive exudate were prepared in order to assess their biological activity with respect to inducing aggregation. Total cuticular extracts were obtained by immersing 10 insects in 1.0 ml of methylene chloride for 1.0 min. Three samples were prepared from each sex. Similar samples were used for bioassays.

Frass produced by a mixture of nymphs and adult males and females was collected from field traps, natural refuges, and laboratory colonies maintained with controlled diets. In each case, approximately 2.0 g of frass was extracted with 2.0 ml of solvent (distilled water, acetone, methylene chloride, and a 1:1 ratio of methylene chloride and distilled water) and concentrated for bioassays. Frass from earwigs raised on exclusive diets of either carrots, cat chow, or bee pollen was extracted in pentane in a similar manner and analyzed by gas chromatography/mass spectrometry (GC-MS). Insect frass equivalents (mean mg frass/day/insect) were determined by sequestering five replicates of 10 males and 10 females, separated by sex, in individual weighed vials. After 24 h, the insects were removed, and the vials reweighed to yield the amount of frass produced per insect per day.

The legs of 25 nymphs were amputated at the femoral-trochanteral joint with a pair of forceps and were placed in 2.0 ml of methylene chloride. A similar sample was also prepared from 50 adults which had been frozen previously. Both extract samples were subjected to GC-MS analysis and used for bioassays.

The defensive exudate from 7-10 individuals of each sex was obtained by pinching or pulling the animal's forceps. The secretion, which was emitted from a pair of specialized glands (Schildknecht and Weis, 1960), exuded onto the insects' dorsal abdomens and was taken up in 5.0 μ l microcapillaries, which were quickly crushed in 1.0 ml of methylene chloride. Identification and quantification of compounds was made using GC analysis.

Chemical Analyses

Several possible sources exist for potential behaviorally active chemicals of earwigs. since insect pheromones have been found on the cuticle (e.g., Howard and Blomquist, 1982), in the frass (e.g., McFarlane and Alli, 1985), and as specially-produced exudates or emissions (e.g., Nagel and Cade, 1982; Teale et al., 1991). Therefore, the chemical profile of the earwig's cuticle and frass was analyzed. Sauphanor (1992) suggested that the tibial glands (Brousse-Gaury, 1983) produce an aggregating compound, so chemicals present only on the legs were also analyzed. *F. auricularia* produce a defensive secretion composed of 2-methyl- and 2-ethylquinone, which is stored in a pair of glands beneath the third and fourth tergites (Schildknecht and Weis, 1960). When disturbed, the earwig extrudes the quinone mixture, and it appears as opaque, yellowish-brown droplets along the dorsal abdomen. The defensive exudate was also analyzed for aggregating potential.

Frass, cuticular and leg washings were analyzed by GC/MS. The defensive exudate was analyzed by gas chromatography. GC analysis was conducted using a Shimadzu GC-9A gas chromatograph equipped with a 30 m x 0.5 mm-ID open DB-17 column with a 1.0 μ m film thickness. The temperature was programmed from 60° to 215° C., set to run at 10° C/min, and the carrier gas flow rate was 15.0 ml/min. On any given day, retention temperatures were reproducible to 1° C. Mass spectra were obtained in the E.I. mode at 70 eV using either a LKB-2091 GC/MS equipped with a 30 m x 0.25 mm I.D. 5% Db-5 column or a Finnigan model 4500 GC/MS equipped with a 30 m x 0.32 mm I.D. column with a 5% DB-1 phase. Normal hydrocarbons, fatty acids, and quinones were identified by comparison of their mass spectra with published data (NIST/EPA/MSDC, 1990). The methyl alkanes were identified from their parent ions and diagnostic fragment ions (Lockey, 1988; Bagneres and Morgan, 1990). Assistance with the GC/MS was provided by Tappey H. Jones and Lewis Pannell of the National Institute of Diabetes and Digestive and Kidney Diseases of the National Institutes of Health, in Bethesda, Maryland.

Aggregation Bioassays

The results of the aggregation experiments and the chemical analyses suggested a series of bioassays in which frass, cuticular washings, leg washings, and individual synthetic chemicals found in frass and/or the cuticle be tested for aggregating ability.

Bioassays were performed by allowing test insects a choice between control and experimental shelters. Experimental compounds were applied to 2.5 x 6.25 cm strips of Fisher Scientific chromatographic paper, and allowed to dry. Control papers were identical except that only the solvent used in the extraction was applied by itself to the paper. In tests of synthetic chemicals, either pentane or methylene chloride was used as the solvent for the compounds, and was applied to the control papers. Papers were folded into quarters and placed in the arena so that they resembled an upside down W-shape (modified from Ross and Tignor, 1986), thus forming artificial shelters. All tests were conducted during daylight hours in a room illuminated by natural light and maintained 20-25° C. Bioassays were performed in arenas of two different designs, one in which a large glass cylinder was inverted over a 645 cm² piece of glass, and the other in which three 11.4 cm-diameter plastic Petri dishes were cut and glued together to form three overlapping chambers with a section of the walls removed to allow movement from one chamber to another, a modification of a design used by Nagel and Cade (1983). In the latter design, the control and experimental papers were placed in the far chambers, and the insects introduced into the central chamber. Twenty test insects were removed from laboratory colonies without regard to sex or body size approximately 1 h before testing. Insects were then sequestered in groups of 20 in 30 ml glass vials, and stoppered with cotton balls. At the start of each experiment, vials were inverted over the central arena, allowing the test insects to be deposited within the central arena.

Position of all insects were recorded 1 h later as on or touching the control paper, on or touching the experimental paper, or neither. Arenas were thoroughly washed with distilled water and dried after each test. No significant ($P>0.05$) differences between insect response to the two bioassay designs were found.

Bioassays 1-6. Response to extracts of frass.

The results of the preliminary experiments suggested that extracts of frass be tested for attractivity to earwigs to eliminate the possibility that frass was attractive solely because it was a food source. Frass (0.602 g) was extracted with 2.0 ml methylene chloride. The extract was divided into approximately 4 equal aliquots, applied to strips of chromatographic paper, and allowed to air dry. Four replicates of the assay were then run.

A more concentrated extract was prepared for a second bioassay. This time, 2.27 g frass was extracted with 2.0 ml methylene chloride. The resulting extract was used for four replicates of 0.5 ml each.

Bioassays 3 through 6 utilized 2.0-2.5 g frass. In Bioassay 3, frass was macerated with a mortar and pestle for about 5 min before dividing into approximately two equal portions and extracting each portion with 2.0 ml methylene chloride. The tubes were then centrifuged for about 2 min at 70 rpm, and the supernatant collected into fresh tubes. Extracts were concentrated to approximately 1.0 ml in each tube under a gentle stream of dry nitrogen under a hood. The extracts were used for eight replicates (0.125 g/replicate). In the fourth bioassay,

frass was extracted with 2.0 ml distilled water and Bioassay 5 used frass extracted with 2.0 ml acetone. For Bioassay 6, frass was extracted with 1.0 ml methylene chloride and, in a separate procedure, with 1.0 ml of distilled water. After concentration, the resulting aqueous extracts were applied separately to papers, allowing the first application of extract to dry before applying the second. Eight replicates of these bioassays were performed.

Bioassays 7-9. Response to natural extracts.

For Bioassay 7, methylene chloride extracts of male cuticle (described previously) were used to determine attractivity. Female cuticle extracts were also evaluated in a separate series of tests. Ten replicates for each sex were performed with the extracts.

Methylene chloride extracts of leg washings were tested in Bioassay 8. Separate analyses of nymph and adult legs were performed. Ten replicates for each age class were performed with the replicates.

The results of Bioassay 8 suggested Bioassay 9 of potential leg "trails", residual compounds which might be left on the substrate by the tibial glands. Sauphanor (1992) suggested that secretions from these glands were attractive. Accordingly, twenty subjects were confined to four 0.5-l jars lined with Whatman filter paper for 24 h, after which papers were removed and extracted and papers not spotted with excreta were extracted in 1.0 ml methylene chloride. Eight replicates were performed with the extracts.

Bioassay 10. Response to synthetic chemicals identified as components of frass and/or cuticle.

Some of the hydrocarbons and fatty acids determined by the GC analysis to be in the frass and/or cuticle were tested for attractivity. Before performing these bioassays, it was not known which, if any, compounds would elicit a response, and how much would be needed. Where possible, as many different concentrations and combinations of chemicals were tested. Ten to twenty replicates of each bioassay were performed, depending on availability of chemicals.

The following compounds were tested:

- 1) Oleic acid (200 μ l of 1.0 M, 200 μ l of 0.1 M, 400 μ l of 0.1 M)
- 2) Linoleic acid (200 μ l of 1.0 M)
- 3) Stearic acid (200 μ l of 1.0 M, 200 μ l of 0.75 M, 200 μ l of 0.5 M, 200 μ l of 0.1 M)
- 4) Palmitic acid (200 μ l of 1.0 M, 200 μ l of 0.75 M, 200 μ l of 0.5 M, 200 μ l of 0.1 M)
- 5) Linoleic acid (200 μ l of 0.1 M) combined with oleic acid (200 μ l of 0.1 M)
- 6) Tricosane (200 μ l of 0.1 M, 400 μ l of 0.1 M)
- 7) Pentacosane (200 μ l of 0.1 M, 400 μ l of 0.1 M)
- 8) Heptacosane (200 μ l of 0.01 M)

9) Pentacosane (100 μ l of 0.1 M) combined with heptacosane (100 μ l of 0.01 M)

Bioassay 11. Response to synthetic quinone.

Since quinones were identified in the defensive secretions, their aggregating (or repelling) potential was also tested. In some insects (Nault and Phelan, 1984), defensive secretions may function secondarily as alarm pheromones to affect the behavior of conspecifics. Ethylquinone was not available for use in testing, but methylquinone was tested at two concentrations and dosages:

1) 0.1 M (200 μ l and 400 μ l)

2) 0.01 M (200 μ l and 400 μ l)

Ten to fifteen replicates of each bioassay were performed.

Statistics

Attractivity of compounds was evaluated by the two sample Student's t-test (Sokal and Rohlf, 1981). Level of attractivity was determined by using the aggregation index (A.I.), in which a value of 0 represents random choice of papers, negative values suggest a tendency toward dispersal, and positive values a tendency toward attraction/aggregation. A.I. is given by $E-C/E+C$, where E=number of insects in the experimental shelter, and C=number of insects in the control shelter (Roth and Cohen, 1973). Regression analysis was used to evaluate the linearity of

relationships (Sokal and Rohlf, 1981). All statistics were computed using the Minitab Release 10 for Windows computer program (Minitab, Inc., 1994).

Results

Preliminary Aggregation Experiments

Some of the insects were attracted to the conditioned papers (Experiments 1 and 2), but tests using a greater sample of test earwigs (Experiment 3) revealed no significant differences between control and conditioned filter papers (Table 2.2). Four of the replicates in Experiment 4 used refrigerated frass which had not been allowed to warm to room temperature; the results from these replicates (no significant ($P > 0.05$) difference between attraction to control and experimental papers) were different from the other 15 replicates, and were not, therefore, included in the analysis. Earwigs were significantly ($P = 0.014$) attracted to papers with room temperature frass (Table 2.2). No significant ($P > 0.05$) differences were found between the response to enclosed earwig corpses versus control cages (Experiment 5, Table 2.2). No significant ($P > 0.05$) differences were found between number of replicates containing two insects in one shelter and number of replicates containing insects in different shelters (Experiment 6, Table 2.2). Experiment 7 was first analyzed for the number of insects which selected the experimental shelter (insect #1), and then number of replicates in which insect #1 and insect #2 were in the

Table 2.2. Response of *F. auricularia* to experimental conditions in preliminary aggregation experiments, in which subjects had a choice between treated (experimental) and untreated (control) areas. Significant ($P < 0.05$) response indicates attraction to the experimental condition.

Experiment	N/replicate	Replicates	Response (P) ^a
1. Conditioned filter paper disk	6	1	NS
2. Conditioned filter paper strip	1	7	NS
3. Conditioned filter paper strip	20	7	NS
4. Frass	20	15	0.014
5. Earwig corpses	20	10	NS
6. Earwigs	2	20	NS
7. Earwigs + conditioned filter paper strips	2	30	
after 1h			<0.025
after 2h			<0.001

^a Student's two-sample t-test (Sokal and Rohlf, 1981)

same shelter. After 1 h, 22 out of 30 insects selected the experimental shelter ($\chi^2=6.5$, $df=1$, $P<0.025$), 7 selected the control shelter, and 1 escaped from its arena. After introduction of the second insect to each arena, and elapse of another h, only 18 of 30 replicates contained insects together in the same shelters, which was not significantly ($P>0.05$) different from the number of replicates in which each insect was in a different shelter. However, 46 of 60 insects were in an experimental arena after 2 h ($\chi^2=17.1$, $df=1$, $P<0.001$), indicating that the experimental paper was significantly more attractive than the control paper. This experiment did not provide any evidence that the insects themselves were attractive (Table 2.2).

Experiment 8. Attraction to new vs. old traps.

Results indicated that earwigs preferred resting in previously occupied traps over those which had not been used by earwigs before (Figure 2.1.). Although attractivity to new traps increased on Day 6 (N=2 replicates), in general, old traps continued to be more attractive for the length of the experiment.

Chemical Analyses of Extracts

Cuticles

A mixture of normal, monomethyl, and dimethylalkanes was identified by GC-MS (Table 2.3, Figures 2.2, 2.3, and 2.4). The hydrocarbons identified comprised >88% of the detectable volatiles. The many unidentified minor components (>30 at

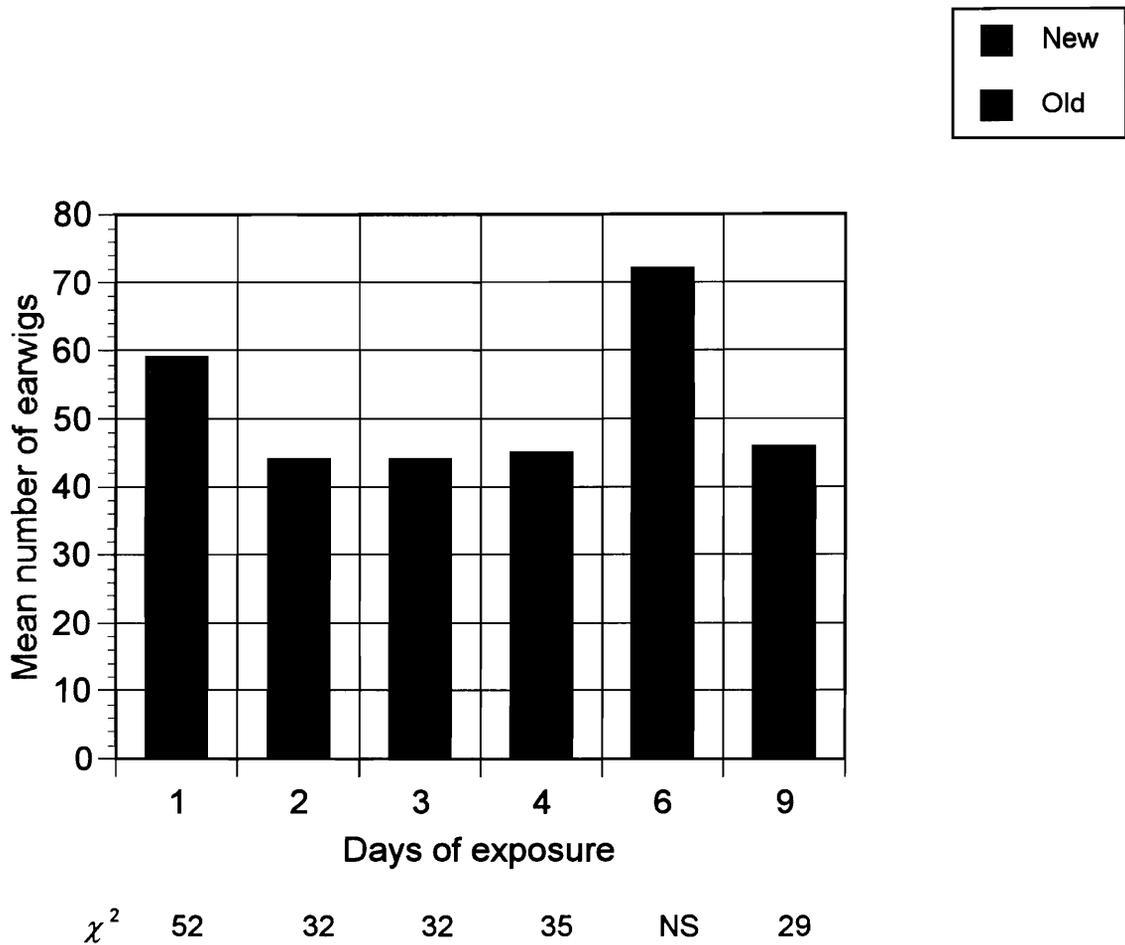
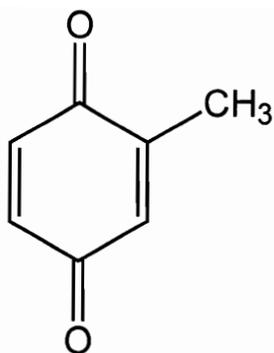


Figure 2.1. Distribution of *F. auricularia* in two adjacent traps (N=6 replicates) in Blacksburg, Virginia, in 1990. One trap had been previously exposed to earwigs (old), and one had not (new). Significant ($P < 0.05$) χ^2 values (df=1) are given. Except for Day 6, $P < 0.001$ for all sampling days.

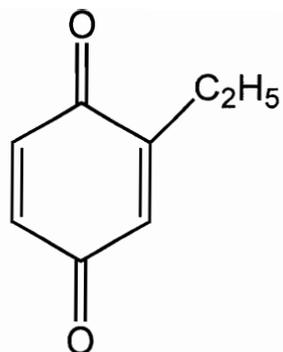
Table 2.3. Saturated cuticular hydrocarbons of *F. auricularia*.

Peak	Percent	Compound	Diagnostic ions	Mol. mass
1	1.0	Tricosane		324
2	5.8	Pentacosane		352
3	1.3	13-MeC ₂₅	196/197	366
7	5.6	Heptacosane		380
8	14.7	9-, 11-, 13-MeC ₂₇	140/141, 280/281; 168/169, 252/253; 196/197, 224/225	394
13	0.5	Nonacosane		408
14	19.1	9-, 11-, 13-, 15-MeC ₂₉	140/141, 308/309; 168/169, 280/281; 196/197, 252/253; 224/225	422
15	5.5	<i>x, y</i> -DiMeC ₂₉		436
16	5.5	9, 21-DiMeC ₂₉	140/141, 323	436
17	16.6	9-, 11-, 13-, 15-MeC ₃₁	140/141, 336/337; 168/169, 308/309; 196/197, 280/281; 224/225, 252/253	450
18	5.5	<i>x, y</i> -DiMeC ₃₁		464
19	5.5	9, 23-DiMeC ₃₁	140/141, 351	464
20	1.2	11-MeC ₃₃	168/169, 336/337	478

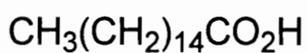
Total 87.8% of detectable components



2-methyl-1,4-benzoquinone



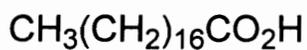
2-ethyl-1,4-benzoquinone



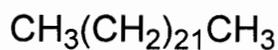
Palmitic acid



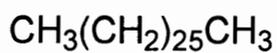
Oleic acid



Stearic acid



Tricosane



Heptacosane

Figure 2.2 Structural formulae for selected chemical components of *F. auricularia* frass, defensive secretions, or cuticle.

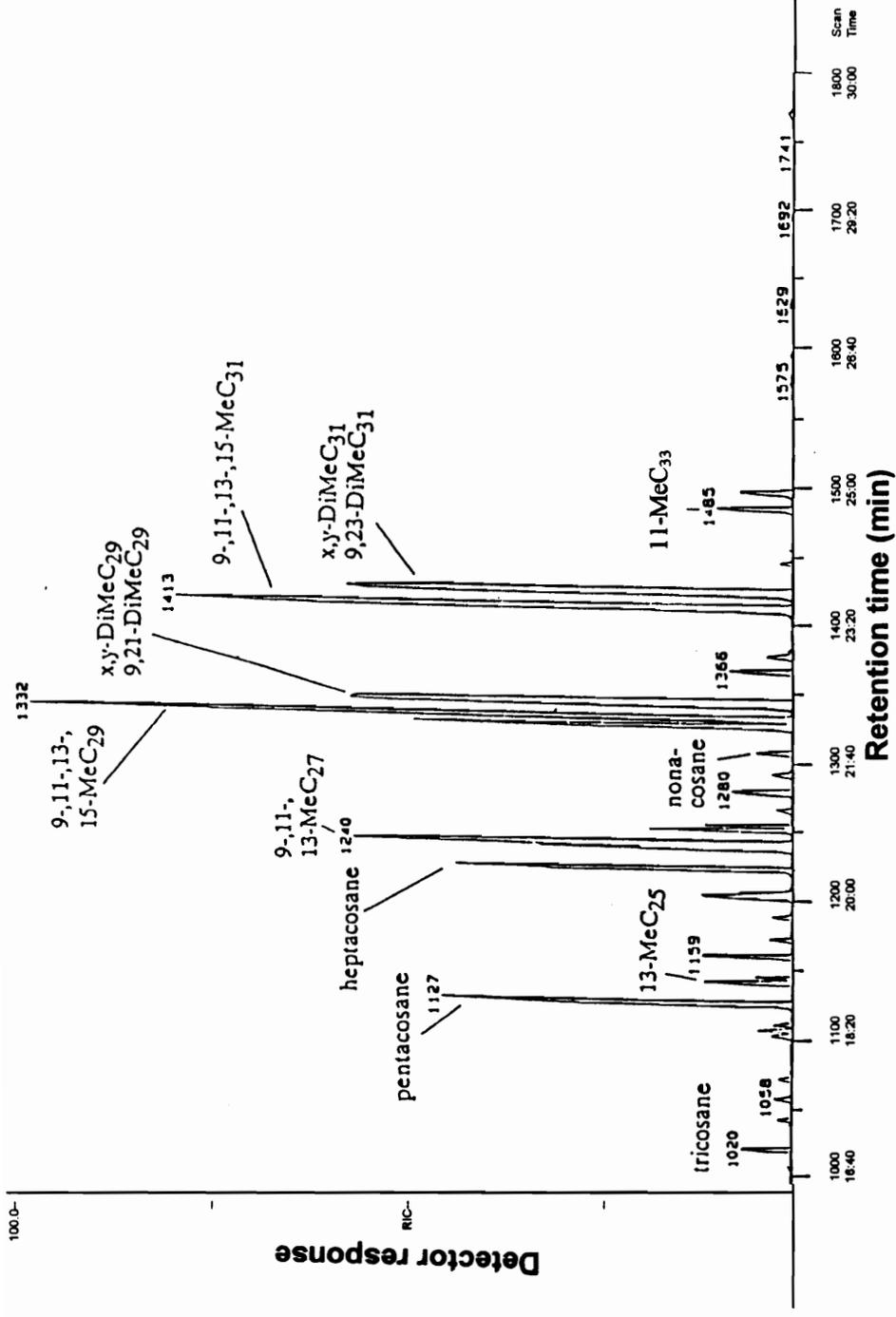


Figure 2.3. Gas chromatogram of methylene chloride washes of female *F. auricularia* cuticle, with identified peaks.

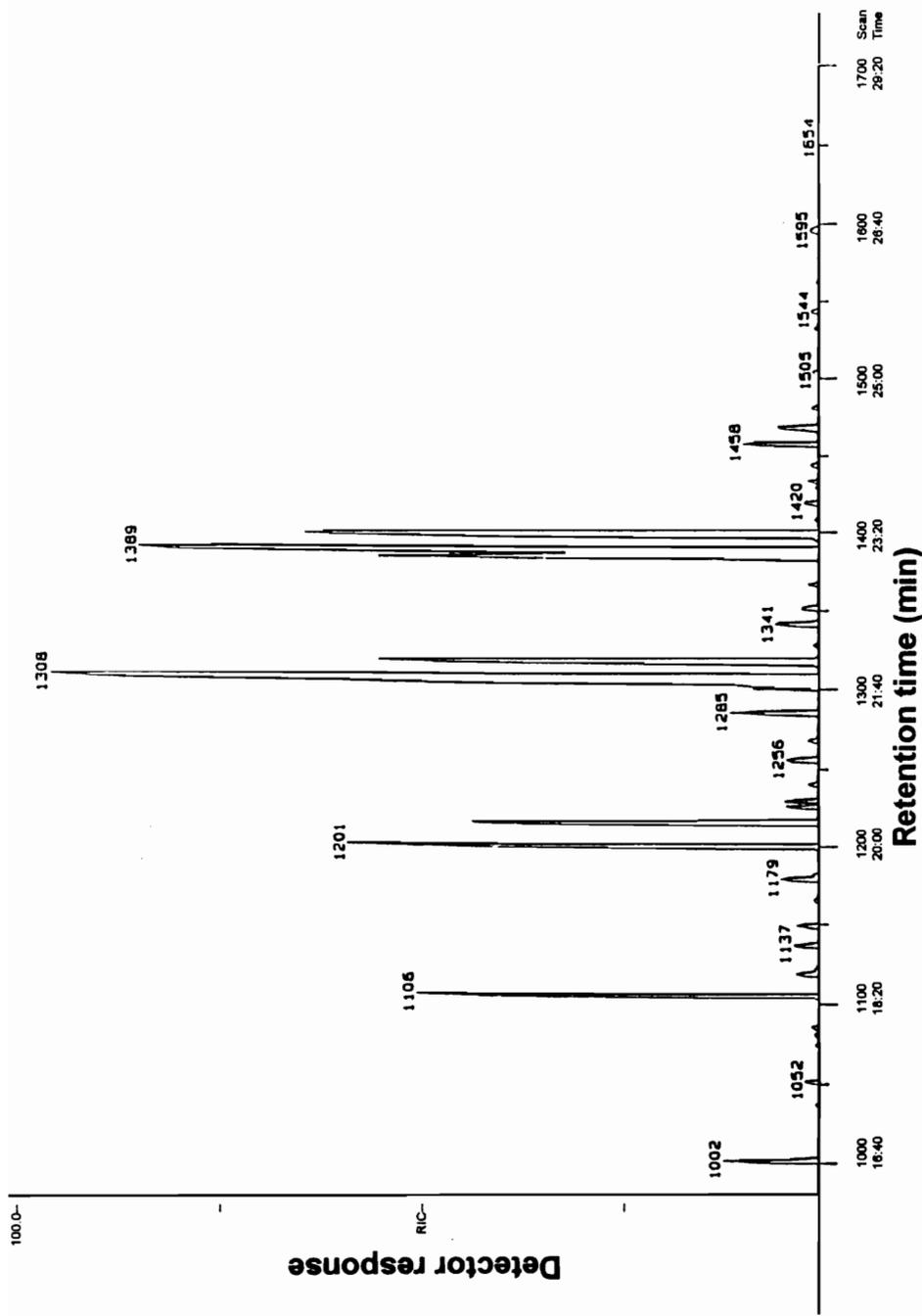


Figure 2.4. Gas chromatogram of methylene chloride washes of male *F. auricularia* cuticle.

less than 1% each) that were detected were present in both male and female washings.

Frass

Mean frass produced/day/male was 1.238 mg (N=10, sd=0.14mg), and mean frass produced/day/female was 1.336 mg (N=10, sd=0.38mg); frass production did not differ significantly ($P>0.05$) by sex.

GC/MS analysis of frass from an exclusive cat food diet revealed the presence of a set of common fatty acids (Table 2.4, Figure 2.5) along with the same pattern of cuticular hydrocarbons shown in Table 2.3. Not all peaks could be identified. In particular, peak no. 1303 (Figure 2.5) was very large, but the chemical it represented could not be determined from the mass spectra. Fatty acids comprised approximately 36% of the chemical constituents, with 57% hydrocarbons, and 7% other compounds. Individual fatty acid percentages were calculated from the GC analysis by measuring each peak, summing together, and computing the percentage of the total represented by each fatty acid. Insect equivalents (IE) were then calculated using these percentages and mean frass/day of 1.3 mg (Table 2.3).

Legs

Analysis of leg extracts revealed the same fatty acids found in the frass (Figure 2.6) except that two, with mass spectra very similar to that of linoleic acid and oleic acid, predominated in the mixture. The usual cuticular hydrocarbons were also detected, along with cholesterol (Table 2.3). In addition, two minor (<5% each)

Table 2.4. Fatty acid content in *F. auricularia* frass.

Peak No	Percent	Acid	Mol. Wt.	IE ^a /d (mg)
2	1.8	Myristic	228	0.008
4	17.9	Palmitic	256	0.083
5	1.0	Heptadecanoic	270	0.005
6	15.2	Linoleic	280	0.071
7	44.6	Oleic	282	0.207
8	18.8	Stearic	284	0.087

^a IE=Insect Equivalent

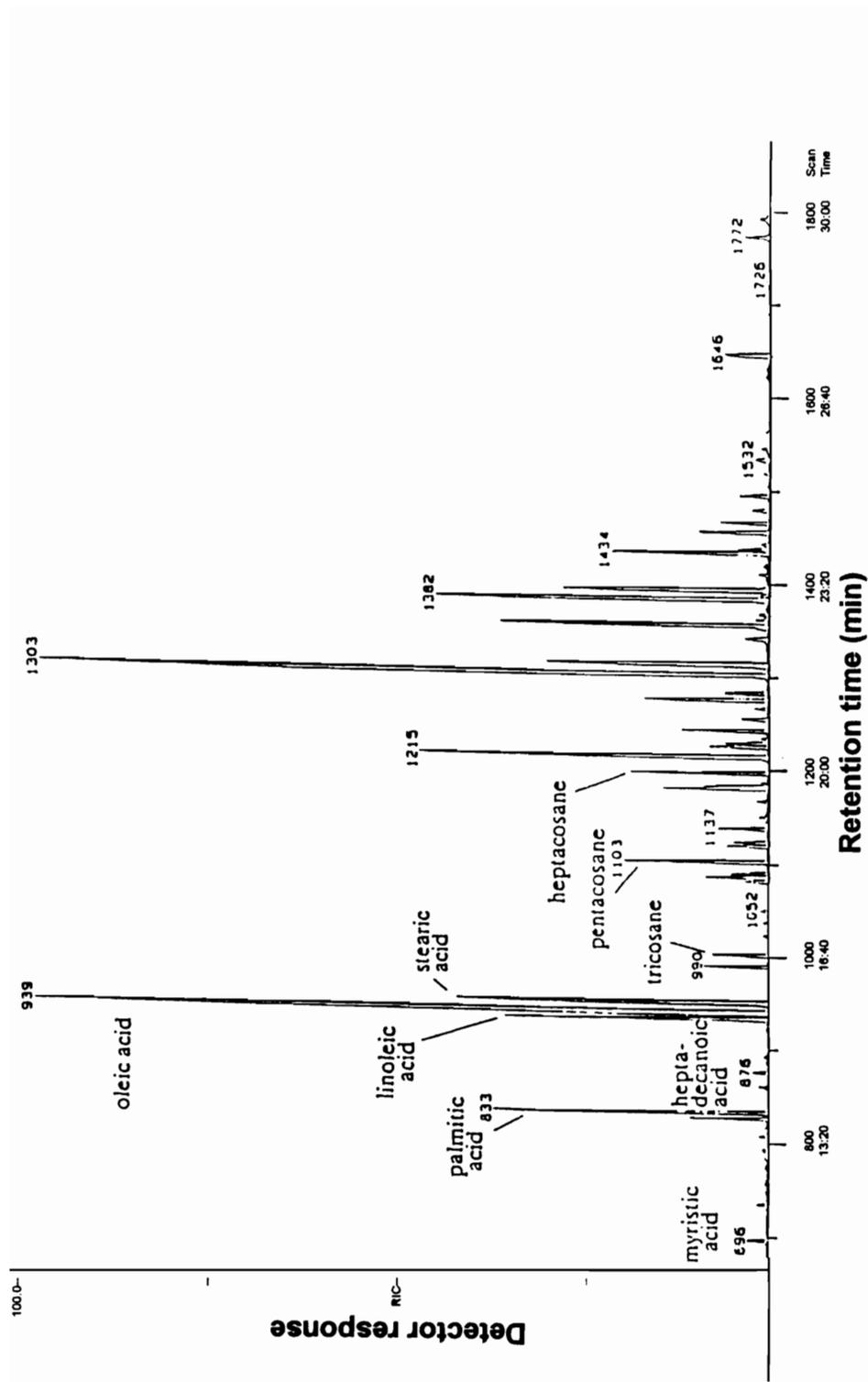


Figure 2.5. Gas chromatogram of methylene chloride washes of *F. auricularia* frass, with identified peaks.

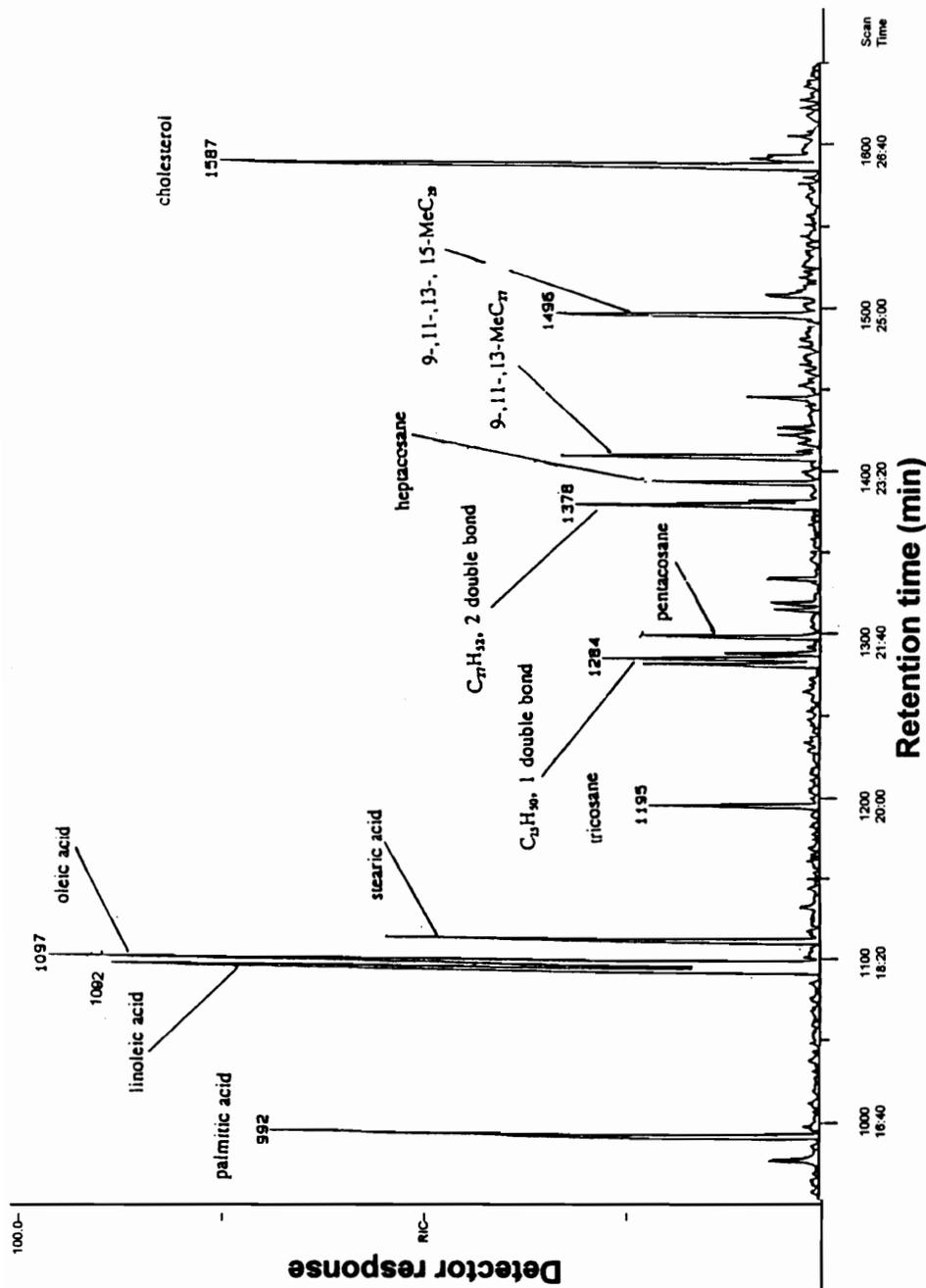


Figure 2.6. Gas chromatogram of methylene chloride washes of *F. auricularia* nymph legs, with identified peaks.

components were detected having mass spectra ($m/z=348$ (M+), 96, 95, 82, 81, 67 (100), 57, and 55; 376 (M+), 110, 96, 95, 82, 81, 67 (100), 57, and 55 indicating C_{25:2} and C_{27:2} alkadienes. These components eluted before the normal alkanes in this mixture.

Defensive exudate

GC-MS analysis indicated the presence of 2-methyl- and 2-ethyl-1,4-benzoquinone. GC analysis consistently showed that the ethylquinone predominated in the defensive chemistry, with about 0.05 $\mu\text{g}/\mu\text{l}$ per sample, or 0.005 $\mu\text{g}/\mu\text{l}$ per animal, and about 0.025 $\mu\text{g}/\mu\text{l}$ methylquinone per sample or 0.0025 $\mu\text{g}/\mu\text{l}$ per animal. There was no discernible sexual dimorphism in quantity of quinones produced.

Behavioral Response to Extracts

Natural extracts

Behavioral bioassays of frass extracts showed that frass is clearly attractive to earwigs, regardless of the solvent used for the extraction (Table 2.5). Initial assays with smaller quantities of frass (e.g., Bioassay 1) did not yield significant ($P>0.05$) results, probably because the threshold level of attractivity had not been reached. Increasing frass quantity and maceration of the frass prior to extraction improved results.

Table 2.5. Aggregation bioassays of natural extracts of *F. auricularia*. Except for frass, all extracts were made with methylene chloride.

Extract	Replicates	Response (P) ^a	A.I. ^b
Frass			
Distilled H ₂ O	8	0.0210	0.375
Acetone	8	0.0030	0.567
CH ₂ Cl ₂	8	0.0001	0.732
Distilled H ₂ O + CH ₂ Cl ₂	8	0.0001	0.825
Cuticle washes			
Male	15	0.034	0.202
Female	15	NS	-0.134
Leg washes			
Nymphs	10	NS	0.034
Adults	10	-0.004	-0.235
Leg "trails"			
	8	NS	-0.133

^a Student's two-sample t-test (Sokal and Rohlf, 1981)

^b A.I. = (Aggregation Index) = E-C/E+C, where E = # insects on experimental paper, C = # insects on control paper (Roth and Cohen, 1973).

Response to frass produced exclusively by nymphs, females or males was not specifically evaluated. However, frass, regardless of origin, appeared to aggregate nymphs and adults of both sexes equally.

Extracts of female cuticle were not attractive, but male extracts were ($P=0.034$) (Table 2.5). Bioassays of nymph leg extract were not significantly ($P>0.05$) attractive. On the contrary, bioassays of adult leg extract were significantly ($P=0.004$) repellent (Table 2.5). Bioassays of leg "trails" extracts were not significantly ($P>0.05$) attractive and were, in fact, slightly, but not significantly ($P>0.05$), repellent (Table 2.5).

Synthetic compounds

Fatty acids

Fatty acids were assayed at concentrations ranging from 27.3 to 788.7 insect equivalents (IE)/day (Table 2.6). IE was determined by dividing the amount tested by the amount excreted in the frass per day (see Table 2.4).

Linoleic and oleic acids were not attractive at any concentration tested. Stearic and palmitic acids were significantly ($P<0.05$) attractive only at higher concentrations, at about 600 insect equivalents (IE)/day. Oleic and linoleic acids, assayed alone and together, were slightly repellent, although this was not significant ($P>0.05$) in any case. In general, aggregation index (A.I.) increased or decreased with increasing IE, but the relationship was not significantly ($P>0.05$) linear (Table 2.6).

Table 2.6. Aggregation response of *F. auricularia* to bioassays of synthetic fatty acids.

Compound	Replicates (20 insects)	Concentration (M)	Amount Tested (μ l)	IE ^a (mg/d)	Response (P) ^b	A.I. ^c
Oleic acid	15	0.1	200	27.3	NS	-0.020
	15	0.1	400	54.6	NS	-0.116
	15	1.0	200	272.5	NS	-0.219
Linoleic acid	15	1.0	200	788.7	NS	-0.148
Linoleic acid and oleic acid	10	1.0	200	788.7	NS	-0.203
		0.1	200	27.3	NS	
Stearic acid	15	0.1	200	65.5	NS	0.113
	15	0.5	200	326.4	NS	0.158
	15	0.75	200	489.6	0.003	0.215
	15	1.0	200	652.8	0.001	0.271
Palmitic acid	15	0.1	200	61.7	NS	0.212
	20	0.5	200	308.4	NS	0.116
	15	0.75	200	462.7	NS	0.116
	15	1.0	200	616.9	0.01	0.270

^a IE = Insect Equivalent

^b Student's two-sample t-test (Sokal and Rohlf, 1981)

^c A.I. = (Aggregation Index) = $E-C/E+C$, where E = # insects on experimental paper,
C = # insects on control paper (Roth and Cohen, 1973)

Hydrocarbons

None of the hydrocarbons tested produced a significant ($P>0.05$) response. Tricosane was weakly, but not significantly ($P>0.05$), repellent. Bioassays of pentacosane and heptacosane, applied singly and together, were not significant ($P>0.05$). As with the fatty acids, A.I. increased or decreased with increasing IE (Table 2.7).

Quinone

2-Methyl-1,4-benzoquinone was significantly ($P<0.05$) repellent at concentrations of 0.01 M and 0.10 M, except for 400 μ l at 0.01 M. Repellency also increased with increasing dosage at the 0.10 M concentration (Table 2.8).

Discussion

The preliminary aggregation experiments were difficult to evaluate in that nonsignificant results may have been due to unrefined experimental designs. However, they did demonstrate that frass promoted aggregation. Experiments 3 and 7 tested response to filter paper exposed to earwigs for 24–48 h; the results of Experiment 7 were significant ($P<0.05$), but those of Experiment 3 were not. The difference is probably due to the greater number of replicates of Experiment 7 (30) versus Experiment 3 (7) (Table 2.2) But the fact that earwigs were attracted to conditioned papers did not explain whether earwigs were attracted to compounds within the spots of excreta, or other compounds deposited on the papers. Since

Table 2.7. Aggregation response of *F. auricularia* to synthetic hydrocarbons.

Compound	Replicates (20 insects)	Conc. (M)	Amount Tested (μ l)	Response (P) ^a	A.I. ^b
Tricosane	15	0.10	200	NS	-0.002
	15	0.10	400	NS	-0.212
Pentacosane	10	0.10	200	NS	0.007
	10	0.10	400	NS	0.061
Heptacosane	10	0.01	200	NS	0.164
Pentacosane + Heptacosane	10	0.10 0.01	100 100	NS	0.046

^a Student's two-sample t-test (Sokal and Rohlf, 1981)

^b A.I. = (Aggregation Index) = $E-C/E+C$, where E = # insects on experimental paper, C = # insects on control paper (Roth and Cohen, 1973).

Table 2.8. Aggregation response of *F. auricularia* to bioassays of synthetic 2-methyl-1,4-benzoquinone.

Replicates (20 insects)	Conc. (M)	Amount tested (μ l)	Response (P) ^a	A.I. ^b
15	0.01	200	0.018	-0.261
10	0.01	400	NS	-0.217
15	0.10	200	0.001	-0.553
10	0.10	400	0.001	-0.731

^a Student's two-sample t-test (Sokal and Rohlf, 1981)

^b A.I. = (Aggregation Index) = $E-C/E+C$, where E = # insects on experimental paper, C = # insects on control paper (Roth and Cohen, 1973).

frass was attractive, it was also possible that aggregation was caused both by the spots of excreta and by other compounds left on the papers by the insects.

Experiment 8 demonstrated that earwigs prefer old to new traps for at least several days. By Day 6, new traps were about equally as attractive as old traps, but 3 days later, old traps were significantly ($P < 0.05$) more attractive again; the reason for this discrepancy is unknown. Extending the trial length in future experiments might reveal equal attractivity after a certain period of exposure time. The mechanism for the results of this experiment appears to be that, given a choice between a trap impregnated with pheromones or attractants, and one without, most earwigs choose the impregnated trap. New traps may become progressively more attractive because a few insects enter the new trap on the first day, and in resting there, may leave aggregants, either in the form of frass or other compounds, on the grooved surfaces of the traps. The deposition of these materials likely attracts more insects to the new traps, and as more insects are recruited, they leave more and more chemical attractants. However, these results did not resolve the question of the origin of the aggregants: was the attraction caused by compounds in the frass, or by other compounds which might be present on the bodies of the insects?

Bioassays were more helpful in elucidating the source of the pheromone. Frass-extract bioassays clearly showed that earwigs are attracted to frass. Since the A.I. obtained with some solvents was higher than with others, it is possible that extraction with those solvents either removed a greater quantity of the aggregating

compound, or additional compounds promoting aggregation. The solvents, by themselves, showed no differential attractivity.

Quinones were significantly ($P < 0.05$) repellent, rather than promoting aggregation, and repellency increased with increasing concentration. This study indicated a much lower quantity of methylquinone secreted per animal— $0.0025 \mu\text{g}/\mu\text{l}$ of methylquinone and $0.005 \mu\text{g}/\mu\text{l}$ ethylquinone/ animal— than did Schildknecht and Weis' (1960) estimate of $20 \mu\text{g}/\text{animal}$. Further work is necessary to reconcile these differences. The analytical chemistry used in this study was considerably more sophisticated than that used by Schildknecht and Weis (1960). However, the true quantity of quinones secreted by *F. auricularia* may be underestimated because of several factors. First, the exudate rapidly coagulated following secretion, preventing total collection. Second, nothing is known about the time required for synthesis of the compounds or "refueling" of secretions after discharge in this species. It is possible that the glands are not completely depleted after one discharge, but it was impossible to know which insects had recently discharged before testing. Third, the quantity of defensive secretion stored per animal probably varies from individual to individual, and factors such as age, gender and reproductive condition have been shown to affect the amount of exudate produced in some insect species (Blum, 1985). Future attempts to quantitate quinones should involve collection directly from the glands.

Aggregation bioassays with cuticular lipids suggested that the aggregation pheromone originates on the male cuticle. The location of the male cuticle for pheromones is not unusual (Schaner and Jackson, 1992). Since earwigs are in close contact with each other and because they regularly consume carcasses and shed exuviae, it is not surprising that frass also promotes gregariousness. Frass mediates aggregation in several insects, including *Blaberus discoidalis*, *Acheta domestica*, *Blattella germanica* (Ishii, 1970; McFarlane and Alli, 1985) and *Phyllocnistis callosus* (Barnes and Capatos, 1989). The same hydrocarbon pattern observed in the cuticle was also seen in frass. Furthermore, if the pheromone originates within the frass rather than on the male cuticle, and the male cuticle only acquires activity through contact with the frass, the female cuticular washings should have shown activity as well, but they did not. The hydrocarbons identified in *F. auricularia* do not seem to play a role in aggregation, since only the cuticular washings of males are attractive. The aggregation pheromone appears to be a minor component of the hydrocarbon profile since male and female cuticular profiles are identical to within a few percent (and nearly 88% of the total hydrocarbons have been identified). Some other insects produce a very small quantity of pheromone compared to total volatiles emitted, such as *Ips pini*, whose primary aggregation compound lanierone constitutes only 0.2% of the amount of ipsdienol emitted (Teale et al., 1991). Fatty acids have been shown to aggregate other insects (McFarlane et al., 1983; Fuchs et al., 1985), but do not appear to be responsible for gregarious

behavior in earwigs since attractive concentrations were greater than those found in frass and, therefore, probably indicate attraction to a food source rather than presence of a pheromone.

Male and female *F. auricularia* produce a nearly identical mixture of cuticular hydrocarbons, which could serve as a taxonomic character (Grunshaw et al., 1990) in future research. It is noteworthy that mono- and dimethylalkanes predominate in this mixture, and that the branching is at odd-numbered carbons and at position C-9 or higher. A review of the literature reveals that this methyl branching pattern is not unusual (Brown et al., 1990). On the other hand, *F. auricularia* are typically found in dark, humid areas, so that cuticular hydrocarbons that form efficient waterproofing layers would not be as essential as in other insects (Lockey, 1976; Howard and Blomquist, 1982). *F. auricularia* are notoriously difficult to grasp, and it may be that their cuticular hydrocarbons serve a defensive function, imparting a characteristic slipperiness to this insect. In addition, since quinones appear to repel *F. auricularia*, these hydrocarbons may enhance the dissolution of the quinones on the surface of the insect's cuticle, increasing the efficacy of the insect's defense, in a manner similar to the tenebrionid beetle *Argoporis alutacea*, which improves its defense by spreading a quinone exudate over its body and that of its attacker (Tschinkel, 1972).

It is not surprising that quinones, produced as defense chemicals to ward off interspecific predators, also apparently act as an intraspecific repellent in earwigs. Whether these compounds work in the same manner in natural populations is

unknown, but if so, would represent an energetically efficient system. Two compounds, synthesized de novo (Schildknecht and Weis, 1960) could be used not only to deter attackers but, in the case of threats involving an aggregation of earwigs and, therefore, secreted by a large number of earwigs, would also function as an alarm pheromone to other earwigs in the periphery of the group or in the area, resulting in dispersal from the threatened area. Defensive secretions also act as alarm pheromones in some other insects, such as membracids, aphids, and cimicids (Nault and Phelan, 1984), which, like earwigs, are frequently gregarious.

Sauphanor (1992) recently suggested that compounds contained within the tibial glands (Brousse-Gaury, 1983) of *F. auricularia* are responsible for its gregarious behavior on the basis that extracts of amputated legs and of filter paper "trails" caused aggregation. The results of the present study, however, showed that neither leg extracts nor leg "trails" aggregated *F. auricularia*-- in fact, extracts of adult legs were repellent, and indeed, oleic acid has been shown to be a generalized repellent (Howard et al., 1982). A probable reason for the discrepancy in the results of the test of leg "trails" was that in our study, we removed areas of paper spotted with excreta before extracting filter papers; since frass is attractive, papers with spots of excreta might bias the results of any test for aggregating ability of possible compounds deposited by the legs. Sauphanor (1992) tested responses of nymphs, whereas we evaluated adult response, but it seems unlikely that only nymphs would be sensitive to the pheromone given that gregarious behavior is so pronounced in

earwigs both in the field and in laboratory colonies, regardless of maturity. Also in contrast to our results, frass extracts were not attractive in the Sauphanor (1992) study. A factor potentially leading to this difference is freshness of the frass: we observed that frass must be fresh in order to aggregate, which likely indicates that aggregants in frass are volatile.

Eventual identification and synthesis of the aggregation pheromone may prove useful in control of *F. auricularia*, as evidenced by the high degree of attractiveness of traps previously inhabited by conspecifics. Augmentation of this natural attractiveness could be accomplished by development of traps impregnated with the pheromone.

CHAPTER 3: BEHAVIORAL REPERTOIRE AND SOCIAL INTERACTIONS

Introduction

Preliminary observations of *F. auricularia* indicate that typical insect behaviors such as feeding, grooming, resting, and locomotion exist, as well as some behaviors involving interactions with conspecifics, such as contact, aggression, and allogrooming. Yet the insect's behavioral repertoire has not previously been described. The description and quantification of individual behaviors into an activity time budget allow an insight into the significance of individual behaviors, as well as uncovering the pattern of behaviors best suited for the insect in its environment (Joern et al., 1986). Time is finite, and animals typically divide it into activities that improve fitness (Sullivan, 1990). Interactions between conspecifics may also give some valuable information on social organization of the species.

In addition to a detailed behavioral repertoire, it is important to assess the effects of several variables on the behavior of the earwig. *F. auricularia* has been described as a nocturnal insect (e.g., Crumb et al., 1941), but no detailed study has been made of the effect of time of day on its activity patterns. If the earwig is indeed nocturnal, adults and nymphs should dedicate more time to activities such as feeding, moving and grooming at night than during the day, and less time to resting.

Gender may also influence behavioral patterns, even in nonreproductive periods. Female insects, especially those providing brood care, require large amounts of nutrition prior to oviposition (Thornhill and Alcock, 1983). Female earwigs reportedly

overwinter for some months prior to oviposition, and subsequently care for nymphs until the second instar, a large majority of the time without feeding (Lamb and Wellington, 1974). If true, then it would be reasonable for females to feed more than males. Juvenile insects also require large amounts of food in order to prepare for the metabolically costly processes of growth and molting (Rust and Appel, 1985). Therefore, it could be predicted that nymphs spend more time feeding than adult males, and possibly as much time as adult females. Since little is known about reproductive behavior, the potential effect of partner gender on behavior would be valuable, especially since it is unknown when *F. auricularia* becomes reproductively active. If male earwigs initiate courtship, as in many insects (Thornhill and Alcock, 1983), males might be expected to contact females more than males. If intrasexual selection is important in this species, males would also probably be more aggressive when paired with males than with females. Adults are dominant over juveniles in many taxa (Wilson, 1975). If this pattern is consistent in earwigs, it is predicted that adults feed more and are more aggressive when paired with juveniles than with adults. Conversely, nymphs should feed less with adults, and spend more time engaged in other behaviors such as locomotion and resting. Nymphs should also be less aggressive toward adult partners, and might be expected to spend more time in allogrooming when paired with adults. Allogrooming, an activity in which one insect cleans another, was first noted in *F. auricularia* by Lamb (1975) with regard to aggregations of nymphs, but he made no further attempts to describe or quantify the

behavior. Allogrooming is common in the social insects, and may have several purposes, including hygiene, such as removal of ectoparasitic mites from nestmates by bees (Buechler et al., 1992; Bozic and Valentinic, 1995) and communication and expression of social position, wherein dominant individuals typically receive more grooming.

Since group-living is the norm for some period of the life of the European earwig, it is also important to investigate the effect of increasing group size on behavior, as well as to characterize any distinctive features of group behavior. Aggression may function to control space, and to gain access to resources and mates (Wilson, 1975). With increased group density, animals come into greater proximity, the encounter rate increases exponentially, and the frequency of aggressive interactions typically increases at the same rate (Wilson, 1975). Sociobiology predicts that the rate of aggression increases with crowding and with group population density (E.O. Wilson, 1971; Marler, 1976). Aggression does increase with increasing group density in several cockroach species (Gautier et al., 1988; Clark and Moore, 1994). High levels of aggression may be responsible for instances of cannibalism in some insects, such as *Heliothis zea* larvae (Dial and Adler, 1990). It would be expected that aggression levels would increase with increasing nymphal density.

Materials and Methods

Videotaping of Earwig Dyads and Groups

Earwig behaviors and interactions were recorded by videotaping pairs of insects. Since there were no prior studies on behavioral interactions of earwigs, these pairs were experimentally manipulated by combining earwigs of varying age and sex, and recording dyads in the daytime and evening. Nymphs cannot be sexed (Crumb et al., 1941), so they represent only an age variable.

Insects were removed from the laboratory stocks described in Chapter 2, and individually sequestered for 1 h in either 3.5 cm-diameter plastic Petri dishes, or in 20.0 ml glass vials stoppered with cotton wool. Immediately before videotaping, insects were taken from the holding receptacles and placed in a 9.0 cm-diameter plastic Petri dish with two small pieces of carrot. To improve photographic contrast, the dish was placed on a white sheet of paper. Evening videotapes were photographed in a dark room, lit only by a lamp with a 25 watt red light bulb.

The following experimental dyads were recorded:

1. Male-male, evening
2. Male-female, evening
3. Male-nymph, evening
4. Male-nymph, day
5. Female-female, evening
6. Female-nymph, evening

7. Female-nymph, day
8. Nymph-nymph, day
9. Nymph-nymph, evening
10. Nymphs in group sizes of 2, 3, 5, and 7; evening

Male-female reproductive behavior was also recorded, and is the subject of Chapt. 4.

For tests involving groups of nymphs, insects were individually marked with Liquid Paper, an opaque typewriting correction fluid. Lamb and Wellington (1974) used plastic paint for marking earwigs, but found the result unsatisfactory since the paint tended to flake off easily due to the earwig's smooth cuticle, and because of frequent grooming by the insects. In this study, Liquid Paper adhered well to the cuticle, frequently remaining on the body until molting, but did not impede mobility. In addition, this product dried very quickly, within 1 min. Because grouped behavioral trials were conducted in the dark under red light, different colors could not be discerned. Therefore, individual nymphs were marked with varying numbers and patterns of dots for identification.

Dyads were videotaped using a Quasar VHS/C-Minicam camera with a 6X-autofocus high speed shutter lens, connected to a Toshiba M 6550-VHS videocassette recorder. Each behavioral sequence was taped for at least 1 h. Videotapes of nymphs and adults were made June through July 1992. Male-male and female-female interactions were recorded between July and August 1992, and

male-female interactions were taped from August to October 1992. Grouped nymphs were videotaped in June 1993. Four of the scenarios (male-male, female-female, male-female, and grouped nymphs) were recorded only in the evening. Adult-nymph and nymph-nymph tapes provided data on daytime activities, which allowed comparison of activity levels and behavioral repertoires during the day and night in some cases. Daytime videotapes were recorded between 1000h and 1400h with natural light, and evening behaviors were recorded between 2100 h and 0200 h.

Six to 15 replicates of each dyad were recorded. The paucity of insects at certain time periods sometimes precluded the recording of more than six replicates: for example, the rapid maturing of nymphs in the summer of 1993, as well as the large number of nymphs needed made it difficult to videotape more than five replicates of each of the scenarios of grouped nymphs in sets of 3, 5, and 7.

Since the behavioral repertoire of *F. auricularia* had not previously been studied, definition of behavioral categories was determined from a preliminary review of videotapes. Discrimination between the end of one behavior and the start of a second behavior was sometimes arbitrary. For example, earwigs frequently rested for long periods of time on or against the bodies of their partners: it was decided that initial contacts (<30 sec) would be defined as contact, but subsequent quiescent contact of long duration would be defined as resting. Division of behaviors into categories was also subjective. Some authors describing other insect

species (e.g., Moore and Wilson, 1993) have divided one category such as aggression into several steps. In this initial study of the European earwig, behavior was divided into broader categories. The following individual behaviors were recorded:

1. Rest
2. Locomotion
3. Groom
4. Feed alone
5. Feed with partner
6. Contact
7. Aggression
8. Dorsal palpation

The first four behaviors were categorized as nonsocial behaviors because they were performed by the insect without any interaction with the insect's partner or partners. However, the initiation of these behaviors may have been influenced by the activities of other insects in the arena. The last four behaviors were considered to be social because they involved some interaction with the partner or partners.

Rest was defined as a quiescent state in which the insect did not move purposefully or perform another activity, such as groom or feed. Instances in which an insect only moved its antennae or briefly moved its head were still defined as

being within the resting state. While resting, some insects rhythmically moved one or two legs very slightly, but this was still categorized as resting.

Locomotion was defined as directed movement by walking or running, either forward or backward, within the arena. The type of slight, undirected movements discussed above were not considered to be locomotion.

Groom was defined as cleaning of the body and its appendages, using the mouthparts and/or the legs. Grooming is a common behavior in many insects, and typically consists of stereotyped cleaning movements which are so distinctive that they can frequently be used for taxonomic classification (E.O. Wilson, 1971). In addition to hygiene, self-grooming also aids in distributing secretions over the body surface (E.O. Wilson, 1971).

Feed alone was indicated when the insect ate, determined by movement of the head and/or mouthparts over the surface of the food. If an insect was observed with its head or body bent over a piece of food, but no movement of the head or mouthparts was seen, it was not scored as feeding. Frequently, earwigs rested on food in the arena, but feed alone was scored only when the insect's mouthparts or head was observed as moving. In addition, feed alone was applied only when the insect was the sole insect feeding at the time.

If more than one insect was feeding at the same food source at the same time, the activity was scored as feed with partner. In situations where one insect was initially feeding alone, the label feed with partner was applied at the moment the

second insect was observed to begin to feed. The presence of a second, or more, insects on or near the food did not result in application of this label; more than one insect had to be feeding at a time.

Contact was defined as touching of a second individual by the insect.

Touching with the antennae alone was not included in this category: contact had to be made using another part of the body, such as the head or legs. More specialized contacts were included in other categories as defined, including aggression and dorsal palpation, defined below, and courtship maneuvers, discussed in Chapter 4. The category contact did not include prolonged (>30 sec) resting against another individual; these activities were defined as rest. Because some situations involved contacts resulting in prolonged resting on or against another insect, it was sometimes difficult to judge when contact had ended and rest had begun.

Aggression was defined as either combative contact of the partner, or such a display directed toward the partner. Earwigs typically use their forceps in aggressive situations (Fulton, 1924; Crumb et al., 1941). In videotaped trials, this behavior appeared most often as a means to defend access to food. Typically, the individual feeding threatened the approaching partner by raising or spreading its forceps. Further advancement by the partner sometimes led to nipping with the forceps by the feeding individual. In this study, aggression consisted primarily of movements of the forceps toward an opposing earwig, including horizontal back-and-forth swipes, curling over the head, and rolling of the abdominal segments and

cerci vertically. The earwig also sometimes slightly opened and closed the forceps at the same time as waving at the approaching earwig. Occasionally, contact was made by nipping at the opponent. Both sexes and age classes used the forceps to threaten, and both sexes were aggressive toward their own and the other sex.

Dorsal palpation was a specialized contact in which the insect used its mouthparts to palpate the dorsum of a partner. This behavior was previously undescribed in *F. auricularia*, and appears to be analogous to allogrooming observed in some other insects.

Total social time was computed by adding durations of feed with partner, contact, dorsal palpation, and aggression. Similarly, total number of social events was determined by summing frequencies for those behaviors.

To examine the effects of time of day, gender, age, partner gender and partner age, numerous different comparisons were made (Table 3.1).

For studies of grouped individuals, only nymphs were utilized. Antennal contact rate was observed as a measure of the insect's assessment of spatial density within the group, and was obtained by counting the number of antennal contacts made by all individuals within a group for each videotape, and dividing by the number of individuals in the group (Gordon et al., 1993). Data on the percentage of time spent in various behaviors were used to construct activity or time budgets.

Table 3.1. Comparisons of dyads of *F. auricularia* used to evaluate the effect of five variables on behavioral durations and frequency. Brackets indicate partner in dyad: [Ny]=nymph, [M]=male, [F]=female. Eve=evening.

Variable	Treatments Compared	
Time of Day		
1.	<u>Male</u> [Ny] day, N=9	vs. <u>Male</u> [Ny] eve, N=9
2.	<u>Female</u> [Ny] day, N=14	vs. <u>Female</u> [Ny] eve, N=14
3.	<u>Nymph</u> [M] day, N=15	vs. <u>Nymph</u> [M] eve, N=9
4.	<u>Nymph</u> [F] day, N=14	vs. <u>Nymph</u> [F] eve, N=9
5.	<u>Nymph</u> [Ny] day, N=33	vs. <u>Nymph</u> [Ny] eve, N=14
Gender		
1.	<u>Male</u> [M] eve, N=34	vs. <u>Female</u> [F] eve, N=14
2.	<u>Nymph</u> [M] eve, N=15	vs. <u>Nymph</u> [F] eve, N=9
Age		
1.	<u>Male</u> [M] eve, N=34	vs. <u>Nymph</u> [Ny] eve, N=12
2.	<u>Female</u> [F] eve, N=14	vs. <u>Nymph</u> [N] eve, N=12
Partner Gender		
1.	<u>Male</u> [M] eve, N=34	vs. <u>Male</u> [F] eve, N=12
2.	<u>Female</u> [F] eve, N=14	vs. <u>Female</u> [M] eve, N=12
3.	<u>Nymph</u> [M] eve, N=12	vs. <u>Nymph</u> [F] eve, N=9
4.	<u>Nymph</u> [M] day, N=15	vs. <u>Nymph</u> [F] day, N=14
Partner Age		
1.	<u>Male</u> [M] eve, N=34	vs. <u>Male</u> [Ny] eve, N=9
2.	<u>Female</u> [F] eve, N=14	vs. <u>Female</u> [Ny] eve, N=14
3.	<u>Nymph</u> [Ny] day, N=12	vs. <u>Nymph</u> [M] eve, N=9
4.	<u>Nymph</u> [Ny] day, N=33	vs. <u>Nymph</u> [M] day, N=15
5.	<u>Nymph</u> [Ny] eve, N=12	vs. <u>Nymph</u> [F] eve, N=9
6.	<u>Nymph</u> [Ny] day, N=33	vs. <u>Nymph</u> [F] day, N=14

Videotape Review

The behavior of each insect in a recorded experimental dyad was analyzed separately with the assistance of the Observer 3.0 software computer program (Noldus Information Technology, 1990). Due to the large number of tapes recorded, and the fact that most behaviors lasted at least 5 sec, most videotapes were reviewed with the fast-forward mechanism of the VCR. Since fast forward on the Toshiba VHS-VCR decreases real time by a factor of 5, duration (sec) of behaviors was then multiplied by 5. Social interactions, however, frequently lasted less than 5 sec. Therefore, each videotape was reviewed a second time for each insect, and social behaviors recorded to the nearest sec with a stopwatch.

Duration and frequency data were compiled and analyzed for the entire 1 h test period for all of the insects videotaped, except for the grouped nymphs. Total duration was expressed as the percentage of time spent by each insect/ behavior/ h.

For analysis of group tapes, two nymphs/tape were randomly selected for behavioral compilation prior to review of the tape. However, to determine rate of antennal contact between earwig nymphs in groups, all antennal contacts by all nymphs in each tape were counted.

Statistics

Activity budgets were constructed using mean percent time spent /behavior/h, rather than medians, in order to account for 100% of the time allocated

to tests. Because antennal contact data were distributed normally, ANOVA was used for their analysis (Sokal and Rohlf, 1981).

Because the behavior of each of the partners within the same test might, in some way, be affected by the behaviors of the other insect, partner behavior within the same tests was not directly compared (e.g., female behavior versus nymphal behavior in female-nymph tests). Instead, comparisons of selected dyads were analyzed to examine the effect of age, gender and time of day on behavior (Table 3.1).

Most of the duration (percent time) data were not distributed normally. Therefore, the nonparametric Mann Whitney U-test was used to test for significant differences in duration of behavior among treatments (Daniel, 1990). Frequency data were analyzed with a test of two proportions of frequencies using a normal approximation (Walpole and Myers, 1989), which required division of data for each behavior into high and low counts, and transformation of high counts into proportions. High counts were individually defined for each behavior:

Feed alone ≥ 8

Feed with partner ≥ 3

Rest ≥ 10

Groom ≥ 7

Locomotion ≥ 13

Contact ≥ 4

Dorsal palpation ≥ 1

Aggression ≥ 1

No. of social events ≥ 9

Correlations of behaviors of individual insects were computed using the Spearman rank correlation test (Daniel, 1990). Except for frequency analyses, which were done manually, statistics were computed using Minitab for Windows 10.0 software (Minitab, Inc., 1994).

Results

Activity Budgets

Males

Males paired with adults spent most of their time resting (50%), grooming (25-35%), or moving around (10%). For males with nymphs, the top three activities were feeding alone (45-50%), resting (30-45%), and grooming (10%), with males in evening trials spending more time feeding alone and males in daytime trials spending more time resting (Figure 3.1).

Time allocated to social behavior (feeding with the partner, dorsal palpation, contact, and aggression) was about 4% for males with adults and with nymphs in the evening, but less than 1% for males with nymphs during the day (Figure 3.2). Males

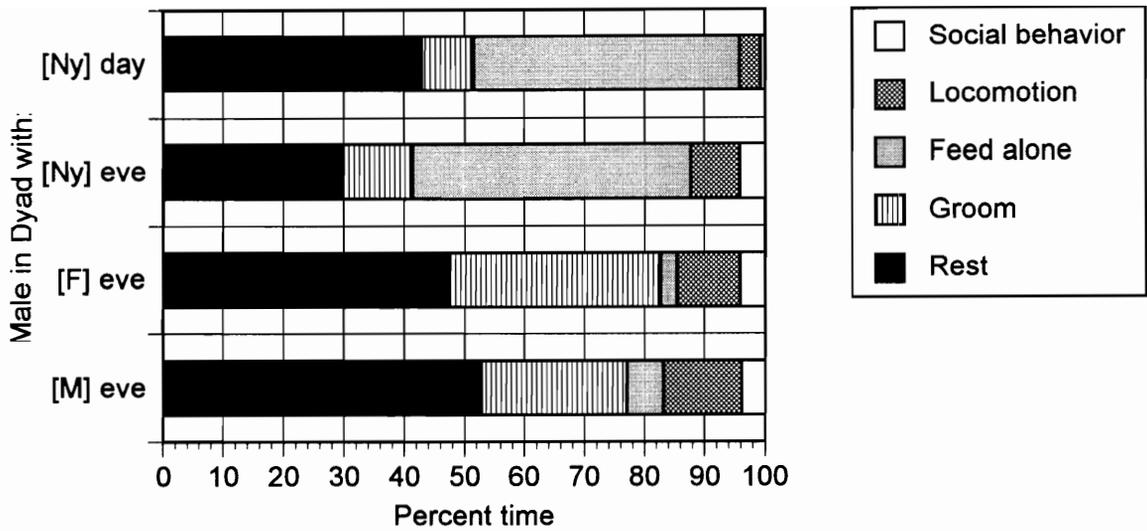


Figure 3.1. Activity budget for male *F. auricularia* (N=64), with percent time allocated to five behaviors. Brackets indicate partner in each dyad: [Ny]=nymph, [M]=male, [F]=female. Eve=evening.

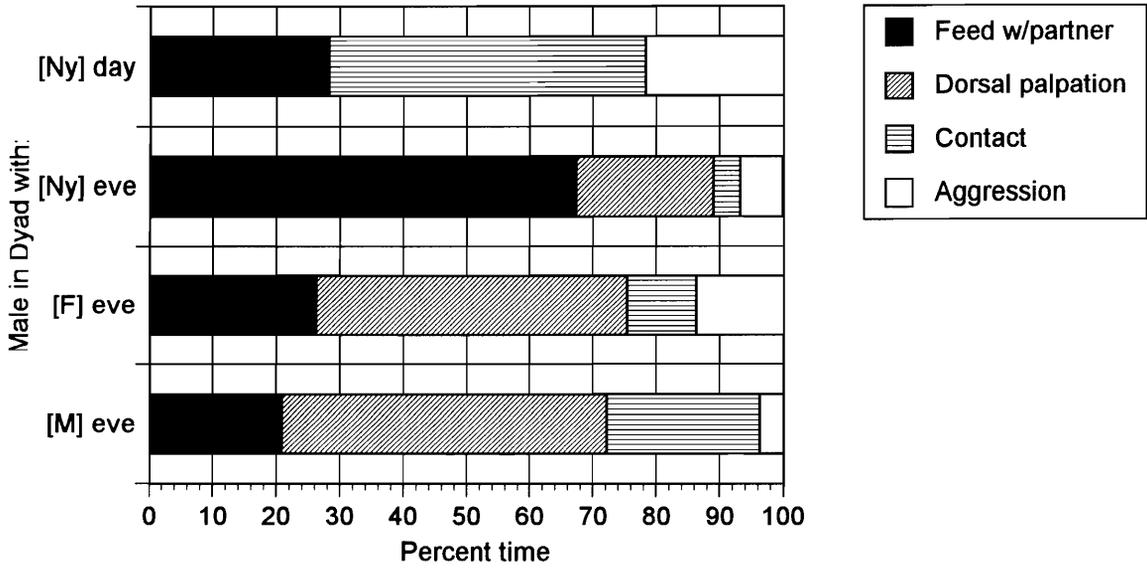


Figure 3.2. Male *F. auricularia* (N=64) time allocation to four social behaviors. Brackets indicate partner in each dyad: [Ny]=nymph, [M]=male, [F]=female. Eve=evening.

with nymphs in the evening spent most (70%) of their social time feeding with their partners, compared to <30% of the time spent by males in the other treatments. Dorsal palpation appears to be an important evening activity for males paired with adults, which spent about 50% of the time allocated to social behaviors engaged in dorsally palpating their partners, compared with <20% for males paired with nymphs. Males in the daytime did not participate in dorsal palpation. On the other hand, they spent more time in aggression than did males in the evening.

Females

Females paired with adults spent most of their time feeding alone (35-40%), resting (35%), and grooming (15%) (Figure 3.3). Females paired with nymphs, on the other hand, invested most of their time in feeding alone (45-50%), resting (15-30%), and grooming (10-15%). Whereas males paired with nymphs in daytime dyads rested about 45% of the time, females with nymphs in the daytime spent the least amount of time (15%) resting of all the female treatments.

Females spent a greater percentage of their activity budget engaged in social behaviors than did males: about 6% of the time for females paired with adults, but 12-15% of the time for females paired with nymphs (Figure 3.4). Females spent much more time feeding with both juvenile and adult partners than did males, and more time was spent by females feeding with nymphal partners than with adult partners. As with males, dorsal palpation appeared to be a more important activity for females with adults.

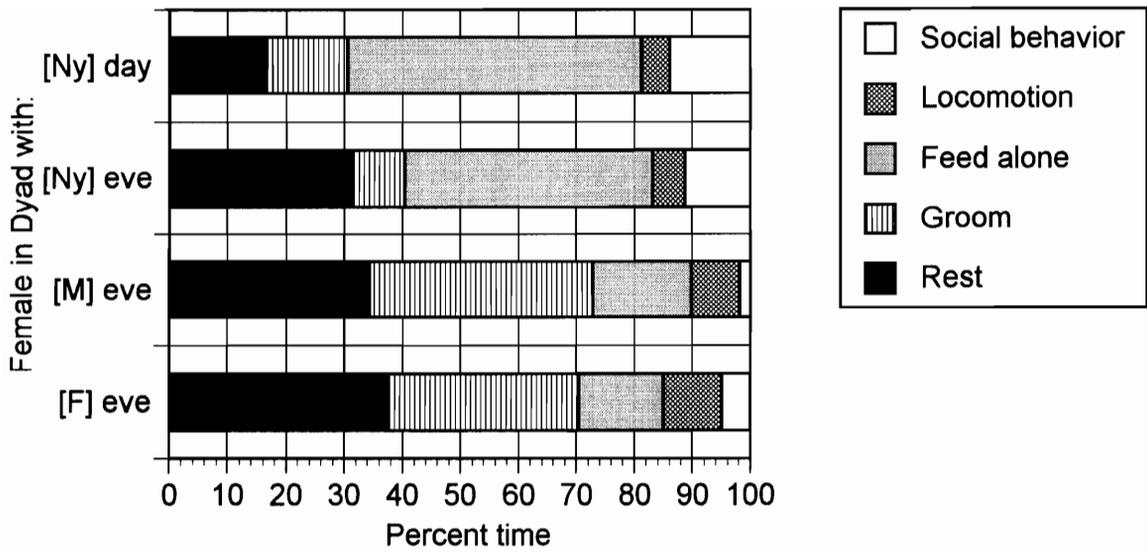


Figure 3.3. Activity budget for female *F. auricularia* (N=54), with percent time allocated to five behaviors. Brackets indicate partner in each dyad: [Ny]=nymph, [M]=male, [F]=female. Eve=evening.

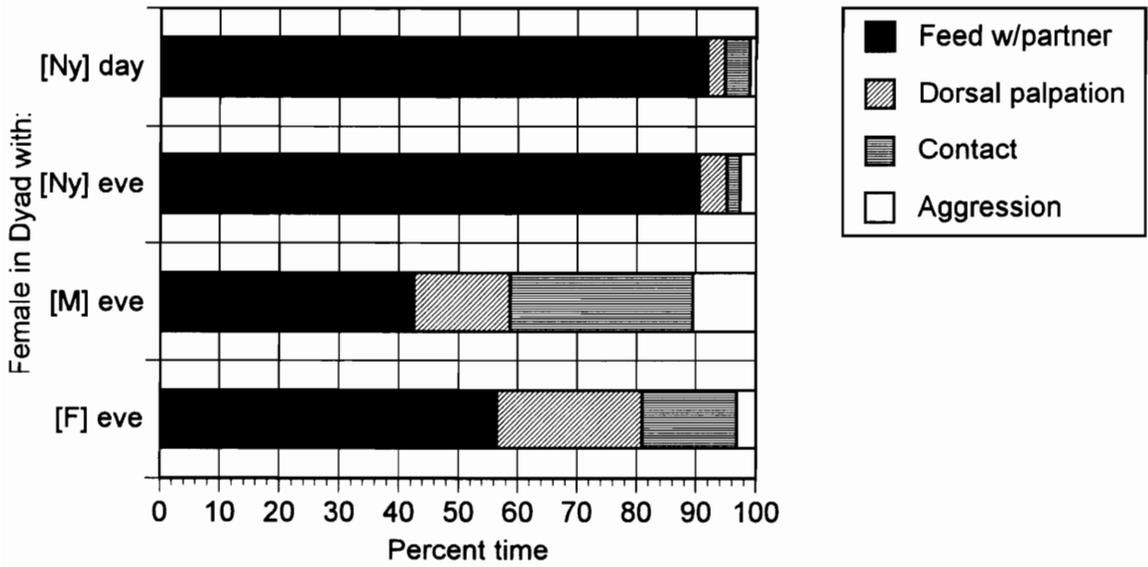


Figure 3.4. Female *F. auricularia* (N=54) time allocation to four social behaviors. Brackets indicate partner in each dyad: [Ny]=nymph, [M]=male, [F]=female. Eve=evening.

Nymphs

Nymphal activity budgets seemed to be more affected by time of day than by partner age or partner gender (Figure 3.5). During the day, nymphs spent most of their time resting (65-70%), grooming (10-12%), and feeding alone (10-12%). In the evening, however, nymphs spent less time resting (40-60%), but more time feeding alone (15-30%), and about the same amount of time grooming (10-15%). In general, nymphs spent more time resting than did adults, and more time feeding alone than males, but less time feeding alone than females.

Somewhat more time was spent in social behaviors in the evening (5-10%) than during the day (1-7%) (Figure 3.6). Feeding with the partner accounted for the greatest portion of the social activity budget of most nymphs (70-95%), except those paired with nymphs or males during the day, which spent most of their social time engaged in dorsal palpation. Nymphs fed with females about the same amount of time regardless of time of day, but nymphs with male partners reduced daytime feeding with partner time from evening dyads.

Effect of Variables on Behavior

Several different variables could have been responsible for significant differences in behavior including gender, age, time of day, partner gender, and partner age. Frequencies and percent amount of time spent in various behaviors for males (Table 3.2), females (Table 3.3), and nymphs (Table 3.4) were used in these comparisons.

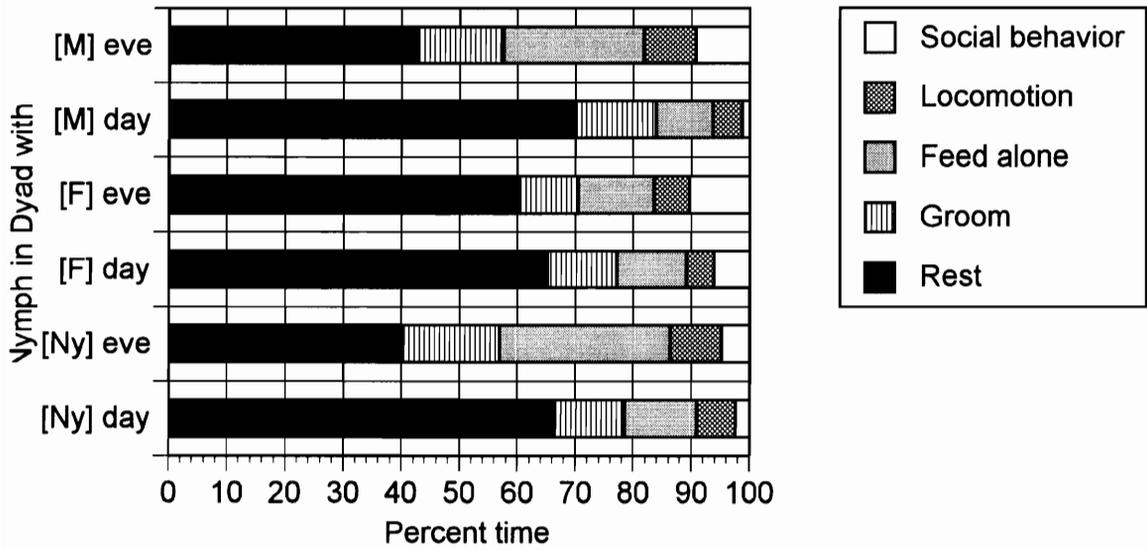


Figure 3.5. Activity budget for *F. auricularia* nymphs (N=94), with percent time allocated to five behaviors. Brackets indicate partner in each dyad: [Ny]=nymph, [M]=male, [F]=female. Eve=evening.

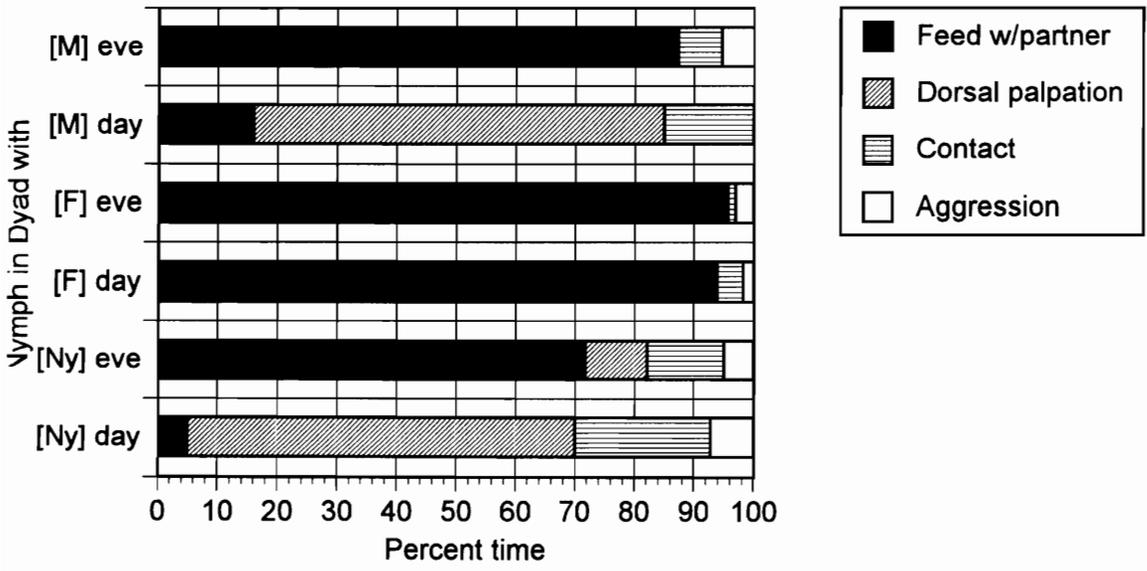


Figure 3.6. *F. auricularia* (N=94) nymphal time allocation to four social behaviors Brackets indicate partner in each dyad: [Ny]=nymph, [M]=male, [F]=female. Eve=evening.

Table 3.2. Frequencies (f) and percent durations (time spent per h)(%d) of behaviors of *F. auricularia* males. Brackets indicate partner in each dyad: [Ny]=nymph, [M]=male, [F]=female. Eve=evening.

Behavior	Male [M] eve, N=34 Median		Male [F] eve, N=12 Median		Male [Ny] eve, N=9 Median		Male [Ny] day, N=9 Median	
	%d	f	%d	f	%d	f	%d	f
Feed alone	0.0	0.0	0.0	0.5	43.3	8.0	33.2	6.0
Feed with partner	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rest	49.7	9.0	40.5	7.5	21.6	5.0	46.9	6.0
Groom	21.8	7.0	37.0	8.0	11.9	8.0	4.8	5.0
Locomotion	9.9	9.0	8.5	9.0	4.8	9.0	3.0	9.0
Contact	0.6	5.0	0.3	2.0	0.1	3.0	0.3	4.0
Aggression	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0
Dorsal palpation	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total social behaviors	1.1	3.0	1.7	7.0	0.4	4.0	0.5	0.0

Table 3.3. Frequencies (f) and percent durations (time spent per h)(%d) of behaviors of *F. auricularia* females. Brackets indicate partner in dyads: [Ny]=nymph, [M]=male, [F]=female. Eve=evening.

Behavior	Female [Ny] eve, N=14 Median		Female [F] eve, N=12 Median		Female [M] eve, N=14 Median		Female [Ny] day, N=14 Median	
	%d	f	%d	f	%d	f	%d	f
Feed alone	10.7	4.5	4.6	0.5	38.1	3.5	56.4	3.5
Feed with partner	0.0	0.0	0.0	0.0	0.0	0.0	5.7	2.0
Rest	40.6	7.0	33.2	7.5	26.0	5.0	11.7	5.0
Groom	34.0	7.0	38.5	7.5	6.1	4.0	14.3	4.0
Locomotion	8.6	14.0	6.0	9.0	5.4	8.0	4.0	8.0
Contact	0.6	8.0	0.0	0.0	0.3	2.0	0.5	2.0
Aggression	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.5
Dorsal palpation	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total social behaviors	1.6	12.5	0.5	3.0	0.8	6.0	7.0	3.5

Table 3.4. Frequencies (f) and percent durations (time spent per h)(%d) of various behaviors of *F. auricularia* nymphs. Brackets indicate partner in dyads, [Ny]=nymph, [M]=male, [F]=female. Eve=evening.

Behavior	Nymph [Ny] day, N=33		Nymph [Ny] eve, N=12		Nymph [F] day, N=14		Nymph [F] eve, N=9		Nymph [M] day, N=15		Nymph [M] eve, N=9	
	%d	f	%d	f	%d	f	%d	f	%d	f	%d	f
Feed Alone	0.2	1.0	24.1	7.0	4.3	0.5	1.2	0.5	6.2	2.5	9.6	3.0
Feed with partner	0.0	0.0	1.8	1.5	3.6	2.0	0.0	0.0	0.0	0.0	0.0	0.0
Rest	71.1	13.0	40.7	7.0	66.9	7.5	70.7	7.5	67.7	12.5	43.1	9.0
Groom	13.6	8.5	18.2	5.0	6.9	3.0	8.8	3.5	17.9	6.5	12.8	5.0
Locomotion	5.2	15.0	6.5	15.5	4.8	7.0	4.6	7.0	3.2	12.0	6.7	12.0
Contact	0.4	3.0	0.5	4.5	0.2	1.0	0.1	1.0	0.0	3.0	0.3	2.0
Aggression	0.0	0.0	0.1	2.0	0.0	1.0	0.0	0.0	0.0	0.0	0.1	0.0
Dorsal palpation	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total social behaviors	0.4	4.5	3.5	11.0	3.9	6.5	0.4	4.5	0.4	0.0	1.0	4.0

Time of Day

The only significant difference in behavior attributable to time of day was for nymphs. As predicted, nymphs spent significantly ($P=0.01$) more time resting during the day than in the evening (Table 3.5). Nymphs also had significantly ($P<0.05$) more bouts of daytime resting and grooming, but significantly ($P<0.05$) more feed alone bouts in the evening. Nymphs engaged in significantly ($P<0.05$) more social interactions in the nighttime (Table 3.6). There were no significant ($P>0.05$) differences between adult nighttime and daytime activity levels or frequencies.

Gender

Females spent more time feeding alone than males (Table 3.5), and had more feed alone bouts than males (Table 3.6).

Partner Gender

Females paired with females spent more time engaged in contact behavior than females paired with males. Females also spent more time socially interacting with female partners than females with male partners. Similarly, nymphs spent more time feeding with female partners than nymphs that had male partners. Nymphs with females also spent more time socially interacting with those partners than nymphs with males (Table 3.5).

Table 3.5. Significant ($P < 0.05$) comparisons of percent duration (time spent per h) of behaviors of *F. auricularia*, analyzed by the Mann-Whitney U-test (Daniel, 1990). Brackets indicate partner in each dyad: [Ny]=nymph, [M]=male, [F]=female. Eve=evening.

Variable	Median	Median	W	P
Time of Day				
<u>Nymph [Ny]</u> day, N=33 Rest	71.1%	<u>Nymph [Ny]</u> eve, N=12 Rest	40.7%	857.0 0.0123
Gender				
<u>Male [M]</u> eve, N=34 Feed alone	0.0%	<u>Female [F]</u> eve, N=14 Feed alone	11.1%	446.5 0.0069
Partner Gender				
<u>Female [F]</u> eve, N=14 Contact Total social behavior	0.6% 1.8%	<u>Female [M]</u> eve, N=12 Contact Total social behavior	0.0% 0.4%	231.5 0.0283 247.0 0.0454
<u>Nymph [M]</u> day, N=15 Feed with partner Total social behavior	0.0% 0.4%	<u>Nymph [F]</u> day, N=14 Feed with partner Total social behavior	3.6% 3.9%	201.5 0.0249 209.0 0.0106
Age				
<u>Male [M]</u> eve, N=34 Feed alone Feed with partner	0.0% 0.0%	<u>Nymph [Ny]</u> eve, N=12 Feed alone Feed with partner	14.5% 1.9%	697.5 0.0265 699.0 0.0128
Partner Age				
<u>Male [M]</u> eve, N=34 Feed alone Rest Contact	10.7% 49.7% 0.6%	<u>Male [Ny]</u> eve, N=9 Feed alone Rest Contact	43.3% 21.6% 0.1%	625.5 0.0001 823.0 0.0261 815.5 0.0438
<u>Female [F]</u> eve, N=14 Feed alone Groom Locomotion Contact	10.7% 34.0% 8.6% 0.6%	<u>Female [Ny]</u> eve, N=14 Feed alone Groom Locomotion Contact	38.1% 6.1% 5.4% 0.3%	145.0 0.0081 282.0 0.0003 248.0 0.0409 255.0 0.0171
<u>Nymph [Ny]</u> eve, N=12 Contact	0.5%	<u>Nymph [F]</u> eve, N=9 Contact	0.1%	218.0 0.0040

Table 3.6. Significant ($P < 0.05$) comparisons of high counts of proportions of behaviors by *F. auricularia*, analyzed with a test of two proportions, using a normal approximation (Walpole and Myers, 1989). Brackets indicate partner in each dyad: [Ny]=nymph, [M]=male, [F]=female. Eve=evening.

Variable	Proportion	Proportion	Z
Time of Day			
<u>Nymph [Ny]</u> day, N=33		<u>Nymph [Ny]</u> eve, N=12	
Feed with partner	0.04	Feed with partner	0.5
Rest	0.81	Rest	0.33
Groom	0.67	Groom	0.11
Social events	0.27	Social events	0.67
			-3.5
			3.0
			2.4
			-2.4
Gender			
<u>Male [M]</u> eve, N=34		<u>Female [F]</u> eve, N=14	
Feed alone	0.0	Feed alone	0.36
			4.0
Age			
<u>Male [M]</u> eve, N=34		<u>Nymph [Ny]</u> eve, N=12	
Feed alone	0.0	Feed alone	0.42
Feed with partner	0.1	Feed with partner	0.5
Locomotion	0.29	Locomotion	0.67
Aggression	0.23	Aggression	0.67
			4.2
			3.7
			2.9
			2.8
Partner Age			
<u>Male [M]</u> eve, N=34		<u>Male [Ny]</u> eve, N=9	
Feed alone	0.0	Feed alone	0.56
			-5.1
<u>Nymph [Ny]</u> eve, N=12		<u>Nymph [F]</u> eve, N=9	
Contact	0.67	Contact	0.27
			3.9

Age

Males spent significantly ($P=0.03$) less time feeding than did nymphs (Table 3.5), and fed significantly ($P<0.05$) fewer times than nymphs (Table 3.6). Males in male-male dyads also fed together significantly ($P=0.01$) more often than nymphs in nymph-nymph dyads (Table 3.5). Nymphs were aggressive and moved around the arena significantly ($P<0.05$) more times than males (Table 3.6).

Partner Age

Adults appeared to dominate nymphs in behavioral interactions. Males in male-nymph dyads spent significantly ($P<0.05$) more time feeding alone than males in male-male pairs, and more time resting and engaged in contact behavior when paired with other males, than when paired with nymphs (Table 3.5). Males also had more feed alone bouts when paired with nymphs than with adults (Table 3.6). Aggression levels did not significantly ($P>0.05$) differ.

Similarly, females spent significantly ($P=0.01$) more time feeding when paired with juveniles than with female partners (Table 3.5). Although median percent time spent in aggressive behavior was not greater for adults when paired with nymphs, adults spent more time feeding than their nymphal partners in the same dyads: for males in the evening, 43.3% versus 9.6% for nymphs, and in the daytime, 33.2% for males versus 6.2% for nymphs; and for females, in the evening, 38.1% versus 4.3% for nymphs, and in the daytime, 56.4% for females versus 1.2% for nymphs. When

with their female partners, females spent more time grooming in contact behavior and in locomotion than females with nymphs.

Nymphs spent more time contacting nymphal partners than female partners (Table 3.5), and contacted juvenile partners significantly ($P < 0.05$) more frequently than female partners (Table 3.6).

Correlations of Individual Behaviors

Resting and grooming were significantly ($P < 0.05$) inversely correlated for most of the dyads tested, as were resting and locomotion (Table 3.7). Some social behaviors were significantly ($P < 0.05$) correlated with nonsocial behaviors: for example, feeding alone and feeding with the partner were positively correlated for female-female dyads; feeding alone and contact were positively correlated in males with females; feeding alone and aggression were positively correlated in nymphs with females; resting was negatively correlated with contact behaviors by nymph-nymph, male female and male-male dyads; aggression and resting were negatively correlated for females with nymphal partners; amount of time allocated to social behaviors was positively correlated with both locomotion and resting in daytime nymph-nymph dyads. There were no instances of significant correlation of two social behaviors.

Group Behavior

Nymphal time allocation varied with group size for only two behaviors. Nymphs spent significantly ($P = 0.015$) less time feeding alone in larger groups

Table 3.7. Significant ($P < 0.05$) correlations of behavioral durations (time spent per h) for *F. auricularia* analyzed with a Spearman rank correlation test (Daniel, 1990). * denotes correlations where $P < 0.01$. Brackets indicate partner in each dyad: [Ny]=nymph, [M]=male, [F]=female. Eve=evening.

Feed alone - Feed with partner	<u>Female</u> [F] eve, N=14	0.738*
Feed Alone - Locomotion	<u>Male</u> [M] eve, N=34	0.444
	<u>Male</u> [F] eve, N=12	0.834*
Feed alone - Contact	<u>Male</u> [F] eve, N=12	0.681
Feed alone - Aggression	<u>Nymph</u> [F] day, N=14	0.654
Feed with partner - Rest	<u>Nymph</u> [Ny] eve, N=12	-0.868*
	<u>Nymph</u> [F] day, N=14	-0.632
	<u>Nymph</u> [F] eve, N=14	-0.708
Feed with partner - Locomotion	<u>Nymph</u> [F] eve, N=14	0.663
Rest - Groom	<u>Male</u> [F] eve, N=12	-0.949*
	<u>Nymph</u> [Ny] day, N=33	-0.641
	<u>Female</u> [Ny] day, N=14	0.639
	<u>Male</u> [M] eve, N=34	-0.626*
Rest - Locomotion	<u>Male</u> [M] eve, N=34	-0.677*
	<u>Male</u> [F] eve, N=12	-0.860*
	<u>Nymph</u> [Ny] day, N=33	-0.655*
Rest - Contact	<u>Nymph</u> [Ny] day, N=33	-0.441
	<u>Male</u> [M] eve, N=34	-0.476
	<u>Male</u> [F] eve, N=12	-0.794*
Rest - Aggression	<u>Female</u> [Ny] eve, N=14	-0.642
Rest - Social Time	<u>Nymph</u> [Ny] day, N=33	0.462

Groom - Locomotion	<u>Female [Ny]</u> eve, N=14	0.645
	<u>Male [F]</u> eve, N=12	0.774
	<u>Nymph [Ny]</u> day, N=33	0.720*
Contact - Groom	<u>Nymph [Ny]</u> day, N=33	0.473
	<u>Male [F]</u> eve, N=12	0.675
Contact - Locomotion	<u>Female [Ny]</u> day, N=14	0.659
	<u>Male [M]</u> eve, N=34	0.448
	<u>Male [F]</u> eve, N=12	0.822*
	<u>Male [Ny]</u> eve, N=9	0.709
	<u>Male [Ny]</u> day, N=8	0.798
	<u>Nymph [Ny]</u> day, N=33	0.598
Social Time - Locomotion	<u>Nymph [Ny]</u> day, N=33	0.565

(Kruskal Wallis test, $H=10.48$, $df=3$, $P=0.015$) (Table 3.8). Nymphs in groups of 2 or 3 spent significantly ($P=0.004$) less time resting than did nymphs in groups of 5 or 7.

Resting duration increased with increasingly larger groups (Kruskal Wallis test, $H=13.15$, $df=3$, $P=0.004$) (Table 3.8). Frequency of behaviors did not vary significantly ($P>0.05$). Antennal-antennal contact rates per individual per h increased significantly ($P=0.02$) with group density (Table 3.9).

Discussion

Activity Budgets

The predominant behaviors for *F. auricularia*, regardless of age or gender, were feeding, resting, and grooming. Social behaviors comprised a very small portion of the insect's activity budget, but appeared to be somewhat more important to females than males. This was especially true for females with nymphal partners: These females spent much more time feeding with juveniles than males in male-juvenile dyads. The importance of these behaviors was difficult to determine, since compared to nonsocial behaviors, they were usually of short duration, and some of them, such as dorsal palpation, occurred only occasionally. It is possible, however, that some or all of these behaviors are integral parts of the insect's behavioral repertoire regardless of their duration and frequency. Certainly, more intensive study of the social behaviors of *F. auricularia* is warranted.

Table 3.8. Comparison of median percent time spent in behaviors by grouped *F. auricularia* nymphs, analyzed by the Kruskal-Wallis test (Daniel, 1990). .

Behavior	Nymphs in groups of	Median % time spent/h	P
Rest	2	40.7a	0.004
	3	57.1a	
	5	81.7b	
	7	79.4b	
Groom	2	18.2	NS
	3	12.2	
	5	10.8	
	7	7.1	
Locomotion	2	6.5	NS
	3	9.2	
	5	4.9	
	7	5.5	
Feed alone	2	24.1a	0.015
	3	6.6ac	
	5	0.0b	
	7	0.0bc	
Feed with partner	2	0.9	NS
	3	0.0	
	5	0.0	
	7	0.0	
Contact	2	0.5	NS
	3	0.8	
	5	0.5	
	7	0.8	
Dorsal palpation	2	2.0	NS
	3	0.1	
	5	0.3	
	7	0.1	
Aggression	2	0.1	NS
	3	0.2	
	5	0.0	
	7	0.0	

Letters indicate medians that are not significantly different.

Table 3.9. Antennal-antennal contact rates for *F. auricularia* nymphs in groups, analyzed with ANOVA (Sokal and Rohlf, 1981).

Nymphs in Groups of	Mean no. antennal-antennal contacts/individual/h	P
2	9.1a	0.002
3	13.4ab	
5	20.5b	
7	20.1b	

F=7.2, df=22, P=0.002

Letters indicate means that are not significantly different.

Consistent with the expectation that females should spend more time engaged in feeding than males, comparison of male and female activity budgets demonstrated that feeding was indeed a less important activity for males than for females, when in adult dyads. However, the activity profiles of both sexes were more similar when paired with nymphs: feeding and grooming durations were about the same. Dorsal palpation also occurred more frequently between adults than between adults and nymphs. Nymphs, but not adults, displayed the nocturnal behavior that has been ascribed to *F. auricularia*.

Behaviors and Social Interactions

The earwig had long been considered a nocturnal insect (e.g., Crumb et al., 1941; Lamb and Wellington, 1974). However, this study showed that behavioral differences due to time of day were significant only for nymphs. Nymphs fed more, rested less, and engaged in more social interactions in the evening than in the daytime. Adult behavior did not significantly ($P>0.05$) change after sundown.

Females may need more food than males to build up nutritional reserves for oogenesis, overwintering, and brood care. Anecdotal evidence (Crumb et al., 1941) suggests that most male earwigs do not survive the winter and do not provide brood care; therefore they may need a smaller energy supply. Sperm are also less costly to produce than are ova (Thornhill and Alcock, 1983).

As predicted, nymphs fed more frequently and for longer periods of time than did males, which may reflect age-related differences in metabolism. Nymphs did

not, however, feed more than females. Nymphs displayed aggressive behavior more often and moved more frequently than did males, but not females.

Females spent significantly ($P=0.02$) more time contacting female partners than male partners. This might be related to female sexual behavior, assuming that contact behavior has, at least at times, a sexual context in courtship. It might be reasonable that females would avoid males and thus have less physical contact with them. However, it seems reasonable that males would spend more time contacting females than males, which was not the case, although there may have been less contact than would be expected, since dyads were taped prior to the onset of reproductive readiness.

Partner age was a significant factor influencing behavior. Adult time allocation shifted when the partner was juvenile: males spent less time resting and contacting nymphs than other adult males; females spent less time grooming, and in locomotory and contact behaviors, and both sexes fed more. Feeding shifts may represent exertion of some degree of adult dominance over nymphs, wherein adults exploit interactions with juveniles to feed for longer periods of time. Nymphs had significantly ($P<0.05$) more bouts of contacting nymphal partners than female, but not male, partners. This is somewhat paradoxical considering that females spent a considerable amount of time socially interacting with nymphs, but may simply mean that females, as adults, may control interactions more than nymphs, and nymphs may be more passive participants in adult-nymph social behavior. An alternative

explanation may be that females and nymphs paired together were unrelated. Also, if contact behaviors are in some way utilized by adults as one means to assess dominance or sexual receptivity, it would be reasonable that adults might contact each other more than juvenile partners. However, contrary to expectation, nymphs were no more aggressive toward nymphal partners than toward adult partners. There was also no significant ($P>0.05$) difference between rates of dorsal palpation, or allogrooming, between nymphs and their nymphal partners versus adult partners. Since dorsal palpation occurred so infrequently, any differences may have been difficult to statistically detect. Allogrooming is observed in many vertebrates, particularly primates, in which it is thought to have social functions such as appeasement or the assertion of social dominance, an expression of close genetic relatedness, or the mutual preference of individuals for each other (Harrison, 1965; Hunkeler et al., 1972; O'Brien, 1993). Allogrooming may also be a method to distribute pheromones, such as in *Cataglyphis niger* ants which transfer cuticular and postpharyngeal gland hydrocarbons to nestmates (Soroker et al., 1995). The termite *Termes saltans* uses mutual grooming as a part of its courtship repertoire (De Szterman, 1992). Allogrooming is apparently rare in nonsocial insects, although some cases exist (e.g., anthribid beetle *Ptychoderis rugicollis* males groom the abdomens of females to remove dust particles following female oviposition in dead wood, Howden, 1992). Mutual grooming may also be a corollary of group-living because of increased exposure to disease organisms and ectoparasites (Alexander,

1974) and, like lowered rates of aggression, may serve to bond the group (Wilson, 1975). In *F. auricularia*, dorsal palpation may serve to distribute the aggregation pheromones originating on the cuticle of the male European earwig (Chapt. 2). Comparison of activity budgets showed that nymphs spent the most time dorsally palpating male partners, and males spent more time dorsally palpating their male partners. But in no instance was there a significant ($P > 0.05$) difference between duration or frequency of this activity between treatments. Dorsal palpation is a more frequent component of male-female interactions during courtship (see Chapt. 4), so this activity may have a clear sexual function as well.

Aggression levels differed little between treatments. If aggression functions primarily during sexual behavior, and these videotapes were made prior to onset of reproductive readiness, one would expect little differences in aggression. It also appeared that aggression is not used very extensively to work out dominance rankings between individuals. Otherwise, more pugnacious behavior would have been observed. As Fulton (1924) noted, the aggressive encounters that did occur rarely erupted into serious fighting. Other types of interactions between individuals rarely resulted in aggression. For example, when moving around the arenas, earwigs frequently walked over their partners. This behavior was generally tolerated by the partner, rarely resulting in forcep displays.

A possible extreme example of aggression, cannibalism in *F. auricularia* was observed both in lab cultures and in aggregation tests (Chapt. 2), but not in these

videotaped trials . The cannibalized individual was typically either in the process of molting, or newly molted, or injured in some way, so that it was unable to adequately defend itself. Corpses were also regularly consumed in lab cultures. All instances of cannibalism occurred when there was ample food in the lab container or arena. It is unknown whether this behavior in *F. auricularia* is typical of natural populations as well, or if it is merely a laboratory artifact. Since earwigs are scavengers, and molting nymphs, injured individuals and corpses probably represent an exploitable source of protein, it would not be surprising if cannibalism occurs in wild populations. As such, it would constitute an aggressive behavior that directly increases the fitness of the aggressor.

Group Dynamics

One effect of group-living may be a heightened degree of social interaction between individuals (Manning and Dawkins, 1992). This did not appear to be the case with *F. auricularia*. Although not statistically significant ($P>0.05$), amount of time allocated to social behaviors decreased as group size increased. Some nonsocial behaviors, however, were affected by group density. Consistent with Lamb's (1976b) finding that body weight of nymphs reared in groups was inversely correlated with group size, the time spent feeding alone significantly ($P=0.015$) decreased with increasing group density. Median percent time spent feeding with group members also decreased in group sizes over 2. Median percent time spent in

dorsal palpation fell off with increasing density. Median percent time spent in contacting group members, however, increased slightly with increasing group size.

Amount of time devoted to aggression did not differ significantly ($P>0.05$) with nymphal density, as was expected, and, in fact, rate of aggression dropped off at higher group densities. Aggression was rarely observed in larger groups, and levels of aggression were greatest at group sizes of 3 nymphs, but tapered to a median of 0% in groups of 5 and 7 nymphs. Instead of heightening levels of aggression, increased group density may cause aggression levels to decrease. Kaufmann (1983) predicted that aggressive behavior will decrease as group members establish stable associations. Judge and de Waal (1993) found that aggressive behavior dropped off with increasing spatial density in rhesus monkeys. They noted that instead of aggression, submissive behavior increased with crowding, possibly as a mechanism to avoid conflict. The gregarious lifestyle of some animals may be incompatible with large degrees of competitive or aggressive behavior because it can disrupt social bonds (Cords, 1992), so that one might expect lower levels of aggression at higher group density in these animals. Since group living is the norm for earwigs, aggression may decrease with increasing group size in order to maintain group stability. Group-living may be advantageous to earwigs in order to exploit favorable microhabitats, such as moist, dark areas, and to bring the sexes together for reproduction.

Individual "awareness" of increased density may have important consequences for the group, such as heightened vigilance for predators and optimization of critical resources such as food and space, and insects might use antennal contacts to determine density, and changes in density (Gordon et al., 1993). Rate of antennal contact rose significantly ($P=0.02$) with increasing group size in *F. auricularia*. Even with 7 nymphs in a Petri dish, there was enough room to maneuver away from group members to avoid contact with them, so that most encounters were probably intentional.

As group density increases, there appears to be less opportunity to conduct personal maintenance activities such as feeding and grooming, but more probability of contacting group members. This suggests that advantages accruing to earwigs by living gregariously outweigh deficits such as less food. And while discrete social behaviors decreased in duration, indicating that group members avoid interacting with each other, the increase in antennal contact rate suggests that perhaps group members intentionally "keep tabs" on the presence and location of other members. It may be advantageous for gregarious insects such as earwigs to adopt a strategy of heightened vigilance if a mass of earwigs is more obvious to predators than lone individuals. The possible use of the defensive secretions as alarm compounds (see Chapt. 2) also aids in group defense.

CHAPTER 4: COURTSHIP AND MATING BEHAVIOR

Introduction

The forceps of earwigs are their most distinctive anatomical feature and the sexual dimorphism of the cerci of most earwig species (Hoffman, 1987) has spawned interest in the evolutionary basis for this dimorphism (Eberhard and Gutierrez, 1991; Moore and Wilson, 1993). The males of some species of Dermaptera, including *F. auricularia*, also have one or more teeth on the inner margin of the cerci (Giles, 1963; Richards and Davies, 1977), whose function is unclear. The frequency distribution of the length of the male cerci of *F. auricularia* has been reported as both bimodal, with a peak of small-forceped males, and a second peak of large-forceped males (Diakonov, 1925; Crumb et al., 1941; Radesater and Halldorsdottir, 1993) and as unimodal (Van Heerdt, 1953; Eberhard and Gutierrez, 1991). Proponents of the "two morph" theory ascribe the length variation primarily to environmental influences (Diakonov, 1925) or to genetics (Crumb et al., 1941). A small minority of males also have one curved "male" forcep and one straight "female" forcep (Crumb et al., 1941); Radesater and Halldorsdottir (1992) suggested that the degree of asymmetry between length of individual cerci may prove to affect male mating success.

Allometry is the relationship between the growth rates of different body parts (Nijhout and Wheeler, 1996). Additional interest in male forcep size is lent by the theory that positive allometry has a greater probability of occurring in secondary

sexual characteristics than in naturally selected characters (Petrie, 1988; 1992; Green, 1992), although it is possible to find evidence of positive allometry in structures of taxa which are unaffected by sexual selection (Green, 1992). Simmons and Tomkins (1996) noted that a sample of British *F. auricularia* did not display positive allometry between male forcep length and pronotum width. However, they used a very small sample size.

The function of earwig forceps has been debated by several authors. Based on anecdotal observations, Goe (1925) reported that males use their cerci as claspers during copulation, but this assertion was later refuted by Fulton (1927). Moore and Wilson (1993) suggested that male toothed earwigs, *Vostox apicedentatus*, use forceps primarily for aggression, but also in courtship.

The courtship and mating behavior of *F. auricularia* has not been examined in detail. In a taxonomic analysis of the Dermaptera, Popham (1965) described the mechanics of the copulatory position of *F. auricularia*, but not its courtship behaviors. Radesater and Halldorsdottir (1993) observed that in aggressive contests between large and small males, larger males seemed to have an advantage, and that larger males gained more copulations. The chief objectives of this study were to determine courtship and mating repertoire, the function of individual behaviors by the male and female, and the importance of the male forceps in courtship and mating. Other factors such as male body size, and male-male interactions in the context of a reproductive situation, were examined to a lesser degree.

Materials and Methods

Courtship Behavioral Repertoire

Insects were field-collected as described in Chapter 2 and maintained in rearing enclosures for at least 24 h before observation. At the beginning of these investigations in 1990, little was known about onset of sexual receptivity, so initial observations began in July, shortly after insects attained sexual maturity. In 1990, 80 pairs of one male and one female were confined to 9.0 cm-diameter plastic Petri dish arenas. Because it was thought that *F. auricularia* was more active at night, all pairs were observed between 2200 and 0500 h in a dark room illuminated by a 25 watt red light bulb. Behavior was observed and recorded in detail every 15 min until courting behavior was observed; at that point, behavior was observed continuously.

From August to December 1992, 20 pairs of one male and one female were videotaped with a Quasar video camera for at least 1 h, between 2200 and 0500 h. If courtship occurred, videotaping continued; if not, the trial was terminated after 1 h.

From August through December 1993, 26 trios of two males and one female were videotaped, as described for 1992. Two males were used in each trial in order to maximize the potential for sexual behavior, and to record male-male interactions in the presence of a female. All three insects were weighed on a Mettler analytical balance to the nearest mg, and body length (minus forceps) and forcep length to the nearest mm was measured with a Nikon dissecting microscope fitted with an ocular micrometer. For each two male-one female trio, one large male and one

comparatively smaller male were used. Large males ($\bar{X} = 72.2 \pm 8.7$ mg (SD)) were significantly heavier (Student's t-test, $df=17$, $P=0.0007$) than small males ($\bar{X} = 54.7 \pm 10.3$ mg), had significantly longer (Student's t-test, $df=11$, $P=0.029$) forceps ($\bar{X} = 40.7 \pm 9.31$ mm) than small males ($\bar{X} = 32.8 \pm 3.49$ mm), and were significantly longer (Student's t-test, $P=0.016$, $df=17$) from head to terminal abdominal segment ($\bar{X} = 96.2 \pm 2.68$ mm) than small males ($\bar{X} = 85.3 \pm 8.31$ mm). In the expectation that virgin males and females might improve sexual receptivity, some of the insects used in mating tests had been isolated and reared from nymphs in separate 20.0 ml glass vials provisioned with cat chow and a cotton-stoppered vial of water.

Videotapes were reviewed in normal motion to describe courtship behaviors for males and females and to determine sequence of courtship behaviors. Durations of courtships were determined by elapsed time as indicated on the videotape. The number of courtships in which a particular transition from one behavior to another was recorded. Transitions may have occurred more than once within a single courtship. Behaviors were transcribed into four first-order preceding-following transition matrices: one for male behaviors, one for female behaviors, a third for male preceding-female following behaviors, and a fourth for female preceding-male following behaviors. Self-transitions (repetitions of the same behavior) were not included. Each matrix was compared to the binomial distribution with a χ^2 test (Fagen and Young, 1978; Daniel, 1990) to determine if the frequency distribution of

behavioral transitions differed significantly ($P < 0.05$) from what would be expected by chance alone. Expected transition frequencies were calculated by

$$E = r \times n / N - r$$

where r = row sum, n = column sum, and N = grand sum (Fagen and Young, 1978). To prevent bias in computation of χ^2 , expected values < 1 were pooled, as well as their corresponding observed values (Zar, 1984). Observed and expected values of individual transitions were converted to proportions and the observed proportion tested for significant deviation from the expected proportion using a normal approximation (Walpole and Myers, 1989).

Male-male Interactions

Although male-male interactions were examined in Chapter 3, this study provided data for male-male interactions in the presence of a female. A female might provoke a greater degree of antagonism between males, especially if the earwig's natural mating system is based on contests between males to gain access to females. Male behaviors were described, but durations of behaviors were not calculated.

Ablated males

In November 1990, 30 males whose cerci had been amputated below the pygidium with a pair of scissors were confined to a 0.5 L jar with 30 intact males and 30 females. Sexual behavior was monitored on an irregular basis for two weeks and

for 5 consecutive days from 2000 to 2400 at 30 min intervals. In 1993, videotapes were made of seven trios of two ablated males and one female.

Body Measurements

To evaluate the conflicting evidence about male forcep size and to collect data on body size for both males and females, 60 female and 218 male field-collected earwigs were measured and weighed. Forcep length, left hind femur length and head width were measured with a Nikon dissecting microscope fitted with an ocular micrometer. Insects were also weighed, either live or dead, to the nearest mg with a Mettler electronic analytical balance. Not all parameters were measured for all insects. For example, dead insects were not measured for total body length since the abdominal segments tend to retract in some specimens, leading to inaccurate values. In addition, dead insects that were missing relevant body parts could not have those structures measured, nor were they weighed.

To examine for allometric growth, log-transformed male forcep length was regressed on log -transformed head width, an indicator of body size. Body size parameters such as head width, femur length, and pronotum width are frequently used in lieu of body length in allometric analyses of insect growth (Nijhout and Wheeler, 1996). In *F. auricularia*, body length was considered an unreliable measure since dry conditions often cause changes in length measurements, and because body length is affected by whether or not females are gravid (Crumb et al., 1941).

Results

Earwigs did not court or mate readily in the laboratory. Virginity did not improve sexual receptivity. Detailed observations were obtained for 13 courtships in 1990, and 41 courtships in 1992 and 1993. Of these 54 courtships, 25 led to mating. Eleven other courtships recorded in 1992 and 1993 contained three or less behavioral transitions, and were not included in any of the analyses.

Courtship Behavioral Repertoire

Sixteen different male behaviors were identified:

1. ***Forcep Wave (FW)***. The male moves his forceps back and forth laterally. He may also hold his cerci perpendicular to the substrate while waving them. The male may direct the cerci toward the female, or may simply wave his cerci in an untargeted fashion.
2. ***Move Backward (MB)***. The male moves backward, with his abdomen and forceps leading.
3. ***Antennate (AN)***. The male contacts the female's body with his antennae.
4. ***Forcep Stroke (FS)***. The male uses his forceps to touch the female in a back and forth motion, along her forceps, abdomen, pronotum and head. His forceps may also be rotated 90 degrees to the side and held perpendicular to the substrate while stroking.

5. **Forcep Bob (FB)**. The male rapidly moves his forceps up and down vertically, parallel to the substrate.
6. **Forcep Encircle (FE)**. The male orients his cerci perpendicular to the substrate (turned 90 degrees), and opens and closes them around the female's head, cervix, abdomen or forceps.
7. **Forcep Raise (FR)**. The male lifts his cerci vertically, from 45 to 90 degrees off the substrate.
8. **Forcep Depress (FD)**. Holding his abdomen parallel to the substrate, the male moves his cerci downward 45 to 90 degrees. The male usually FD against the female's abdomen, and, less frequently, her forceps.
9. **Forcep Splay (FSP)**. The male slowly opens his cerci wide. This is generally a display, done without contacting the female.
10. **Abdomen Curve (AC)**. The male curls his abdomen toward the female, often so that his abdomen is nearly doubled back on itself.
11. **Leg Rock (LR)**. The male stands near the female and bounces his legs back and forth without raising them off the substrate.
12. **Forcep Lift (FL)**. The male slides his forceps under the female's abdomen or forceps, and uses his cerci as a lever to raise her abdomen off the substrate.

13. **Push (PUSH)**. The abdomen and forceps are used to forcibly move the female across the substrate.
14. **Abdomen Twist (ATW)**. The male twists his abdomen 180 degrees in preparation for alignment of his genitalia with the female's ventral abdomen and genitalia.
15. **Slide Backward (SLB)**. The male pushes his abdomen, usually with the ventral side up, under the female's ventral abdomen.
16. **Copulate (COP)**. The male inserts his aedeagus into the female's vagina.

Ten discrete behaviors were identified for females:

1. **Retreat (RT)**. The female moves away from the courting male.
2. **Stationary (ST)**. As the male approaches or courts, the female remains still.
3. **Raise Abdomen (RA)**. The female lifts the terminal segments of her abdomen.
4. **Forcep Wave (FW)**. The female moves her cerci back and forth laterally, as in the male FW.
5. **Forcep Bob (FB)**. Similar to the male FB.
6. **Forcep Stroke (FS)**. Similar to the male FS.
7. **Abdomen Curve (AC)**. Similar to the male AC.
8. **Move Backward (MB)**. Similar to the male MB.

9. **Abdomen Twist (ATW)**. The female rotates her abdomen 60 to 120 degrees.

10. **Forcep Splay (FSP)**. Similar to the male FSP.

Courtship typically starts with male forcep waves (FW) that are not specifically directed toward the female or to any other insect in the arena (Figures 4.1 and 4.2). In a few seconds, however, the male begins directing FWs at the female, and then may move in a backward fashion (MB) toward the female, with his forceps directed toward her abdomen and forceps. Sometimes, the male turns around and antennates (AN) the female's antennae, head or pronotum before proceeding to other courtship maneuvers. The female may either retreat (RT) or may remain stationary (ST). If the female RTs, the male usually follows her by MB or, more usually, by turning around to chase the female, and then to turn back again, point his forceps toward her abdomen and FW. FW usually becomes more precisely targeted toward the female as courtship progresses.

If the female remains ST, the male may proceed with one or more other behaviors employing his forceps, such as forcep bobbing (FB), forcep stroking (FS), forcep raising (FR) or forcep splaying (FSP) in the female's direction. When the male FSs, he strokes the female with his forceps, along the sides, dorsum and venter of her abdomen, in a back and forth motion. Less frequently, he strokes her head or pronotum. FS may frequently involve stroking of the female's entire body, from cervix to cerci, and, in late courtship, is frequently directed specifically at the

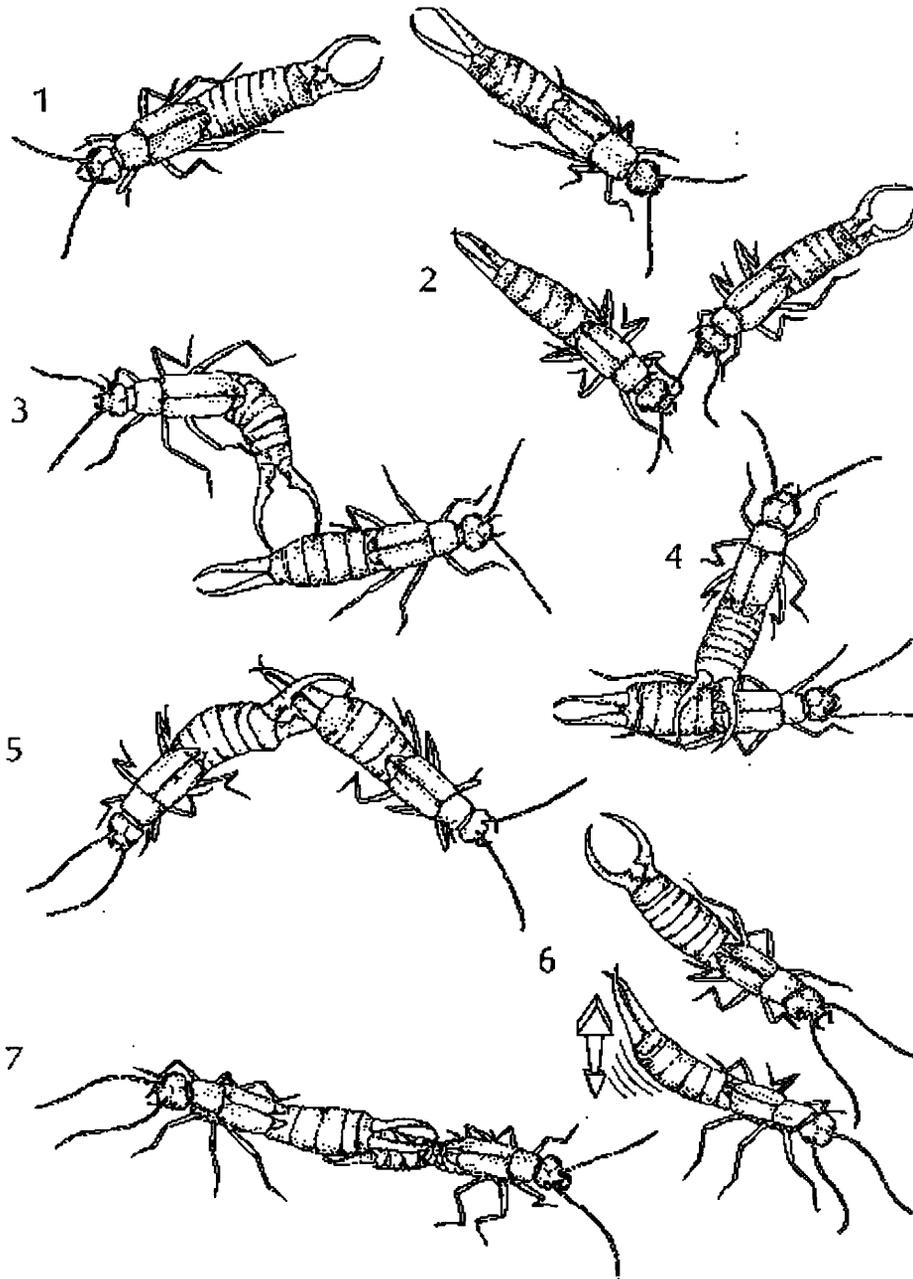


Figure 4.1. Selected courtship behaviors of *F. auricularia*.

1. Male moves backward toward female.
2. Male antennates female.
3. Male waves forceps toward female.
4. Male strokes female with forceps.
5. Male encircles female's cerci with forceps.
6. Female raises abdomen.
7. Copulation.

Male Behaviors

Female Behaviors

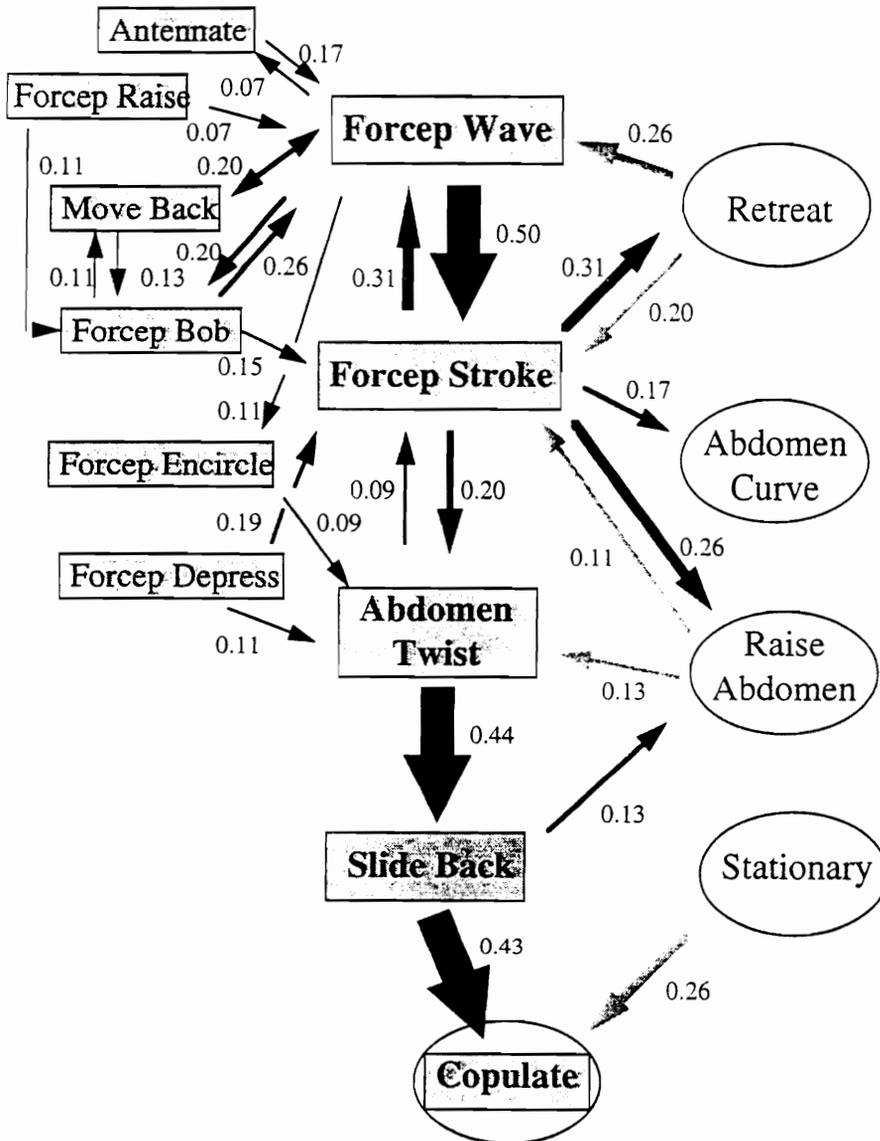


Figure 4.2. Flow diagram of male (rectangles) and female (ovals) *F. auricularia* courtship behaviors, based on 54 courtships. Arrows indicate the direction of behavioral flow. Numbers represent frequencies of courtships/54 in which a particular transition was observed (transitions occurring <0.07 were not included). Less frequently observed male behaviors are denoted by smaller rectangles.

female's ventral abdomen. FR and FSP, while directed toward the female's body, do not involve contact with her, and as such, are displays. When FB, or FR, the male generally turns around and aligns his abdomen and forceps directly opposing the female's abdomen and forceps, or at a 90 degree angle to her abdomen and forceps.

At some point during courtship, the male may begin forcep encircling (FE). He opens his forceps and uses them to enclose the female's head, cervix, abdomen or forceps. Sometimes the male then moves his forceps laterally, back and forth, while they are still closed around the female. Males sometimes engage in this behavior for relatively long periods of time (>1 h), while the female remains ST.

If the female is unreceptive, she responds to male FW, FS, FB and/or FE by retreating (RT) or, if she is receptive, by arching and bobbing her abdomen (FB) in the male's direction, or simply by raising her abdomen (RA). Less frequently, the female strokes the male's forceps with her cerci (FS), waves her forceps (FW) or splays them (FSP) at the male. The female also sometimes moves backward (MB) in the direction of the male, frequently with her abdomen curved toward him (AC); combined with the same maneuvers by the male, the pair sometimes spend several minutes circling around a small area of the arena, with their abdomens and forceps pointed at each other. Two females rotated their abdomens approximately 60 to 120 degrees in response to male FS. At any point in the courtship, a seemingly receptive female may break off courtship and RT. This generally elicits an earlier

sequence of behaviors from the male such as FW and FS. Sequences may be repeated several times in which the female AC, FB or RA, but then RT prior to copulation attempts by the male. Copulation never occurred in sequences in which the female did not perform one or more of these behaviors: FW, FS, RA, FB, FSP, and AC (Chi-square test, N=21, $\chi^2=21.0$, df=1, P=0.00).

Male forcep depression (FD) occurs later in courtship, after the female has indicated some level of receptivity. The forceps are held with the tips against the female's abdomen or forceps for several seconds. The male also frequently curves his abdomen into a "C" shape (AC) while courting the female. Leg rocking (LR) is usually performed after the male has devoted some time to courting a female which continues to break off courtship by RT. When the male LRs, he stands a short distance from the female, and is not in contact with her. When the female is ST, but does not RA or AC toward the male, the male may use his cerci as a lever to raise her forceps and abdomen off the substrate. He may also use his forceps to push the female's abdomen or forceps so that she is moved a small distance across the substrate. FL and PUSH were never observed in courtships that eventually led to mating.

If the female is receptive, the male backs toward the caudal end of the female and to twist the posterior abdominal segments (ATW) in an anticlockwise direction 180 degrees so that the left side is moved over the right, bringing the ventral part of the abdomen beneath the ventral part of the female's abdomen (Popham, 1965). He

then slides backward (SLB), in an attempt to copulate. ATW and SLB were the best predictors of male mating success: 80% of the time ATW appeared in a sequence, the male eventually copulated with the female (Chi-square test, $N=24$, $\chi^2=8.2$, $df=1$, $P=0.000$). Every copulation was preceded by a male SLB.

Copulation occurs in the apposed position previously described by Popham (1965). The male does not use the forceps as claspers to hold the female while mating. The male generally remains quiescent during copulation, except for occasional abdominal pulsing observed in some, but not all, copulating males. Females, however, frequently groom or even eat while in copula; they may also move around the arena, antennating the surface in front of them, dragging the attached male with them. Multiple copulations were common: nine individual pairs mated more than once. One pair copulated 7 times and a second mated 6 times within a 24-h period. Some females in the two males- one female treatment also had multiple mates.

The matrix of male preceding-following behavioral transitions departed significantly from a binomial distribution (Chi-square test, $\chi^2=538.2$, $df=225$, $P<0.05$) (Table 4.1). Courtship sequences were not highly stereotyped: almost 100 different behavioral transitions for males alone were recorded. Three of these transitions occurred significantly ($P<0.05$) more often than would be expected by

Table 4.1. Behavioral transition matrix for male *F. auricularia*, based on 54 courtships. The top value in each cell indicates the observed frequency of that particular transition, the bottom value indicates the expected frequency. Significant transitions are highlighted. FS=forcep stroke, FW=forcep wave, MB=move backward, FR=forcep raise, FB=forcep bob, FL=forcep lift, AC=abdomen curve, FD=forcep depress, ATW=abdomen twist, AN=antennate, FE=forcep encircle, SLB=slide back, COP=copulate, FSP=forcep splay, LR=leg rock.

Preceding Behavior	Following Behavior														Sum		
	FS	FW	MB	FR	FB	FL	AC	FD	ATW	AN	FE	SLB	COP	FSP		LR	PUSH
FS	17 14.8	7	6.9	2	9.5	2	0	9	11	0	9	6	0	2	1	0	73
FW	27 18.7	11	7.5	1	14	0	1	3	6	4	6	0	0	3	2	0	78
MB	3 5.7	4 4.9	0	1	7	0	0	1	1	1	0	0	0	0	1	1	28
FR	1	4	0	2	3.5	0	0	0	0	0	0	0	0	1	1	0	9
FB	8	10	6	4	1.1	0	1	3	3	0	1	1	0	1	0	0	38
FL	2	1	0.5	0	0	0.6	0	1	0	0	0	1	0	0	0	1	6
AC	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
FD	10	1	0	0	0.4	0	0	0.2	6	0	0	1	0	0	0	1	18
ATW	5	0	2	0	2.2	1	1	1	1.8	0	0	2.4	0	0	0	0	37
AN	3	9	0	2	4.8	0	0	1	0	0.8	1.9	0	2.5	1.0	0.6	0.5	16
FE	4	1	1	0	6	1	0	0	5	0	0.8	0	1.0	0.4	0.3	0.2	18
SLB	2	2	1	0	2.2	0.2	0	1.0	1.6	0.3	1.1	1.6	1.1	0.4	0.3	0.2	31
COP	0	0	0	0	0	0	0	0	0	0	0	0	2.0	0.8	0.5	0.4	1
FSP	3	2	1	0	2	0	1	1	0	0.2	0.05	0.1	0	0.02	0.02	0.01	12
LR	3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5
PUSH	1	1	0	0	0.4	1	0	0	0.4	0	0.2	0.4	0.3	0.1	0	0.1	3
Column Sum	72	62	29	10	44	5	4	20	32	7	18	33	23	9	6	5	379

chance alone: MB followed by FW, ATW followed by SLB, and SLB followed by COP. The distribution of transitions in the remaining three matrices (male preceding-female following, female preceding-male following, and female preceding-female following) was not significantly ($P>0.05$) different from the binomial distribution. However, several transitions occurred at a fairly high frequency: male FS followed by female RA in 10/54 courtships, male FS followed by female RT in 16/54 courtships, female ST followed by male COP in 14/54 courtships, and female RT followed by male FS in 11/54 courtships.

Males that eventually copulated ($N=17$) spent significantly (Student's t-test, $df=22$, $P=0.00009$) less time ($\bar{X}=13.4 \pm 11.6$ min (SD)) in courtship than males ($N=23$) which did not ($\bar{X}=59.8 \pm 53.6$ min). Unsuccessful males rarely quit courting, instead alternating periods of courtship with periods of rest or grooming.

Although sample size was small, body size did not appear to affect male mating success: of 13 copulations in two male-one female trios, 7 were by the large male, and 6 were by the small male. Large males ($N=17$) also did not court significantly ($P>0.05$) more often than small males ($N=13$). Latency time to copulation did not differ significantly ($P>0.05$) between large ($\bar{X}=16.3 \pm 15.0$ min, $N=7$) and small ($\bar{X}=12.6 \pm 10.74$ min, $N=6$) males. Females that eventually copulated were not significantly bigger nor heavier than females that did not. Since

courting occurred in 70% of all trios videotaped after early September of both 1992 and 1993, males appeared to accept the majority of females, regardless of size.

Male-male Interactions

A majority (64%, N=35) of taped two male-one female sequences where courting of the female occurred also contained male courtship behaviors directed at the other male, and sometimes, both males courted each other. Initially, these behaviors appeared to be indiscriminately directed at either the female or the other male. Males frequently alternated between courting the female and the other male, switching to the second insect when the first moved away. In some cases, males courted the second male prior to directing these behaviors toward the female. Male-targeted courtship behaviors were restricted to movements utilized early in courtship, such as FW, FR, FB and FS. In a single instance, one male FE the other male's abdomen. No ATW or SLB movements were seen. Even when males courted the other male, more time was spent courting the female. The recipient male usually responded by moving away from the courting male, or, more rarely, by an aggressive display of the forceps, or contact such as using the forceps to scissor the courting male's forceps.

Clearly definable male-male aggressive behaviors appeared in 36% (N=19) of the two male-one female videotapes. Surprisingly, this incidence was lower than that observed in the summer-early fall videotapes of males (\bar{X} = 38.4%), females

(\bar{X} =37.3%), or nymphs (\bar{X} =48.3%) (see Chapt. 3). Most of the behaviors in the fall-winter tapes involved aggression by one male in order to prevent courting of the female, or disruption of a copulation in progress. Body size did not appear to affect aggressive interactions: large males retreated from small males (N=15) as often as small males retreated from large males (N=15). All of the males attempting to interrupt a copulation were small males, while the copulating males were large. When these interruptions occurred, the trial began with the large male exclusively courting the female. Only after the large male successfully copulated with the female did the small male begin to make courting movements of his own toward the female, or to try to break up the mating. Small males usually disrupted copulations by FW and FS the female, and sometimes the large male as well, but more often directing aggressive movements toward the male, such as pushes and lunges with the forceps and abdomen. Small males also repeatedly FS the ventral part of both the male's and female's abdomens, near the point of engagement of their genitalia. The result of these actions was to cause the copulating pair to move away from the small male and, eventually, for the copulation to be broken. The small male was usually successful in disrupting a mating, although never successful in then gaining a copulation for himself.

Dorsal Palpation

Dorsal palpation occurs in interactions between males and females, and courtship was frequently interrupted for bouts of this activity. Dorsal palpation

occurred at a greater frequency (100% of trials) in these fall-winter videotapes than in the summer-early fall videotapes (\bar{X} = 19.9% of trials) (Chapt. 3). Females in the two-males-one female treatments performed this behavior (N=115/264 total DPs) significantly more often (Chi-square test, $\chi^2=14.9$, df=2, P<0.05) than did males (N=85 by the large male, and 64 by the small male), using a hypothesis that DP, if not affected by gender, would be equally likely to occur in the behavior of any of the three participants of the test (expected DP rate of 88 DPs per individual). However, there was no significant (P>0.05) difference between frequency of DPs given by females to large (N=63) males versus those given by females to small males (N=52). Assuming that all three insects in the two males-one female treatments have an equal chance of receiving DPs, there was no significant (P>0.05) difference between frequency of DPs received by any of the participants (females received 79, large males, 89, and small males, 96). Small (N=64 DPs) and large males (N=84 DPs) also did not differ significantly (P>0.05) with respect to frequency of DPs performed.

Ablated Males

In observations of amputated versus intact males, courtship behaviors using the forceps (in the case of ablated males, the cercal stump was observed to move) were displayed by both sets of males. However, only intact males (N=11) were observed to mate (Chi-square test, $\chi^2=11.0$, df=1, P<0.001). One of the females in

a videotaped sequence responded to courtship by an ablated male by AC and MB toward him, but courtship went no further.

Body Measurements

Females were significantly heavier than males (Student's t-test, $df=66$, $P=0.0000$) and had longer left hind femurs (Student's t-test, $df=76$, $P=0.0000$) but males had significantly bigger heads (Student's t-test, $df=17$, $P=0.0000$) and longer forceps (Student's t-test, $df=243$, $P=0.0000$) than did females (Table 4.2). The frequency distribution of male forcep length significantly deviated from normal (Kolmogorov-Smirnov goodness-of-fit test, $D=0.0639$, $P<0.05$, Sokal and Rohlf, 1981), with one peak at about 4.5 mm and a smaller peak at about 7.0 mm (Figure 4.3). Female forcep length was unimodally distributed (Figure 4.4). Male forcep length showed positive allometry when regressed on head width, an indicator of body size (Figure 4.5). The slope of the regression line (2.07) was significantly ($P=0.001$) different from 1, which indicates that forcep length grows proportionately twice the rate of head width.

All male body size parameters were significantly ($P<0.05$) correlated with each other, including forcep length with dry weight, head width, and femur length. Only dry weight and femur length, dry weight and head width, and wet weight and body length were significantly ($P<0.05$) correlated with each other for females (Table 4.3).

Table 4.2. Mean body measurements for male and female *F. auricularia*.

	Males		Females	
	$\bar{X} \pm \text{sd}$	N	$\bar{X} \pm \text{sd}$	N
Head width (mm)	2.29 ± 0.18	174	2.11 ± 0.11	45
Femur length (mm)	2.16 ± 0.29	165	2.42 ± 0.21	39
Forcep length (mm)	5.38 ± 1.33	192	3.26 ± 0.33	58
Dry weight (mg)	15.7 ± 6.50	144	29.5 ± 6.60	44
Wet weight (mg)	61.6 ± 15.00	28	64.1 ± 9.30	16

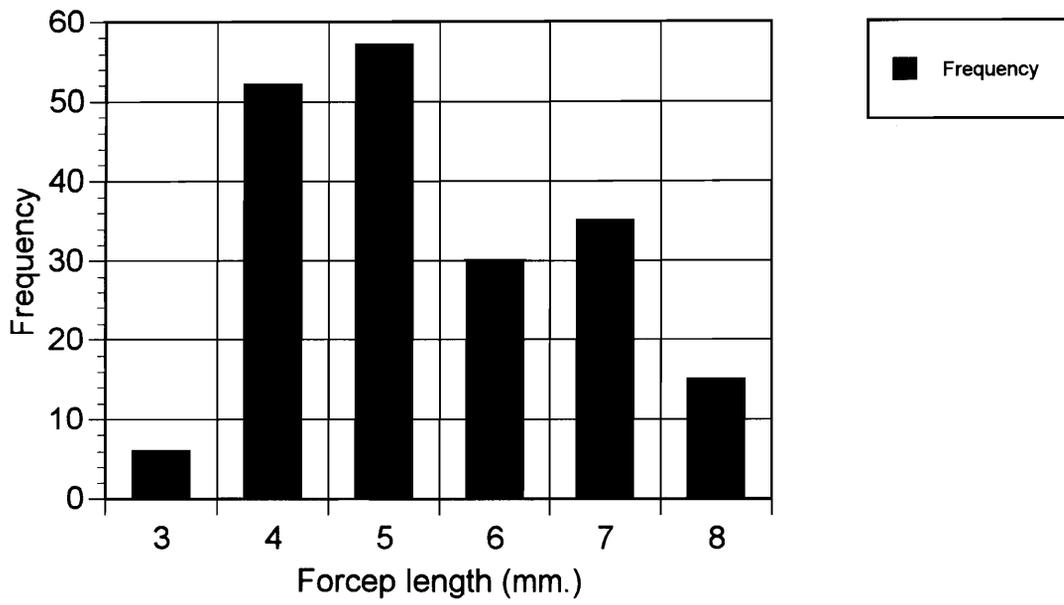


Figure 4.3. Frequency distribution of male *F. auricularia* forcep length (N=243).

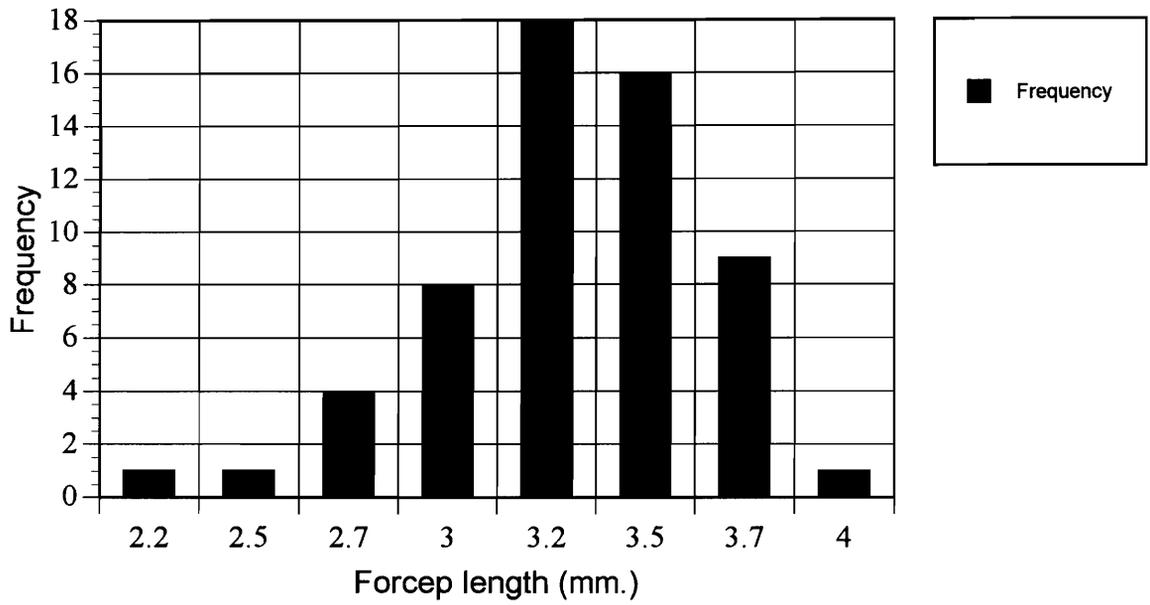


Figure 4.4. Frequency distribution of female *F. auricularia* forcep length (N=60).

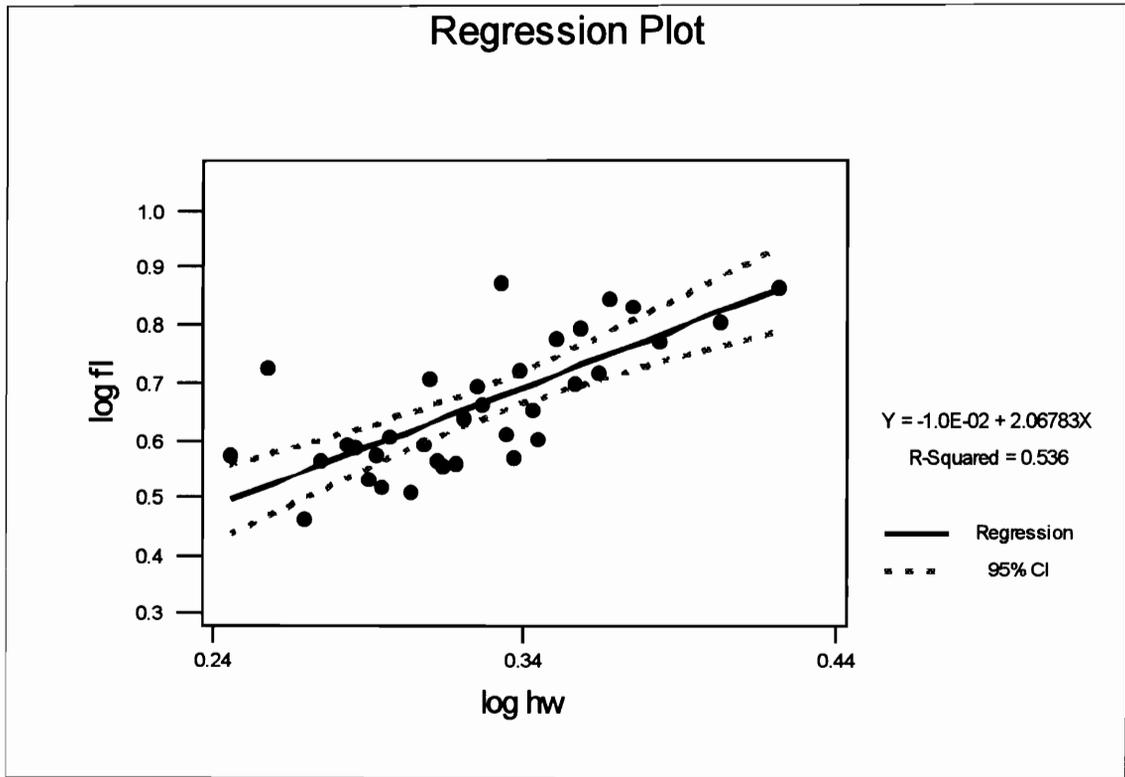


Figure 4.5. Relationship between forcep length (fl) and head width (hw) of male *F. auricularia* (N=174). The regression was significant, $F=38.06$, $df=34$, $P=0.000$.

Table 4.3. Correlations of body measurements for male and female *F. auricularia*, analyzed with the Pearson product moment correlation (Sokal and Rohlf, 1981).

Females		Males	
	r		r
Head width - femur length (N=39)	0.256	Head width - femur length (N=165)	0.187*
Head width - forcep length (N=45)	0.283	Head width - forcep length (N=174)	0.680*
Head width - dry weight (N=44)	0.317*	Head width - dry weight (N=144)	0.237*
Femur length - dry weight (N=39)	0.499*	Femur length - dry weight (N=144)	0.431*
Forcep length - dry weight (N=44)	0.272	Forcep length - dry weight (N=144)	0.482*
Femur length - forcep length (N=39)	0.330	Femur length - forcep length (N=165)	0.371*
Wet weight - body length (N=13)	0.705*	Wet weight - forcep length (N=28)	0.729*

* Significant ($P < 0.05$) correlations.

Discussion

Courtship and mating in *Forficula auricularia* are relatively non-stereotyped, consisting of almost 100 different behavioral transitions for males alone. Early courtship consists primarily of male displays with the forceps and abdomen, progressing to tactile stimulation by males and, sometimes, by females. In this context, the most important male morphological structures are the cerci, which are waved and bobbed and later, used to stroke and encircle the female's body. Insect cerci often serve as sensory receptors for tactile stimuli, but can be adapted for other purposes as well (Chapman, 1982). Male nongenitalic structures which come into contact with the female during sexual behavior may have become specialized and evolved into secondary sexual characters (Eberhard, 1985). Insect examples of such adapted structures include the parameres of the male carabid beetle *Pasimachus punctulatus*, which are used to tap against the female's abdomen during copulation (Alexander, 1959) and the distal teeth and hooks of the valves near the male genitals of the nymphalid butterfly *Limenitis* which are used to rub female's abdomen (Platt, 1978).

The males of some other dermapterans also use their forceps in courting. Caussanel (1970) described stroking and waving movements of the cerci by courting male striped earwigs, *Labidura riparia*, similar to the FW and FS described here for *F. auricularia*. Giles (1970) observed that males and females of some tropical Australian earwigs grip each other with their forceps. Males of the desert-

dwelling toothed earwig, *Vostox apicedentatus*, use their forceps in stroking and tapping the female (Moore and Wilson, 1993). Other examples of male earwigs that use their forceps in courtship are the African earwig, *Euborellia annulipes* (Bharadwaj, 1966) and the seaside earwig, *Anisolabis maritima* (Bennett, 1904). However, none of these species have male forcep-encircling behaviors as does *F. auricularia*.

Although ablated males were able to move the remaining proximal portion of the cerci (the stump) by flexing the abdomen, none were seen mating. This may suggest that the male cerci are necessary for reproductive success, either as secondary sexual characters that play an integral part in courtship maneuvers to win mates, or as weapons in male-male interactions. Aggressive interactions between males were not studied in this context, but males were relatively passive toward each other most of the time. Since copulations occurred in less than 50 % of the mating trials, it is also possible that it is simply due to chance that no ablated males mated. One of the males in the two males-one female treatments had only one forcep. While a female that he courted responded to him, they did not mate.

Based on this behavioral repertoire, the importance of the cerci in reproductive behavior appears restricted to courtship since males do not use the forceps as claspers to hold the female, as suggested by Goe (1925), and do not move the forceps while in copula.

At least two morphological factors may be significant in the use of the cerci in male reproductive behavior: length and shape. Forcep length was, indeed, bimodally distributed as previously reported by Diakonov (1925) and Radesater and Halldorsdottir (1993). The results of Eberhard and Gutierrez (1991) may differ because they relied on Diakonov's (1925) data, instead of measuring field-collected specimens. Eberhard and Gutierrez's (1991) conclusions differed from those of Diakonov (1925) because of the statistical techniques applied (Eberhard and Gutierrez, 1991). Kuhl (1928, in Van Heerdt, 1953) and Van Heerdt, 1953) questioned the validity of Diakonov's (1925) conclusions since he used metal tweezers to retrieve males from hiding places in the field, a technique which might bias the results in favor of males with longer forceps. Together with the observations here of intensive male use of the forceps in courtship, the data on allometry of forcep length lend further support to the hypothesis that sexually selected traits show positive allometry (Petrie, 1988; 1992). In their study of the male forcep length of 42 species of earwigs, Simmons and Tomkins (1996) did not find a regression slope for *F. auricularia* significantly ($P < 0.05$) different from 1 unless they divided males into those with long forceps and those with short forceps. In that case, they found that short-forceped male forcep and pronotum width (their chosen body size indicator) were isometric, while long-forceped males exhibited positive allometry. In the present study, strong positive allometry was seen in a field collected sample of 173 males which were not divided by forcep length before

statistical analysis. These results may differ because Simmons and Tomkins measured less than 45 insects, and those were curatorial specimens collected by others; or because the genetic frequencies for forcep length of their British population may differ appreciably from the population genetics of this American population. In addition, the collectors of these museum specimens may have used the same questionable method as Diakonov (1925). However, the limited data on large male-small male contests here did not suggest a large-male or long-forcep advantage, unlike in Radesater and Halldorsdottir (1993), where larger males won aggressive intermale contests more often than did small males, and also copulated more often. Although Radesater and Halldorsdottir (1993) asserted that large-forceped males enjoyed greater mating success, it was difficult to determine the contribution made by body size apart from forcep length and vice versa. If it is true that longer forceps suggest greater mating success, then the dimorphism may be maintained by a trade-off between lower energetic investment in cercus length resulting in greater survival for shorter-forceped males, and greater investment in cercus length, resulting in lower survival for longer-forceped males (Gadgil, 1972). Thus, shorter-forceped males may have a lower degree of reproductive success due to impaired competitive ability relative to longer-forceped males, but live longer. If, however, males with longer forceps do not, as suggested by the data in this study, have an advantage, the means for maintenance of the dimorphism—as opposed to the development of a normally distributed frequency distribution—in the population

are more problematical. Further examination of the effect of forcep length, controlling for body size, on mating success is warranted to resolve this issue.

The shape of the male's cerci might also affect mating success. Forceps appear to be dual-purpose structures for both sexes: for aggression and defense (Morgan, 1923; Fulton, 1924; Crumb et al., 1941), and for courtship. Use of the cerci as weaponry in the observed aggressive displays and rare nipping could select for longer forceps, since longer cerci might be more impressive in threatening opponents. However, aggression probably is not responsible for sexual differences in shape, since both sexes use the cerci to warn opponents. A possible hypothesis is that this sexual dimorphism is related to the use of this structure in sexual behavior (Gadgil, 1972; Moore and Wilson, 1993). In addition, the sequence of courtship behaviors may offer some explanation for the dimorphism of cerci between the sexes. While the waving, bobbing and stroking movements observed could as easily be performed with straight forceps such as those borne by the female, the male encircling behaviors may be responsible for the evolution of the dimorphism in cercus morphology. And although the female uses the cerci in reproductive behavior, she does not open and close her forceps around the male's body and, indeed, this would be difficult to accomplish with straight forceps. Forcep-encircling has not been seen in aggressive actions by males. Difference in male cercal shape has been found in at least one North American earwig species, *Pyragropsis buscki*. *P. buscki* has two distinct male morphs, differing in forcep shape, not length: one

with arcuate forceps, the other with elongate forceps (Hoffman, 1987). Provided that *P. buscki* males also use their cerci in courtship, this may present an intriguing opportunity to explore different ways of employing the male forceps in reproductive behavior within the same species.

An important correlate for mating success for many insects is large body size (e.g., Hughes and Hughes, 1982; McLain and Boromisa, 1987). In this study larger males—in terms of forcep length, total body length, and wet weight—did not mate significantly ($P > 0.05$) more often than did smaller males. These results contradict those of Radesater and Halldorsdottir (1993). While males which disrupted copulations in this study were all small, large males retreated from aggressive interactions with small males as often as small males retreated from large males, therefore suggesting little advantage accruing to size. Nonreproductive male-female interactions indicated that males were more aggressive toward females than toward other males. Aggression was not quantified in reproductive interactions, but some males were aggressive to reluctant females. It is possible that these results differ from those of Radesater and Halldorsdottir (1993) because fewer courtships and copulations took place in this study, or because the earwigs that they studied in Sweden represent a different race of *F. auricularia* with a different ecology and habits than that in the U.S. It is possible that, in contests with smaller males, larger males do obtain more initial copulations, and that because of this, smaller males employ a different reproductive strategy of letting the large male get the first mating, then

disrupting it and taking over. Since courtship in *F. auricularia* is sometimes labor intensive and is costly in terms of energetics, such a strategy might be beneficial to small males, particularly if less time is required to disrupt a copulation than to initiate one, and if sperm precedence is operational in this species. It is not unusual for "lower quality" males to employ a different strategy to obtain mates (e.g., King et al., 1969; Alcock, 1979). Male earwigs disrupting copulations frequently used their forceps to stroke the copulating male's ventral abdomen. This is similar to actions taken by some small male brentid weevils, *Brenthus anchorago*, which use their snouts to club at the genitalia of copulating males, interrupting matings (Johnson, 1982). However, in this study, none of the small males, all of which successfully disrupted matings, then mated.

Since males begin courtship and it is initially not focused on a particular insect, courtship behaviors appear to be elicited by reproductive readiness of the male. Earwigs naturally dwell in large associations, so precisely focused male courtship may not be necessary: males ready to mate will probably have a high likelihood of finding a receptive female nearby quite easily. If the first few females that the male encounters are unreceptive, they will move away from him, and he will likely find a responsive female without traveling too far or expending too much energy. The female-biased sex ratios found in the field in late summer and early fall (Chapt. 1), the usual mating time for this population, would make it even easier for males to locate females for courting.

Male-targeted male courtship, or homosexual behavior, is not unusual in insects. Males may be so primed to mate that they fail to discriminate between males and females, and therefore, end up mounting other males (e.g., *Drosophila melanogaster*, Tompkins et al., 1980). Another insect in which males frequently mount other males is the corixid water bug, *Palmarcorixa nana*, which lives in large aggregations (Aiken, 1981) like *F. auricularia*. It is probable that the earwig does not have a sex pheromone since the insects are brought into close association by the aggregation pheromone. The earwig's gregarious lifestyle would render signaling by sex pheromones energetically wasteful; males can merely wave their forceps and move around until encountering a favorable response as a raised female abdomen. Females were rarely aggressive to courting males, passively rebuffing them instead by moving away, so indiscriminate males would not be at risk to injury by females.

Like the females of various other insect species (e.g., Deka and Hazarika, 1996), female *F. auricularia* frequently move about and feed while in copula. This may be motivated by the intensive nutritional requirements of female insects (Thornhill and Alcock, 1983), especially in species in which the female provides brood care, such as *F. auricularia*. Female European earwigs reportedly feed very little, if at all, during brood care (Lamb, 1976a). Although the time from beginning of copulation to locomotion of the female was not measured, it is noteworthy that females did not generally begin to move about or to feed until copulation had been underway for some time. Data on time to transfer spermatozoa by the male would

be useful in this regard; females moving about before sperm transfer was complete would be risking loss of the sperm through possible disruption of the copulation. If, however, the frequently long copulations in European earwigs result from male strategies to protect paternity such as guarding, benefits to the female from feeding would outweigh those from maintaining the pair bond once sperm transfer is complete.

The European earwig's reproductive behavior is unusual in that females may actively participate in courtship. The females of most other earwig species remain still if receptive (e.g., Caussanel, 1970; Moore and Wilson, 1993), and do not use the forceps in interactions with the male other than in aggression. Because only about 50% of courted females eventually copulated and females frequently indicated receptivity only to later break off courtship—sometimes repeatedly with the same male—some measure of female choice may be operational. Forcing males to prolong courtship, especially when male behaviors are so many and varied, may give females the opportunity to evaluate the genetic quality of the male. Further experiments with tethered males of differing features such as body size or forcep length should help illuminate this issue.

The results indicated that dorsal palpation may have an important sexual role in behavioral interactions between male and female *F. auricularia*. Females performed this behavior significantly ($P < 0.05$) more frequently than did males. This may be related to the evidence that males produce the aggregation pheromone on

the cuticle. Additional experimental work involving several females as well as males may elucidate whether females dorsally palpate other females as often as males.

Sex ratios of field populations (Chapt. 1) were significantly ($P < 0.05$) female-biased for most of the season, including the early fall, when mating was first observed in the laboratory. Although an excess of females might lead to the expectation that they should be less discriminating in mate selection, these observations suggest that this is not the case. It might also be expected that most, if not all, males would be ready to court. But for unknown reasons, not all males courted in lab trials. Perhaps males not exhibiting a copulatory interest in the female were not physiologically ready to mate, either due to lack of maturity or because they had recently copulated, and were, thus, in a refractory period.

CONCLUSIONS

The European earwig's behavior had been largely unexplored, prior to this study. These results afford a better understanding of the insect's life history in Virginia, its aggregation behavior, and its social behavior.

Information about southwestern Virginia populations of earwigs was provided by this research. Because of its relatively cool, humid summers, Blacksburg, and surrounding areas in southwestern Virginia, are favorable to earwig outbreaks. In 1990, 1991, and 1992, nymphs emerged about mid-May, and appeared in groove-board traps by late May, where they predominated until about mid-late June. Adults were collected from early June, peaking in mid-late July, until no more insects could be found in September or October. Populations were lower in 1991 than in 1990, correlated with the hotter, drier summer of 1991. Sex ratios were female-biased (about 60% female) throughout the season at most of the 11 sites that were sampled, and this bias became more marked by fall. There were several differences between this southwestern Virginia population and those studied by previous investigators (e.g., Crumb et al., 1941; Lamb and Wellington, 1975; Maxwell, 1988). For example, some of these other studies found equal sex ratios in spring, but an excess of females by fall, as well as adult males in spring traps and mating pairs in late summer traps. In addition, because nymphs were not collected later than mid-July, there was no evidence for multiple brooding in the Virginia population, as suggested by Crumb et al. (1941) and Lamb and Wellington (1975). The disparities

between these studies may be due to the effects of regional differences in climate and geography on earwig ecology.

The earwig's pest status in southwestern Virginia is primarily based on its propensity for aggregating in large numbers inside and outside the home in highly visible areas. This research showed that aggregation occurs as a result of a pheromone which originates on the male cuticle, and is quite probably a minor component of the male cuticular hydrocarbon profile. About 88% of the hydrocarbons found in extracts of cuticles were identified, and although males and females produce a nearly identical mixture of cuticular hydrocarbons, only extracts of male cuticle were attractive. Frass was also attractive but because earwigs regularly eat shed skins and carcasses of other earwigs, this was not surprising. If frass contained the pheromone, and the male cuticle had merely become attractive due to close association of the insects with the frass, then the female cuticle would be expected to be attractive as well, which it was not. This study also refuted the results of Sauphanor (1992), who asserted that the aggregation pheromone was contained in tibial glands in the legs. On the contrary, the chemical analyses in this study showed that earwig legs contain a relatively large amount of oleic acid, a generalized repellent (Howard et al., 1982), and behavioral bioassays in this study showed that leg extracts and leg "trails" extracts were significantly repellent rather than attractive. Also, quinones were significantly repellent, and repellency

increased with increasing concentration. Quinones may serve dual roles of defensive secretion and alarm pheromone for earwigs.

The earwig's hydrocarbon profile may serve as a taxonomic character (Grunshaw et al., 1990) in future research. Mono- and dimethylalkanes predominate, and branching is at odd-numbered carbons and at position C-9 or higher. Since the earwig is notoriously difficult to grasp, it could be that cuticular hydrocarbons augment the earwig's defensive weaponry of quinones by imparting a slipperiness to the cuticle of the insect. The hydrocarbons may also enhance the dissolution of quinones over the earwig's body, and that of its attacker.

F. auricularia has been widely considered a nocturnal insect (e.g., Crumb et al., 1941; Lamb and Wellington, 1975), but this research indicates that while nymphs are more active at night, adults are not. Based on activity budgets, adult behavior did not significantly ($P>0.05$) change after sundown. Gender-based differences in behavior included greater time expenditure by females in feeding than by males. Age was responsible for several behavioral differences: nymphs fed, moved around and were more aggressive than adult males. Partner age affected behavioral interactions in that adults rested and groomed less when paired with juveniles, but fed more. When with nymphs, adults monopolized food. Nymphs paired with nymphs were more aggressive than nymphs paired with females. Social behaviors generally comprised <10% of the total activity budget of the earwig. Aggression involved use of the forceps by both sexes, and appeared most often as

defense of access to food. Dorsal palpation is probably a form of allogrooming, and may have several functions such as distribution of the aggregation pheromones originating on the male cuticle, and use in courtship. Dorsal palpation not only occurred at a much higher rate in courtship videotapes, but females perform the behavior on males more frequently than males on females.

Since group-living is an integral part of the earwig's lifestyle, the behavior of grouped insects and the effect of increasing group density was of interest. As group size increased, nymphs spent significantly ($P < 0.05$) less time feeding alone and grooming, but more time resting, which might be expected if food resources had to be divided between more individuals. Contrary to what might have been expected (e.g. Marler, 1976), aggression did not increase with group size. Lowered or neutral rates of agonism may be necessary to maintain group stability (Judge and de Waal, 1993) in gregarious animals such as earwigs. It was expected that social interactions might increase with group density, but the reverse occurred: time spent in social behaviors decreased with increasing group size. Median percent time spent contacting group members went up slightly, however, with group size, and antennal contact rate increased significantly ($P < 0.05$) with group size. Individual earwigs in groups may need to keep informed of group density for resource utilization, and predator protection.

The aggregation pheromone appears to bring earwigs in close proximity, and then males indiscriminately perform courtship behaviors until obtaining a favorable

response, evidenced by the great amount of male-targeted male courtship behavior in two male-one female trios. Because of the relatively low courtship and copulation rate, and the fact that females frequently broke off courtships at stages just prior to copulation, some measure of female choice may be operational. The female European earwig also appears to be unusual in its courtship behavior because she may actively participate in courtship. Similar to some other female insects (e.g., Deka and Hazarika, 1996), however, the female typically feeds during copulation, probably to increase nutritional reserves.

The examination of courtship and mating behavior uncovered an extensive repertoire of male and female acts which combined to form a complicated flow of behavioral transitions. Males initiate courtship primarily with displays, and progress to tactile stimulation; the male's forceps figure prominently in both displays and contact. Males that had most of the cerci removed were able to move the proximal portion of the cerci, and could perform some courtship maneuvers, but none were seen mating, which suggests that the forceps are an important determinant of reproductive success for males. Forcep length and shape may also be important. The Virginia population had a bimodal distribution of male forcep length, but there was no evidence that males with longer forceps were more successful in getting mates than males with smaller ones. Although the males of some other earwig species (e.g., Bharadwaj, 1966; Moore and Wilson, 1993) use their forceps in stroking and waving motions similar to those described here, there appear to be no

similar encircling motions with the male cerci, as found for *F. auricularia*. Further support for the hypothesis that the curved shape of the male forceps may be due to sexual function is lent by the fact that males do not use their forceps to encircle the bodies or cerci of opponents in aggressive interactions, and females, with their relatively straight cerci, are not able to perform this behavior.

Male *F. auricularia* with larger bodies did not appear to have a reproductive advantage over small males, as seen by Radesater and Halldorsdottir (1993). However, it is interesting that in two male-one female trios, the only males which disrupted courtships were small males, and they never courted the female until after the large male had successfully mated with the female. These observations could indicate that small males do have a disadvantage, and in some cases employ an alternative strategy for obtaining matings.

Our knowledge of the behavior of the European earwig still leaves many unanswered questions. Since this insect has been little studied compared to many other insects, much remains to be done. In particular, identification of the aggregation pheromone would be useful, especially in the context of producing a synthetic chemical which could be used in control, or perhaps collection of populations of *F. auricularia* in geographic regions where it can be useful as a biological control agent. Further examination of the significance of the male forcep length and shape should be undertaken to more definitively determine its role in reproductive success. The effect of male and female body size should be further

analyzed, especially to resolve the conflicting results of this study and that of Radesater and Halldorsdottir (1993). The social interactions of the earwig deserve more attention, especially dorsal palpation, an apparently uncommon behavior in non-eusocial insects.

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