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Population dynamics, spatial distribution, dispersal behavior and life history of the predaceous histerid, Carcinops pumilio (Erichson), with observations of other members of the poultry manure arthropod community.

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POPULATION DYNAMICS, SPATIAL DISTRIBUTION, DISPERSAL BEHAVIOR AND LIFE HISTORY OF THE PREDACEOUS HISTERID, *CARCINOPS PUMILIO* (ERICHSON), WITH OBSERVATIONS OF OTHER MEMBERS OF THE POULTRY MANURE ARTHROPOD COMMUNITY

A Dissertation Presented

By

CHRISTOPHER JOHN GEDEN

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DEDICATION

To my parents, George F. and Doris L. Geden, for all their years of encouragement, love, and emotional support.

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ABSTRACT

Population Dynamics, Spatial Distribution, Dispersal Behavior and Life History of the Predaceous Histerid, Carcinops pumilio (Erichson), with Observations of Other Members of the Poultry Manure Arthropod Community.

February 1984

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Directed by: Dr. John G. Stoffolano, Jr.

Succession of arthropods associated with poultry manure was monitored in 2 poultry houses throughout a manure accumulation cycle. Sphaerocerid flies and cereal mites were the first arthropods to become established, followed by Macrocheles muscadomesticae and Carcinops pumilio. Macrocheles abundance peaked at 10 weeks post-cleanout, then declined, while Carcinops adults increased in number throughout the cycle. Carcinops sex ratios were male-biased early in the cycle, approached 1:1 in the middle weeks, and became male-biased again in later weeks. Significantly smaller-sized beetle

adults appeared following peaks of numbers of immatures. Adults during peaks of predator abundance had significantly less-developed ovaries than those from lower density populations.

Spatial distribution studies showed that Carcinops adults and larvae were concentrated within a narrow band of the manure surface and were more abundant near the crest than the base of manure rows. Carcinops and sphaerocerid adults showed no significant preference for wetter or drier manure; immatures of these species, Macrocheles adults and cereal mites were significantly correlated with higher manure moisture content. Predators preferred older to fresh manure, even when the latter was rich in dipteran prey.

At peak Carcinops densities in the field, beetles were observed to fly. Flight was not correlated with physiological age, sex, body size, mating condition or ovarian state. Flight propensity was reversed in the lab via administration of prey. Flight was induced in the lab by witholding prey.

Carcinops was successfully colonized using Coproica hirtula as a prey source and Ralston-Purina house fly diet as a medium. Adult longevity averaged ca. 90 days; no major difference was observed between male and female survival. Development time from egg to adult was 21.6 days at 30-31^{o} C. Females would mate immediately after emergence; males required 5-6 days of prey-feeding before mating. A partial life table was developed for this species under optimal colony conditions.

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INTRODUCTION

In terms of total revenue generated by agriculture in Massachusetts, egg production ranks third, representing 12% of total cash receipts. This contribution to the state's agricultural economy is eclipsed only by that of the dairy and greeenhouse/nursery industries. A major problem faced by all egg producers is regulation of the common house fly, Musca domestica L., which, when unchecked, can build up to enormous population levels in the large manure accumulations typically associated with modern egg production practices. Maintaining populations of this pest below levels acceptable to public health officials and the local citizenry has historically been problematic for virtually all individuals involved with animal agriculture.

In recent years, fly control on poultry farms has become increasingly difficult for three principal reasons. First, in order to increase farm revenue, many egg producers are increasing the number of birds per unit of housing, resulting in greater accumulations of manure, where larvae of this pest breed. Second, changing demographic patterns, in particular, a shift of people from urban to suburban and rural settings, have placed previously isolated producers in close proximity to human dwellings and population centers. These changes, along with increasing public intolerance of filth flies, have resulted in the need for producers to maintain more vigilance with respect to

fly control than has historically been practiced. Third, traditional chemical methods of fly control have become less satisfactory due to the high insecticide resistance shown by house flies, increasing cost of application, and public demand for lessened pesticide residues in food products and the environment.

Caught in the squeeze between public fly control demands and the high cost, restriction and ineffectiveness of chemical control measures, many New England producers now face a crisis situation. Dozens of once-profitable poultry farms in Southern New England have been forced into closure in recent years by these conflicting, and at times, irreconcilable pressures.

Clearly, alternative control methods for house flies are sorely needed. Most research to date on biological control of filth flies has centered on manipulation and mass-releases of parasitic wasps, especially members of the family Pteromalidae. The results of over 30 years of work with these parasites have largely been discouraging; wasps have generally been found to be cost-ineffective and have failed to suppress fly populations below acceptable nuisance thresholds. These drawbacks are further compounded by the shortcomings of many private insectaries with respect to parasite quality control.

As a consequence of these factors, recent years have witnessed renewed interest in predators of filth fly immatures in accumulating animal manure. In Massachusetts, the two most important predatory species are the mite, Macrocheles muscadomesticae (Scolopi), and the histerid, Carcinops pumilio (Erichson).

M. muscadomesticae is a well documented, highly effective predator of fly eggs and newly hatched larvae, and has been extensively studied. Carcinops, on the other hand, although frequently the most abundant and clearly the most important coleopteran predator of fly immatures, has received comparatively little attention. At the start of this project, very little was known of the population dynamics, prey range, ecology, behavior and life history of this beneficial insect. Sound pest management practices dictate a thorough understanding of the biology and dynamics of natural enemy, as well as pest, species. Without such knowledge, sampling and surveillance have neither heuristic nor predictive significance. It was this need which formed the basis of the present dissertation.

LITERATURE REVIEW

The House Fly, *Musca domestica* L.

Historical and epidemiological significance. Since the plague of flies was visited upon the Egyptians in Biblical times (Exodus 8:24), filth flies and, in particular, the common house fly (*Musca domestica* L.), have been viewed as being among the primary arthropodan pests of man. Although medieval and early modern physicians speculated on the role of house flies in the transmission of disease, Raimbert (1869) was the first to clearly demonstrate the potential of these pests in the mechanical transmission of pathogens (anthrax). Nicholas (1873) pointed out that the habit of flies to alternately alight on human food and refuse was cause for concern with respect to public health, and it is felt that this report provided the impetus for much of the subsequent work by others on the behavior and bionomics of filth flies (West 1951). In the years following 1896, L. O. Howard, who may be viewed as the father of the study of flies, investigated numerous aspects of the biology and epidemiological importance of the house fly. This work culminated in the first authoritative text on this pest in 1911 (Howard 1911), and was shortly followed by the publication of similar volumes by Hewitt (1914) and Graham-Smith (1914). Because of the importance of filth flies in the mechanical

transmission of the agents of disease, Howard (1909) proposed changing the common name of M. domestica to "the typhoid fly", however, the term "house fly" prevailed due to extensive prior usage and convention.

In the years since the publication of the above texts, there has been an "explosion" in the volume of literature dealing with Musca and other non-biting flies in relation to disease. Major diseases in which flies have been thought to play an epidemiological role include dysentery, infantile diarrhea, typhoid fever, food poisoning, cholera, helminthoses, poliomyelitis, hepatitus, salmonellosis and yaws. For further information on the epidemiological significance of house fly, the reader should consult Greenburg (1973), Keiding (1976), Lindsay (1956) or West (1951).

Economic status of house fly as a pest. In most of the developed world, where improved sanitation and health care have essentially eliminated fly-born disease, the status of house fly and other filth flies has largely been redirected from epidemiological to economic considerations. Fly populations readily develop in and around animal agriculture facilities due to the large accumulations of manure typically associated with modern intensive production practices. A major obstacle to the development of pest manaement approaches to filth fly control has been, and remains, the ambiguous and enigmatic economic status of these pests. Unlike plant pests, where meaningful correlations can be made between pest densities and crop losses

(Metcalf and Luckmann 1975), there is virtually no evidence which indicates that house fly causes any direct economic damage to livestock, poultry or swine production (Anonymous 1979, Campbell 1981).

As a consequence, house fly is regarded as a "nuisance" pest, whose economic status depends on a variety of environmental, cultural and demographic factors, including the distance between breeding sites and nearest neighbor, population densities of both flies and humans, and the tolerance of local communities towards flies. Completely isolated producers can thus accept fly populations of sizes approaching infinity, while those abutting human population centers may be required to maintain near-zero levels. As a result of the great variation in these factors, the prospects for developing fly "nuisance thresholds" which have any meaning over large areas are discouraging.

As pointed out at a meeting sponsored by U.S.D.A. on livesock pest management (Anonymous 1979), the fact remains that house fly is a pest, regardless of the reasons, and large amounts of precious farm capital are expended on its control. Hard data on losses to M. domestica are extremely difficult to generate and, with the exception of a few attempts by workers in the early part of the century (L. O. Howard 1909, C. W. Howard 1917), nearly all of the available information on this subject is based on U.S.D.A estimates. In 1976, U.S.D.A. (Anonymous 1976) estimated total losses to house fly at $115,000,000 per year. (This figure was, in turn, largely derived by

extrapolation from California estimates of $20,000,000/year (Robinson 1975).) According to U.S.D.A., losses can be further broken down by commodity as follows: beef = $30 million, dairy = $30 million, swine = $25 million, poultry = $25 million, and horses = $5 million (Anonymous 1976). Most of these losses are due to control costs in the form of pesticide applications. It has been estimated that 10.8 million pounds of insecticide are applied annually to control pests of livestock and poultry, at a cost of $60 million for the chemicals alone, independent of the associated equipment, energy and labor expenses (Anonymous 1979).

Sampling methods for adult house flies. Another factor which further clouds the already murky picture of house fly economics is the lack of a universally accepted sampling method with which thresholds can be established. Light traps emitting large amounts of ultraviolet radiation in the range of 330 to 370 nanometers have been found to be effective in attracting flies (Tarry et al. 1971). Trap efficiency can be greatly augmented by the addition of heated baits (Pickens et al. 1975). Although light traps can collect over 400 flies per day (Morgan et al. 1970), their use for survey purposes is limited by the high variation in capture rates with respect to trap height and position (Driggers 1971, Hienton 1974, Pickens et al. 1972, 1975).

Baited traps for house fly control and surveillance were first examined by Morrill (1914), who found that ripened bananas were highly attractive to flies. Since that time, most research on baits has

concentrated on combinations of sugar and attractants such as ammonium carbonate or yeast (Mulla et al. 1977, Pickens et al. 1973, Wicht and Rodriguez 1970) or the sex pheromone "Muscalure" (Carlson and Beroza 1973). As with light traps, however, the utility of bait stations is limited by high capture-rate variation associated with trap position (Willson and Mulla 1973, 1975). A further drawback to baited traps is that they must be changed at least every 1-2 days or else the accumulating fly cadavers become attractive to blow flies (Patterson 1981).

The "Scudder grid" (Scudder 1947) sampling method has been in use for many years, and has the advantage of providing an immediate estimate of fly numbers by making visual counts of alighting flies per unit of time. Despite the simplicity and immediacy provided by this method, obvious drawbacks of the grid include the need for care in maintaining consistency between sampling periods with respect to grid location, time of day and counting time. There is also considerable variation among different individuals using the grid under similar conditions (Patteron 1981).

A number of other methods have been developed which exploit the tendency of flies to rest on the edges of hanging objects (West 1951). These include fly paper and strips, rigid sticky strips (Patterson et al. 1980) and modifications of the "Wiliams trap", which was originally designed for stable flies (Williams 1973). Another common method for estimating fly densities which requires neither immediate counting nor sticky materials is the use of "spot cards", which are

hung near fly resting places. The number of fly specks deposited over time can thus be used as indicator of relative changes in the abundance of flies (Axtell 1970).

The wide variety of population estimation methods makes meaningful comparison of annoyance thresholds difficult to make. In Georgia, control measures are recommended when 3 X 5 inch index cards contain greater than 25 specks after 24 hours (Nolan 1981), while in North Corolina the threshold is expressed as 350 flies per baited trap per week (Rutz 1980). In Nebraska, the action threshold is "arbitrarily" set at 100 flies per sticky trap per two-week interval (Campbell 1981).

Nolan (1981) has taken initial steps to attempt to compare and correlate fly number estimates obtained by some of these methods. Based on work done in Georgia poultry houses, he found that 7.54 adult flies per square foot is the equivalent of 14.8 fly specks per 3 X 5 index card per day and 34.9 fly landings per Scudder grid (Nolan 1981).

Cultural and Chemical Fly Management Strategies

Cultural control. House fly larvae develop optimally in manure with a 60-75% moisture range (Miller et al. 1974). At levels above above 80%, manure becomes anaerobic and larvae will not penetrate below the surface layer. This fairly narrow tolerance interval has given rise to the development of manure management practices which drive moisture

levels towards one extreme or the other, leading to the expression "wet it or dry it" (Loomis 1981). Under "wet" systems, manure is removed, liquefied and held in lagoons, tank trucks or underground storage pits (Bell et al. 1965, Fairbank 1963, Ostrander 1966). In "dry" systems, manure drying is promoted by proper ventillation, low bird densities and water management (Card and Nesheim 1975, Winter and Funk 1941). In recent years, additional manure aeration by mechanical stirring, or "rotovation", has been advocated by some workers in Florida (Hinton 1977, Hogsette 1979).

Both the frequency and timing of manure removal can have a major impact on potential fly populations. Removal on a very frequent basis will break the breeding cycle of the fly (Wilson and Card 1956), although this is impractical except where completely automated systems are in operation. Removal on a bi-weekly or monthly basis creates conditions which are optimal for fly outbreaks (Peck and Anderson 1970), while very long accumulation times (>3 months) encourage manure drying and favor the establishment of natural enemy populations (Bills 1973, Legner 1971, Peck and Anderson 1969).

Chemical control. Where manure management fails to prevent the development of fly populations, insecticides have been and remain the primary method of fly control. In poultry houses, pesticides are generally applied as space sprays (mists and fogs) or as residuals on walls and ceilings. Poison baits are also used on occasion, as are larvicides which are applied to the manure surface, although the

latter adversely affect natural enemies in the manure as well. In addition, there has been an increased amount of work in recent years on "feed-through" insect growth regulators and chitin synthesis inhibitors (Ables et al. 1975, Georghiou et al. 1978, Morgan et al. 1975, Weaver and Begley 1982). A thorough treatment of chemical control of house fly is beyond the the scope of this review. For general information on insecticidal control of house fly, the reader should consult Keiding (1974, 1976) and Pal and Wharton (1974), while discussions of insecticide resistance and resistance management may be found in Brown and Pal (1971), Georghiou (1972), Keiding (1976), Rawlins et al. (1982), Roush and Plapp (1982) and Vinson and Plapp (1974).

Natural Enemies of Fly Immatures

Because of the cosmopolitan distribution and long-standing public health/economic importance of the house fly, there has been a considerable amount of research conducted on natural enemies of this pest. In 1964, Jenkins reported that there were 135 known pathogens and parasites of synanthropic flies, and 83 predator species (Jenkins 1964). Since that time, the list has grown much longer as efforts have continued to locate, assess and import exotic predators and parasites of filth flies (Hoyer 1981, Legner et al. 1974, 1983). Despite the large number of parasitic, predatory and scavenger species which have been examined, a relatively small number have been found to

possess real potential for utilization in fly IPM programs. The following review is restricted to the most important and promising natural enemies of fly immatures.

Parasites. There is a large volume of literature dealing with insect parasites of house fly (Ables and Shephard 1974a,b, 1976, Beard 1964, Legner 1967a, Legner and Dietrick 1972, 1974, Legner and Gerling 1967, Legner and Greathead 1969, Legner and Olton 1970, Legner et al. 1965, 67, 76, Morgan 1981, Morgan and Patterson, 1975, 1977, Morgan et al. 1975a,b, 1976a,b, 1978, Propp and Morgan 1983). Nearly all of this work has focused on parasitic wasps of the family Pteromalidae, although some research has been conducted on staphylinid parasites of the genus Aleochara as well (Lesne and Mercier 1922, Moore and Legner 1971, 1973, White and Legner 1966).

The pupal parasite Nasonia vitripennis (Walker) received a great deal of attention in the years between 1955 and 1970, and was used as a model system for studying population dynamics, host discrimination and other aspects of parasite-host interactions under laboratory conditions (Edwards, 1961, Madden and Pimentel 1966, Nagel and Pimentel 1963, Varley and Edwards 1957, Wylie 1958, 1965, 1966). As was pointed out by Legner, however, this species has little potential for fly suppression in the field due to its inability to locate fly pupae which are not directly exposed on the manure surface (Legner 1967a). Despite its poor biocontrol potential, many commercial insectaries continue to market these parasites for fly control, either

deliberately, because of the ease with which they can be mass-reared, or inadvertently, since they frequently contaminate colonies of other beneficial species (Legner 1981, Stage and Patterson 1981).

Pteromalid parasites which hold the greatest potential for fly suppression belong to the genera Spalangia and Muscidifurax (Morgan 1981), although under certain environmental conditions Spheigigaster and Pachycrepoideus species appear to be effective as well (Legner 1977, Legner et al. 1974, Pickens 1981). With house fly, as with other species, the question of whether single or multiple species introductions will provide maximal pest suppression remains problemmatic (Axtell 1981), however, the most spectacular successes have been acheived via sustained releases of single species, particularly Spalangia endius Walker (Morgan and Patterson 1977, Morgan et al. 1975a, Morgan 1981).

It has been pointed out that despite the apparent effectiveness of S. endius under mass-release conditions, it appears to be competitively inferior to other species such as Muscidifurax raptor (Legner 1977), which raises doubts about the persistance of these parasites in the field following augmentative releases. In lab colonies, M. raptor readily outcompetes and displaces S. endius due its shorter development time (Legner 1981). Spalangia is capable of detecting and avoiding Muscidifurax-parasitized fly pupae, while M. raptor will readily oviposit in Spalangia-parasitized pupae. In multiparasitized pupae, Muscidifurax is generally the survivor (Propp and Morgan 1983). In the field, however, there is evidence that

parasites tend to search different areas within the habitat, with Muscidifurax concentrating on the manure surface and Spalangia searching in deeper zones (Legner 1977). Such niche-partitioning under field conditions may therefore neutralize the apparent competitive advantage which M. raptor has over S. endius.

Predators of fly immatures.

Hymenoptera. In more tropical regions of the world, ants have been found to exert considerable predation pressure on house fly larvae. Simmonds (1940) noted that Pheidole megacephala appeared to bring about a noticable decrease in fly numbers following its accidental introduction into Fiji in 1910, and similar observations were made on this species in Hawaii (Phillips 1934). A closely related species of the Pheidologelon affinis group was observed to effect a degree of fly suppression due to its high rate of predation on fy eggs in Puerto Rico (Pimentel 1957) and the Philippines (Pimentel and Uhler 1971).

Acarina. Although there are many species of predaceous mites in accumulating animal wastes (Axtell 1963b), Macrocheles muscadomesticae (Scolopi) appears to be the most important and abundant mite predator in poultry manure (Peck 1968, Axtell 1981). The predatory nature of M. muscadomesticae was first noted by Pereira and deCastro (1945), who observed the mites feeding on house fly eggs and, to a lesser extent, on first-instar larvae. Since that time, numerous authors have attempted to assess the predation potential of Macrocheles under a

variety of experimental and field conditions (Axtell 1961, 1963a, Filiponni 1955, Kinn 1966, Peck 1968,1969, Singh et al. 1966, Willis and Axtell 1968).

Under laboratory conditions of 80°F, 15h L: 9h D photoperiod and 55-60% RH, Wade and Rodriguez (1961) found that development from egg to adult was completed in only 54.5 hours for males and 56.4 hours for females when mites were provided with abundant frozen house fly eggs. One advantage that Macrocheles has over some other predators is that it readily feeds on naturally-occurring nematodes in the manure, and thus persists during the winter months and other periods when dipteran prey availability is low (Rodriguez et al 1962). Singh and Rodriguez (1966) later developed a mass-rearing method for M. muscadomesticae based on large-scale production of a common manure-inhabiting nematode, Rhabditella leptura Cobb. Wallwork and Rodriguez (1963) noted that ammonia, which is an oviposition stimulant for the house fly (Detier 1947), also serves as a releasing cue for biting and puncturing behavior by the mites. This response could be elicited in mites even after feeding to repletion on fly eggs (Wallwork and Rodriguez 1963).

Diptera. A number of fly species have been found to prey on house fly immatures, with most work having been done on members of the genus Ophyra. O. leucostoma is a cosmopolitan species which has been found in privies, carrion, swallows' nests, rabbit droppings nad poultry manure (Peck 1968), while O. capensis and O. aenescens appear to be restricted to poultry houses in Britain and Florida,

respectively (Hogsette 1979). Seguy (1923) first noted that Ophyra immatures were predaceous, and this observation was later confirmed by morphological (Keilin and Tate 1930) and experimental (Peck 1968, 1969, Hogsette 1979) studies.

Another fly which has received considerable attention in recent years is the black soldier fly, Hermetia illuscens L. Although this species does not appear to be predaceous, it sometimes eliminates house fly larvae from manure by effecting physico-chemical changes in the medium which drive moisture levels above house fly's upper threshold (Hogsette 1979). Since most manure management strategies strive for drier manure, this species is probably of limited value for fly IPM programs.

Coleoptera. Legner and Olton (1970) and Pfeiffer (1978) have provided exhaustive lists of coleopteran predator and scavenger species associated with accumulating manure, while Peck and Anderson (1969) and Legner et al. (1975) examined seasonal changes in population densities of key species in poultry manure. The most important species appear to be staphylinids of the genus Philonthus and the histerids Gnathoncus nanus (Scriba) and Carcinops pumilio (Erichson). The lesser mealworm Alphitobius diaperinus (Panzer) also feeds on fly immatures to some extent and aids in manure aeration, however, the habit of larvae to bore into styrofoam insulation to construct pupal cells renders them unsuitable biocontrol agents (Gall 1980, Pfeiffer 1978).

Of all coleopteran predators, C. pumilio appears to be the most

effective in regulating populations of house flies (Bills 1973, Legner 1971, Pec 1968, 1969, Peck and Anderson 1969). In the laboratory, Peck (1968, 1969) found this species to be as effective as Macrocheles in locating and consuming fly immatures when predator body size and longevity were taken into account. Carcinops appears to be an opportunistic predator and scavenger which feeds readily on flies and a variety of other food items including mites (Smith 1975) stored product pests (Hinton 1945) birds eggs and dead arthropods (Geden, personal observations). While little is known of its evolutionary history, C. pumilio appears to have radiated from the nests of wild avian species (Hicks 1959) into modern poultry production facilities, with their associated "monocultures" of bird manure. At the start of the present project, little was known of the population dynamics, niche characteristics, behavior or life history of Carcinops. The objective of this dissertation was therefore to gather much-needed biological information on this potential biocontrol agent.

C H A P T E R II

POPULATION DYNAMICS OF ARTHROPODS ASSOCIATED WITH POULTRY MANURE IN MASSACHUSETTS, WITH OBSERVATIONS ON SEX RATIOS, OVARIAN STATE AND BODY SIZE OF THE PREDACEOUS HISTERID, CARCINOPS PUMILIO (ERICHSON)

Introduction

Increasing efforts have been mounted in recent years to identify and determine the effectiveness of natural enemies of filth fly immatures in poultry manure (U.S.D.A. 1981). To date, nearly all of this work has been conducted in warmer areas of the U.S., especially California (Anderson and Poorbaugh 1964, Anderson et al. 1968, Legner 1971, 1981, Legner and Brydon 1966, Legner and Dietrick 1972, 1974, Legner and Olton, 1968, 1971, Legner et al. 1975a, b, Olton and Legner 1975, Peck 1969, Peck and Anderson 1969, 1970), North Carolina (Axtell 1961, 1963a, b, 1969, 1970a, b, 1981, Pfeiffer 1978, Pfeiffer and Axtell 1980, Rutz and Axtell 1979) and Florida (Hogsette 1980, Morgan and Patterson 1977, Morgan et al. 1975a, b). In these regions, climatic factors and, frequently, open-sided house design, promote the establishment of a highly diverse community of predator and scavenger arthropod species.

In Massachusetts, where houses are closed and environmentally

regulated throughout the year, this community is much simpler. House fly parasites are rarely encountered (Ruggles 1979) and the predator complex is essentially comprised of two species. These are the mite, Macrocheles muscadomesticae (Scolopi), and the histerid, Carcinops pumilio (Erichson). M. muscadomesticae is a predator of house fly eggs and newly hatched larvae in animal manure, and has been extensively studied (Axtell 1961, 1963a, b, 1969, 1970a, b, 1981, Filipponi 1955, 1960, Filipponi and diDelupis 1963, Filipponi and Petrelli 1967, Kinn 1966, Rodriguez and Wade 1961, Singh and Rodriguez 1969, Singh et al. 1966, Wade and Rodriguez 1961, Wicht and Rodriguez 1970).

Carcinops, on the other hand, has received comparatively little attention. In the laboratory, Peck (1968, 1969) found this species to be as effective as Macrocheles in suppressing house fly production, and Smith (1975) has provided valuable information on Carcinops life history. Aside from observations of seasonal abundance of beetles in poultry houses in California (Peck 1968, Peck and Anderson 1969, 1970) and North Carolina (Pfeiffer 1978, Pfeiffer and Axtell 1980), very little research has been done on the ecology and feeding habits of C. pumilio in the field.

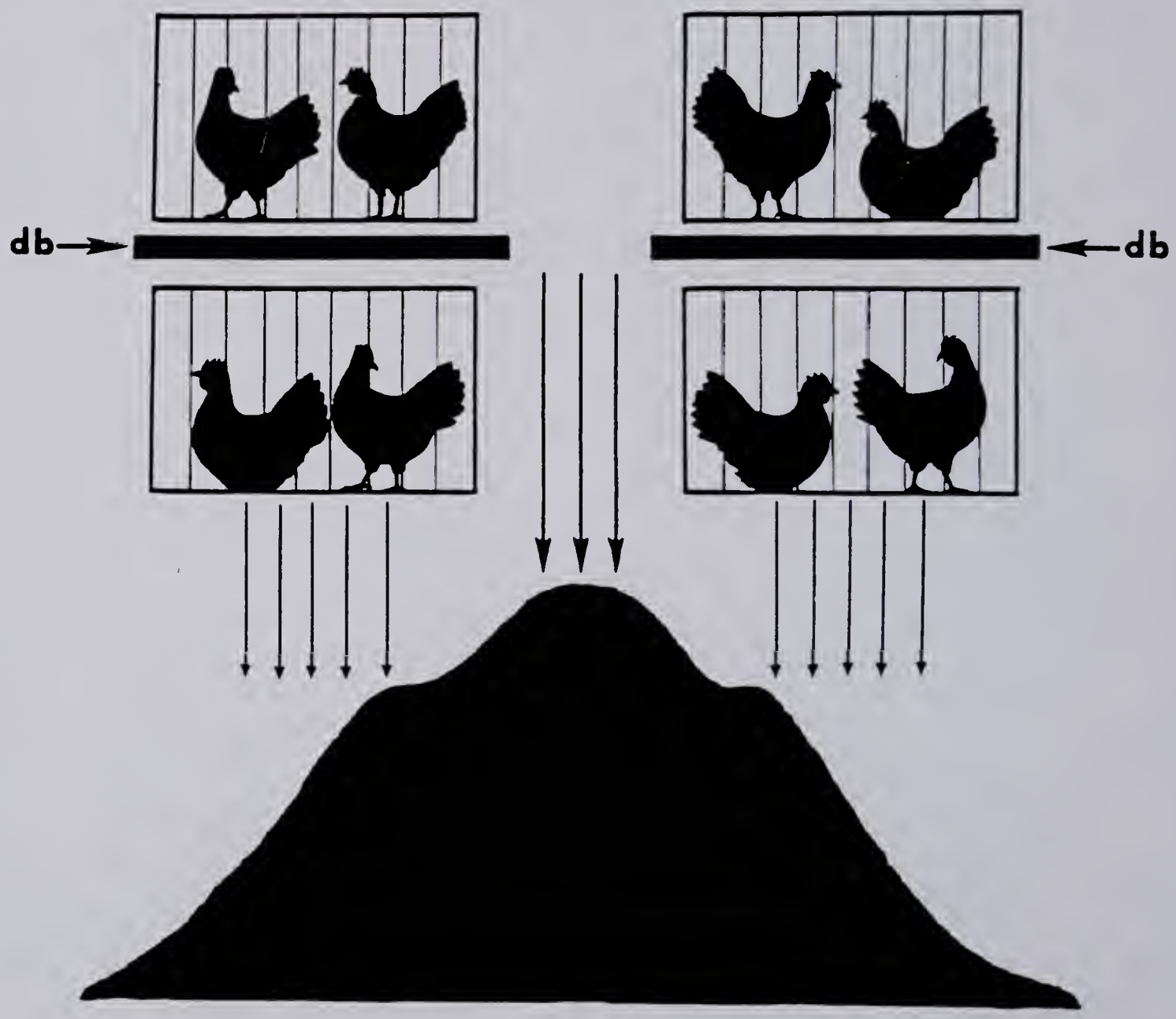
This study was part of a larger project to investigate the ecology, life history and behavior of C. pumilio in relation to other members of the manure arthropod community. Specifically, the objectives of the present study were as follows: 1) to monitor seasonal population dynamics of principal community members throughout

a complete manure accumulation cycle; 2) to compare the relative influences of calender date and manure accumulation time on arthropod population sizes by sampling from two adjacent poultry houses on different manure removal schedules; 3) to monitor temperature changes in regions of the manure where predators are most abundant in relation to ambient and manure-air interface temperatures; and, 4) to assess seasonal changes in Carcinops populations with respect to sex ratios, ovarian state and body size.

Materials and Methods

Study site and weekly arthropod collections. Sampling was conducted at a small commercial egg production facility in Hubbardston, MA, owned by Mr. Maitland Hill. At the time of this study (1980) the farm consisted of three caged-layer houses and a separate breeder house. Each of the layer houses contained ca. 25,000 white leghorn hens which were maintained under conditions typical of producers in Massachusetts. Hens were housed in paired, two-tiered rows of cages suspended ca. 1.2 m over a concrete floor. Manure from birds in the upper tiers dropped onto so-called "dropping boards", where it accumulated for 24 h before being scraped onto the main manure rows beneath the lower birds (Fig. 1). Five of these rows of paired cages were present in each house and were separated by concrete walkways. Manure was completely removed from the houses every 3-4 months on a staggered schedule such that, at any one time, the three houses had

Fig. 1. Schematic illustration of manure accumulation in a typical Massachusetts poultry house. Light arrows indicate manure dropping continuously from lower tiers of birds. Manure from upper tiers collects on dropping boards (db) and is scraped every 24 hr onto the main manure row. Dark arrows represent this once-daily deposition of dropping board manure onto the crest of the main row below.


db
db

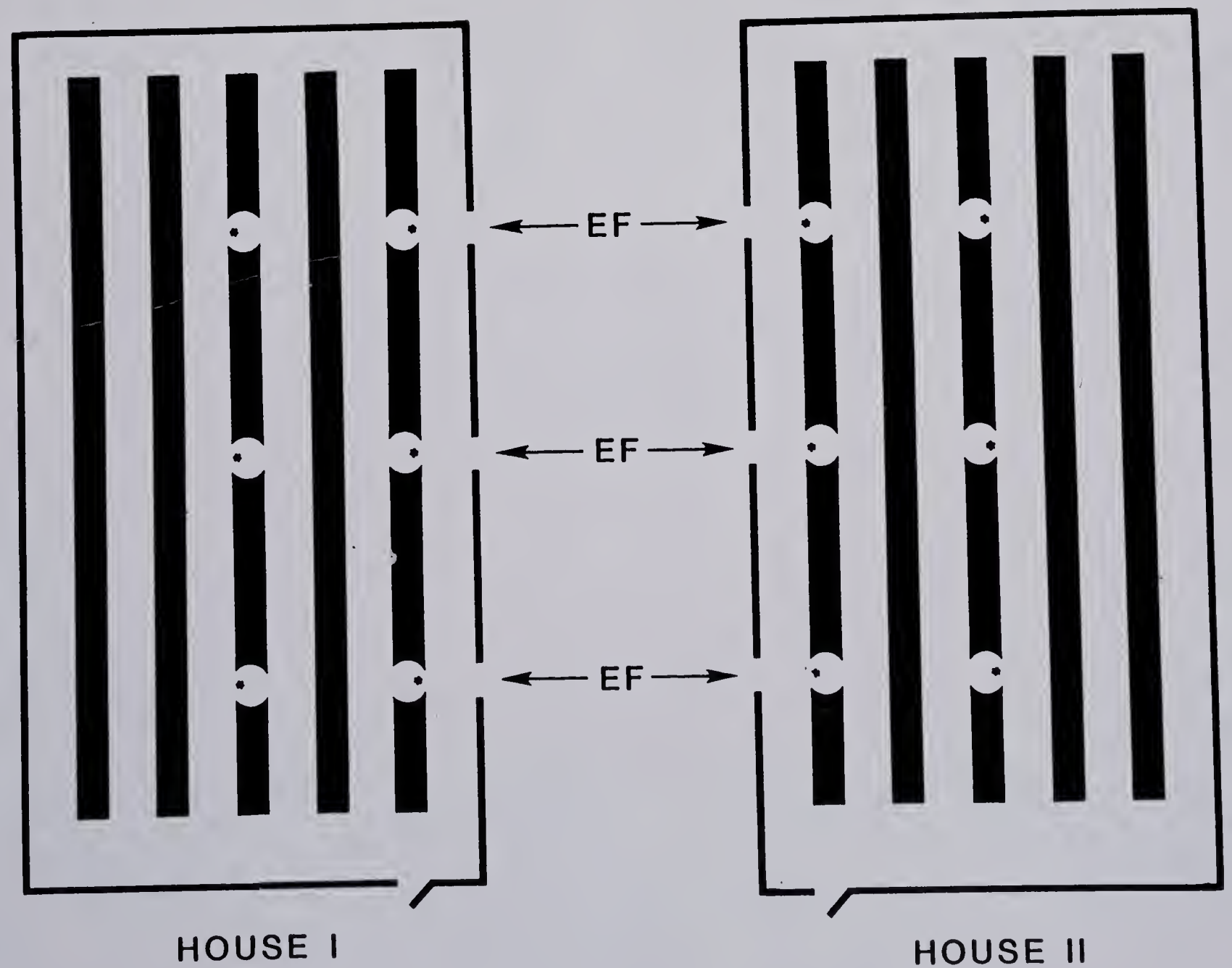
manure of different accumulation times. Following house cleanouts, manure was left in a pile behind the houses for 4-5 weeks to allow predator movement into newly accumulating droppings before it was removed from the farm.

According to the producer, extension service records and neighbors' reports, no serious filth fly outbreaks had occurred on the farm for at least seven years prior to the present study, due to the combined factors of manure management, water regulation and predators (Ruggles 1979). During this seven year period, the producer reported that he had never used insecticides for fly control.

All samples were taken from two of the layer houses, which were parallel along the long axes and were structural "mirror images" with respect to the position of the exhaust fans and house entrances (Fig. 2). House I was sampled weekly throughout a complete manure accumulation cycle, starting on May 19, 1980, one day before manure removal, and ending on Sept. 2, several days before the next cleanout. House II was sampled weekly from May 26, 1980, at which time the manure had accumulated for five weeks, through July 29, several days before the next removal.

On each sampling date, manure samples were taken from each of six positions in each house (Fig. 2) with a polyvinylchlorine core sampler which had a volume of 1.5 liters (diam. = 10.3 cm, length = 18 cm). When a sufficient volume of manure was present to fill the corer, samples were taken by inserting the corer at a 45 ^{o} angle into the manure at a position halfway up the row. During the first several

Fig. 2. Schematic illustration of study site. Stars along rows indicate locations of the six sample positions in each house. Breaks along the facing walls represent positions of the exhaust fans (EF).


EF
EF
EF
HOUSE I
HOUSE II

weeks post-cleanout (hereafter designated as PC) in House I, when the height of the manure was less than the length of the corer, a hand trowel was used to fill the corer with manure from the area immediately surrounding the sample site. Following sample removal, the site was marked with a red flag and avoided in subsequent weeks to minimize the effect of sequential habitat removal on arthropod counts.

Samples were placed in medium-sized trash bags, loosely tied at the top, and returned to the lab, where they were extracted through modified Tullgren funnels into 80% ethanol. Arthropods were separated from debris in the alcohol via water flotation and selective screening. All stages of C. pumilio, sphaerocerids (mostly Coproica hirtula Rondani) and adults of M. muscadomesticae were counted individually. Counts of cereal mites and other non-predaceus acarines were determined volumetrically by first removing all other arthropods from the alcohol by hand and counting mite numbers in subsample aliquots of known dilution. Three mite subsamples were counted for each sample, the mean number per subsample was determined, and the total number in the original sample was estimated by multiplying this mean figure by the dilution factor. Immature M. muscadomesticae were disregarded in these samples since the generation time of this species is less than three days (Axtell 1981).

Temperature data. At each sample position, the temperature was recorded at three locations. One reading was taken ca. 1 m above the sample site, a second at a position 1 cm above the site, and a third

was taken within the manure at a depth of ca. 6 cm, for a total of 18 temperature readings per house. The ambient temperature was also recorded from a shaded area outside the houses. Samples and temperature readings were taken between 1:00 and 4:00 PM on each weekly visit to the farm.

Sex ratios and ovarian state of C. pumilio. To monitor changes in C. pumilio sex ratios throughout a complete manure accumulation cycle during the fly season, 100 beetles were selected at random on each sampling date from House I and dissected in alcohol for sex determinations. Most beetles were obtained from samples which were collected as part of the weekly survey discussed above. On June 17-July 1, when Carcinops populations were very small, additional beetles were collected as needed to yield a total of 100 per week.

Of the females which were identified during these sex determinations, 20 were also examined each week (except May 19) with respect to ovarian state. C. pumilio has four ovarioles/ovary and deposits eggs singly such that, at any one time, one rarely finds more than one fully developed, chorionated egg per female, and seldom more than two oocytes with substantial yolk deposition (Chapter V). The length of the two most developed oocytes (1/ovary) was therefore measured for each female under a dissecting microscope with an ocular micrometer. For purposes of analysis, data were pooled to form three groups, representing the first, middle and last five weeks since manure removal on May 20.

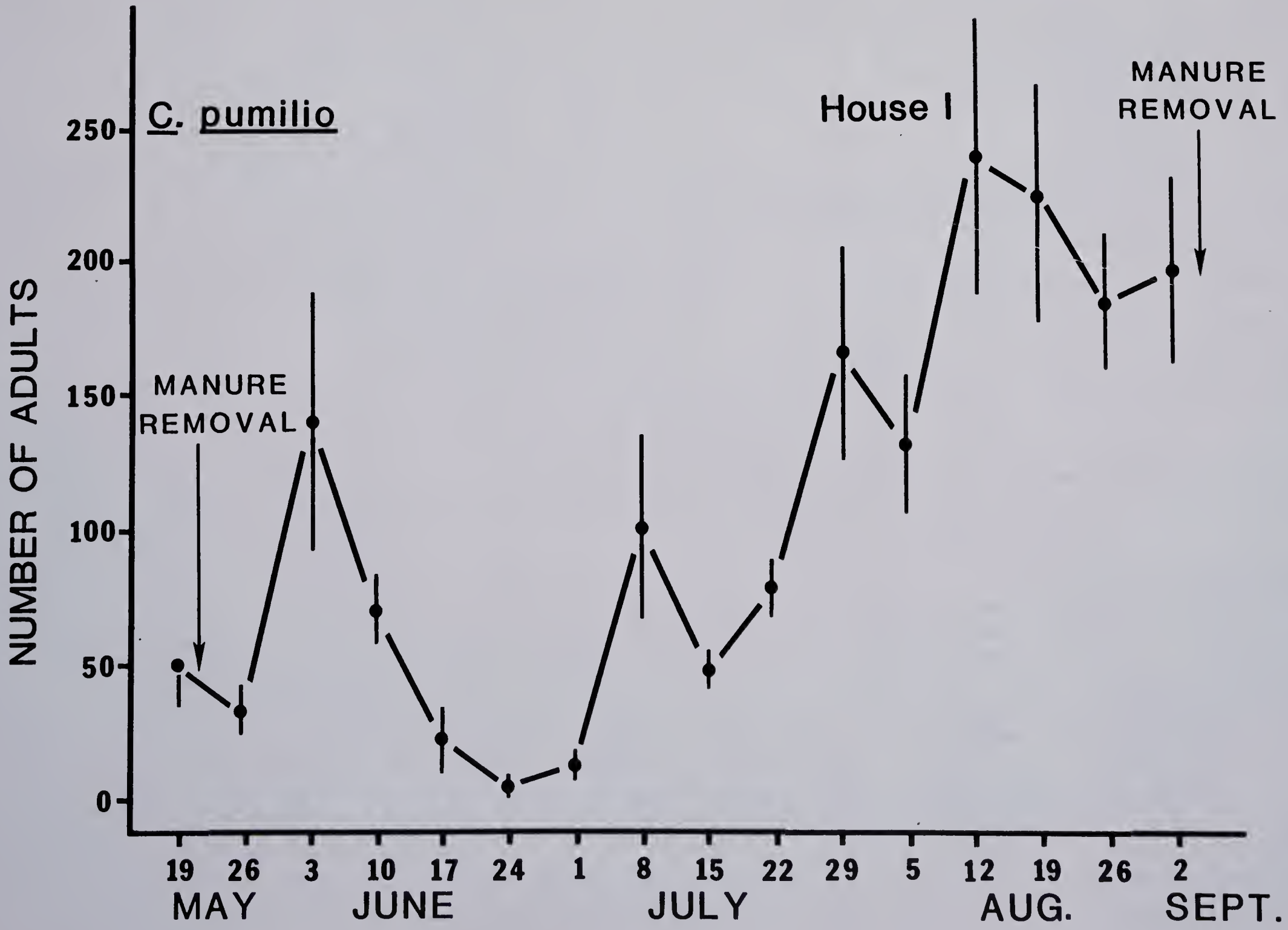
Morphometric analysis of C. pumilio. Changes in body size of Carcinops throughout the season were assessed by measuring the length of the following characters from 20 females per week from House I: pronotal width at the head (PWH), maximum pronotal width (PWM), right elytral width at anterior end (EWA), maximum right elytral length (ELM), and the diagonal length of the right elytron from inner left (anteriorly) to outer right (posteriorly) points (ELD). Measurements were made of alcohol-preserved specimens as described above. For analysis, data were pooled into three groups as above.

In addition to these meaurements, 100 male and 100 female beetles were examined from Aug. 5-Sept. 2 to determine whether there were any diagnostic morphometric characters for sex determination, since the sexes appear to be externally cryptic in this species. The following characters, as well as the five described above (PWH,PWM,EWA,ELM,ELD) were examined and measured: head width across eyes (HW), maximum pronotal length (PLM), and the lengths of the fore-, middle- and hind femora (FF,MF,MT) and tibiae (FT,MT,HT).

Results

Weekly survey of manure arthropod populations. Results of weekly manure samples for arthropod populations are presented in Figs. 3-12. C. pumilio adults (Fig. 3) were present in relatively low numbers on the day prior to manure removal in House I (51.1 $\pm$ 16.8/1.5 liter

Fig. 3. Mean number of C. pumilio adults collected weekly from six 1.5-liter core samples of poultry manure throughout a complete manure accumulation cycle in House I.


C. pumilio
House I
MANURE REMOVAL
MANURE REMOVAL
NUMBER OF ADULTS
250
200
150
100
50
0
19 26 3 10 17 24 1 8 15 22 29 5 12 19 26 2
MAY JUNE JULY AUG. SEPT.

sample). On May 26, several days following house cleanout, numbers of this species dropped slightly (32.0 ± 9.9/sample), then appeared to have increased by the following week (140.2 ± 61.9/sample). This early peak gave the impression of greater beetle numbers than were present before the cleanout, however, this was an artifact of the smaller amount of surface area provided by newly accumulating droppings in the first several weeks PC. Carcinops adults declined over the next three weeks, reaching a minimum of less than 5 beetles per sample on June 24 (5 weeks PC). Beetle numbers were also low on July 1 (6 weeks PC), then gradually increased over the next 6 weeks, peaking on Aug. 12 (12 weeks PC) at 232.2 ± 64.7/sample. Beetle numbers remained high, at over 170 per sample, for the remaining three weeks before the next manure removal. In House II (Fig. 4), where manure had accumulated for 5 weeks prior to sampling, beetle numbers were much higher than in House I during the period from May 26-July 15. On the initial sampling date of May 26, beetles were present in relatively low numbers (73.7 ± 23.0/sample). On June 3, 2 weeks following the cleanout of House I, Carcinops were considerably more abundant in House II (145.3 ± 30.0) and remained high, at over 100 beetles per sample, until July 1, when numbers fell to 87.0 ± 14.5/sample. On the final sampling date of July 29, several days before cleanout, beetles were also present in lower numbers (72.1 ± 13.6/sample).

Numbers of Carcinops immatures dropped sharply following the first cleanout of House I (Fig. 5), and were present at very low

Fig. 4. Mean number of C. pumilio adults collected weekly from six 1.5-liter core samples of poultry manure from House II, where manure had accumulated for six weeks prior to sampling.

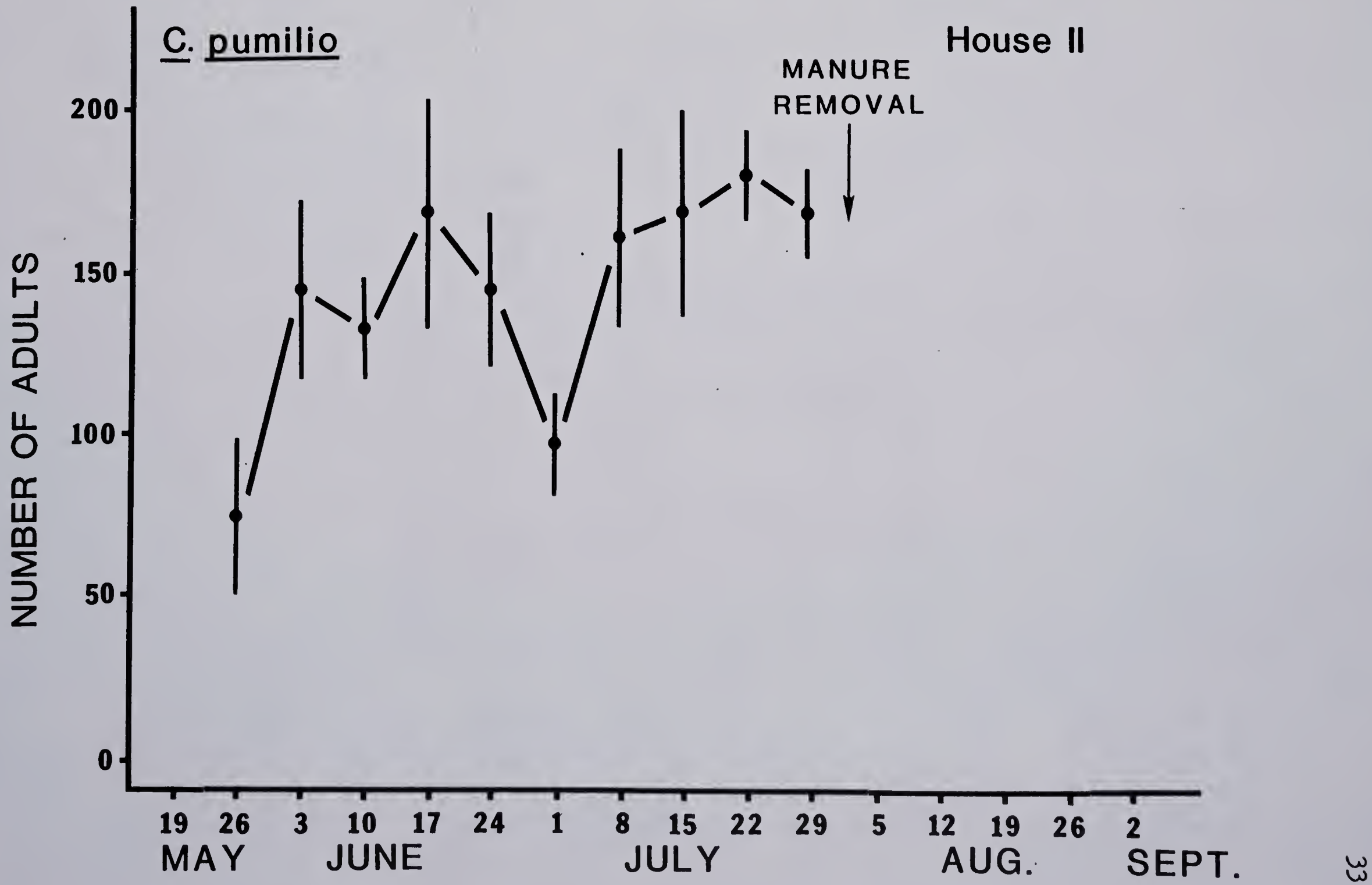
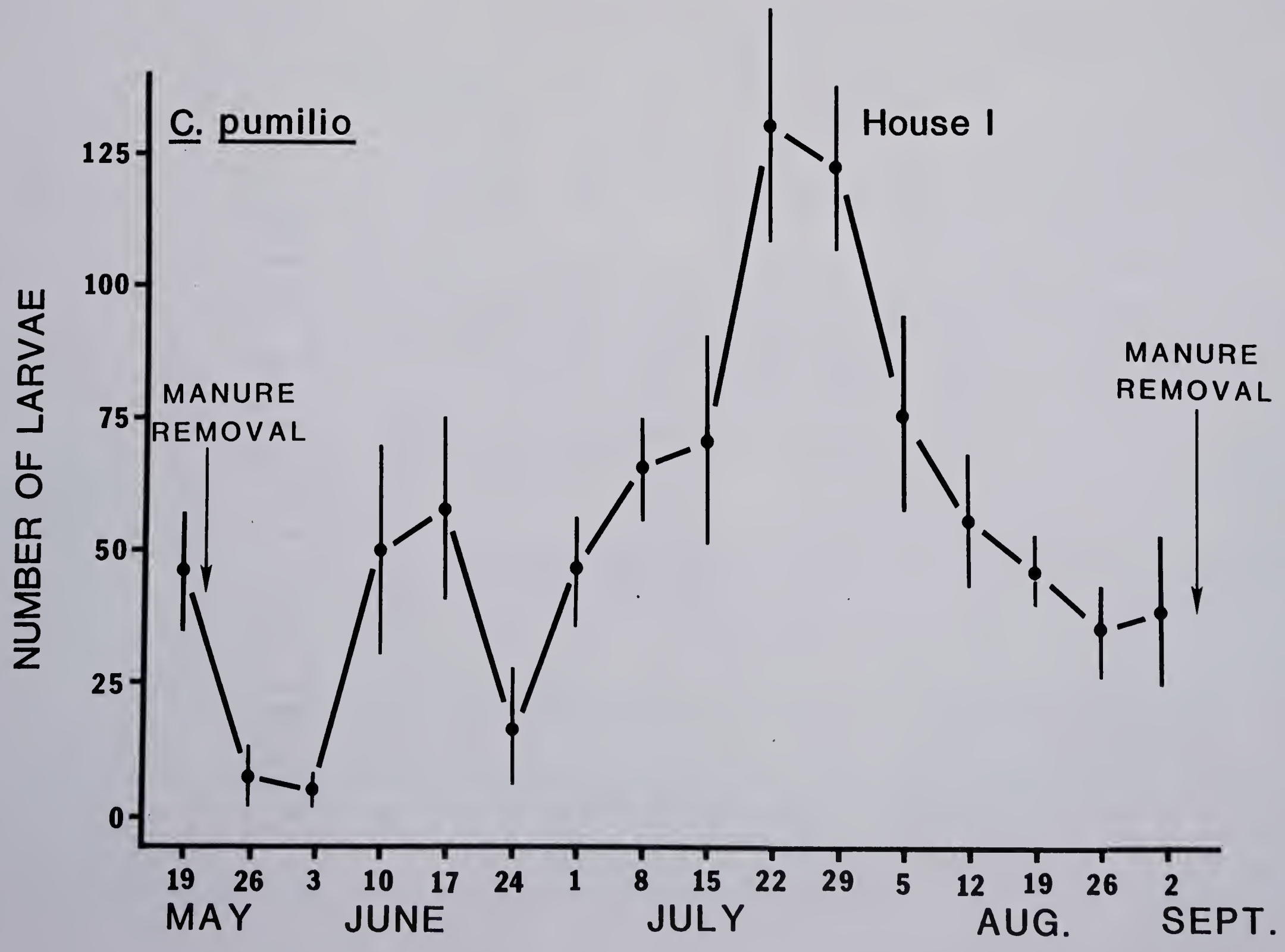

C. pumilio
House II
MANURE
REMOVAL
NUMBER OF ADULTS
200
150
100
50
0
19
26
3
10
17
24
1
8
15
22
29
5
12
19
26
2
MAY
JUNE
JULY
AUG.
SEPT.

Fig. 5. Mean number of C. pumilio larvae collected weekly from six 1.5-liter core samples of poultry manure throughout a complete manure accumulation cycle in House I.


C. pumilio
House I
MANURE REMOVAL
MANURE REMOVAL
NUMBER OF LARVAE
125
100
75
50
25
0
19
26
3
10
17
24
1
8
15
22
29
5
12
19
26
2
MAY
JUNE
JULY
AUG.
SEPT.

levels for the first two weeks PC. On June 10 and June 17 (weeks 3 and 4 PC), larval numbers increased (49.5 ± 17.2 and 57.8 ± 15.9/sample, respectively), then declined to 16.8 ± 8.1/sample on June 24. Immature numbers gradually increased over the following four weeks and peaked at 128.8 ± 23.1/sample on July 22 (9 weeks PC), preceding the adult peak in this house by 3 weeks. Larval counts remained high on July 29, then declined steadily until Aug 26 (14 weeks PC), reaching a minimum of 36.7 ± 9.8/sample on that date. In House II (Fig. 6), larval numbers were high, at over 145 per sample, during the first 3 weeks of sampling (weeks 6-8 PC). This was followed by a decline to 82.0 ± 19.4 and 100.3 ± 7.5/sample on June 17 and June 24, respectively, at which time adult beetle numbers in this house were at their peak. From July 1 through July 22, larvae were present in numbers exceeding 160 per sample, and peaked at 174.0 ± 26.1 on July 8. Numbers of larvae dropped sharply on the final sampling date of July 29 (47.6 ± 7.5/sample).

Changes in population sizes of adult Macrocheles muscadomesticae are presented in Figs. 7 and 8 for House I and House II, respectively. In House I, manure cleanout was accompanied by a drop of mite numbers from 141.3 ± 50.6 to 24.7 ± 12.1/sample. Numbers remained low for the following 4 weeks, then increased sharply on July 1 and July 8 (weeks 6 and 7 PC), peaking on the latter date at 1,032.7 ± 247.3/sample. Mite abundance then declined, but remained at levels of between 250 and 500 per sample, through the remainder of July. On Aug. 5, mites declined in number to 142.7 ± 25.3/sample and remained low, below 150

Fig. 6. Mean number of C. pumilio larvae collected weekly from six 1.5-liter core samples of poultry manure from House II, where manure had accumulated for six weeks prior to sampling.

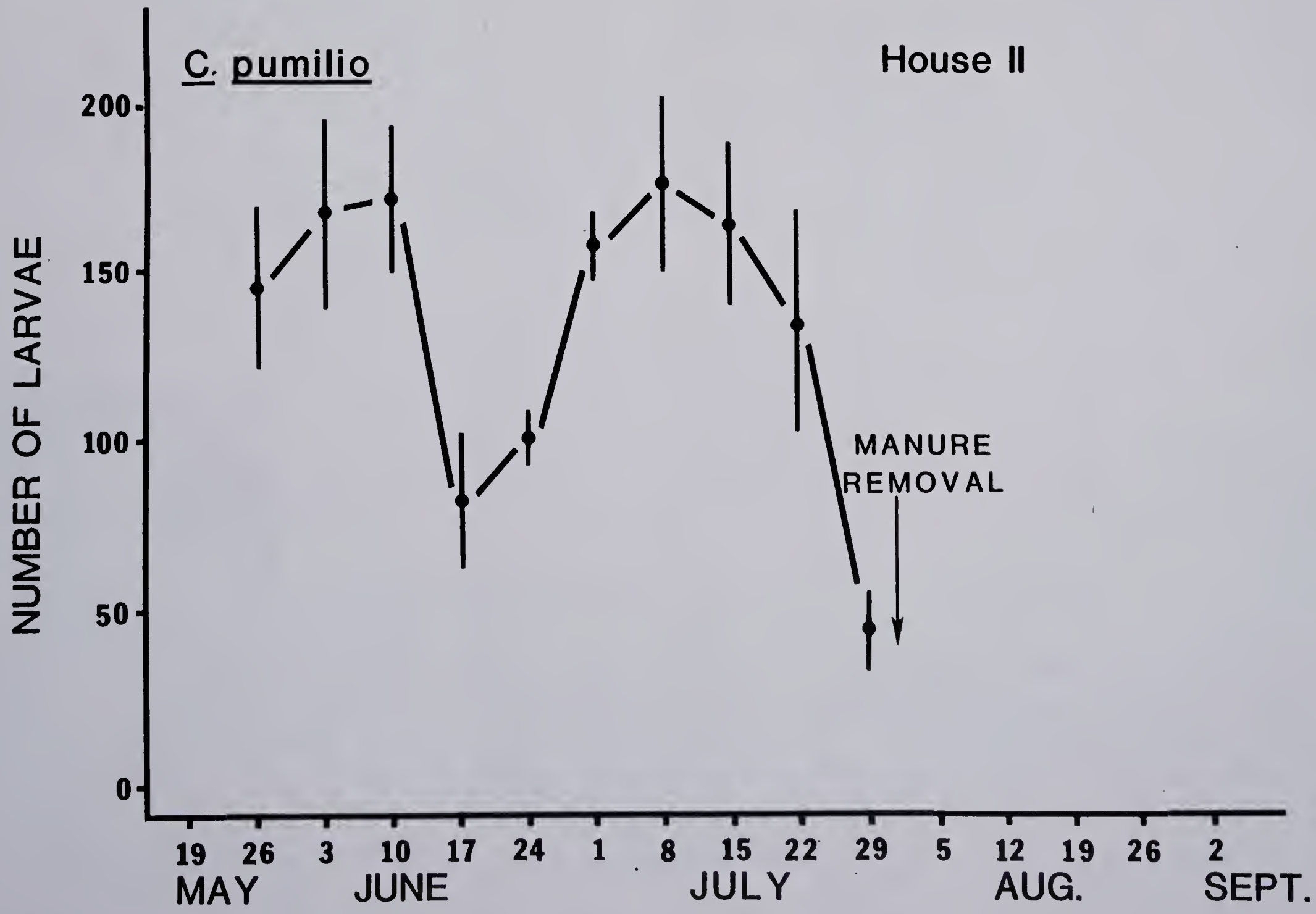

C. pumilio
House II
NUMBER OF LARVAE
200
150
100
50
0
MANURE
REMOVAL
19
26
3
10
17
24
1
8
15
22
29
5
12
19
26
2
MAY
JUNE
JULY
AUG.
SEPT.

Fig. 7. Mean number of M. muscadomesticae adults collected weekly from six 1.5-liter core samples of poultry manure throughout a complete manure accumulation cycle in House I.

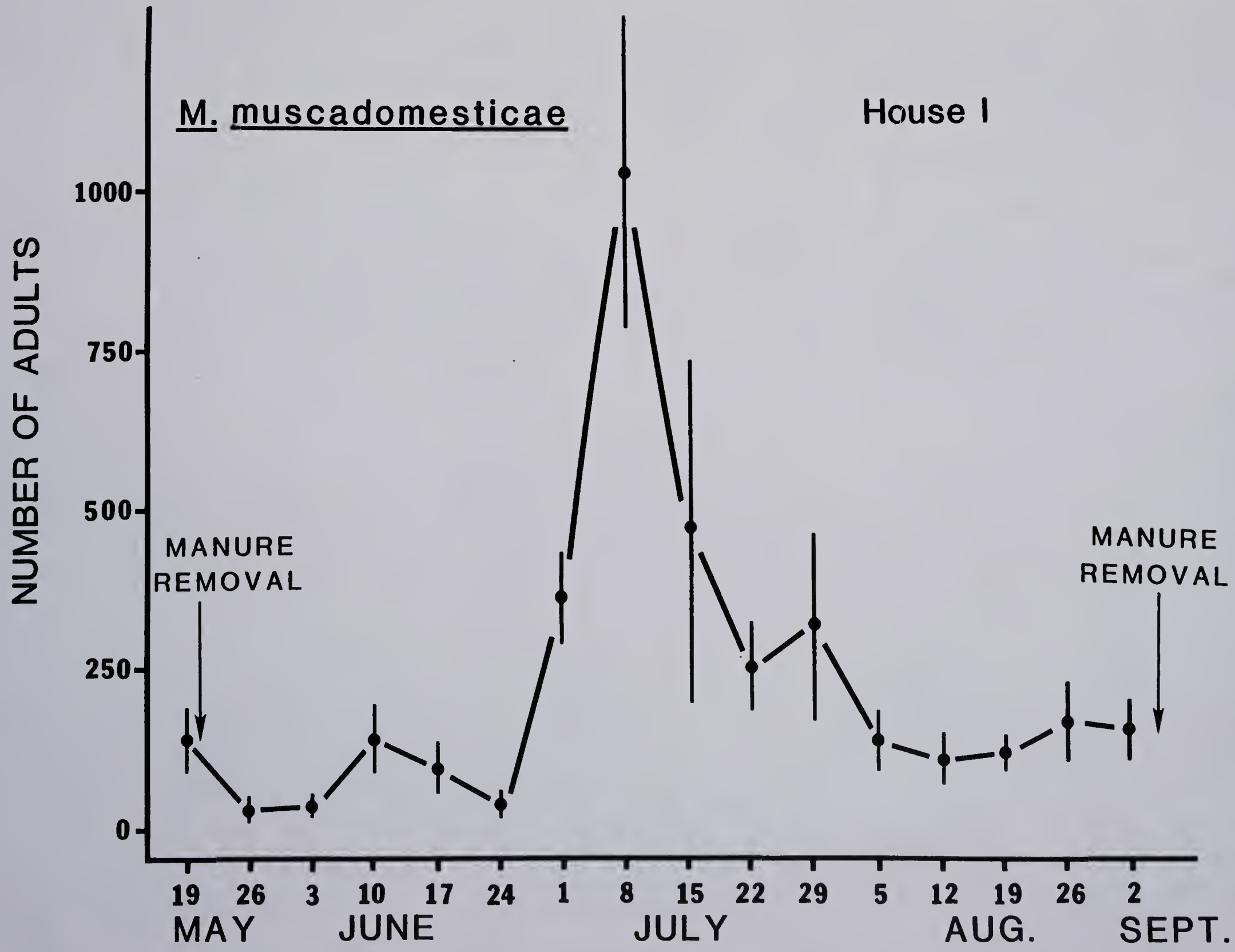
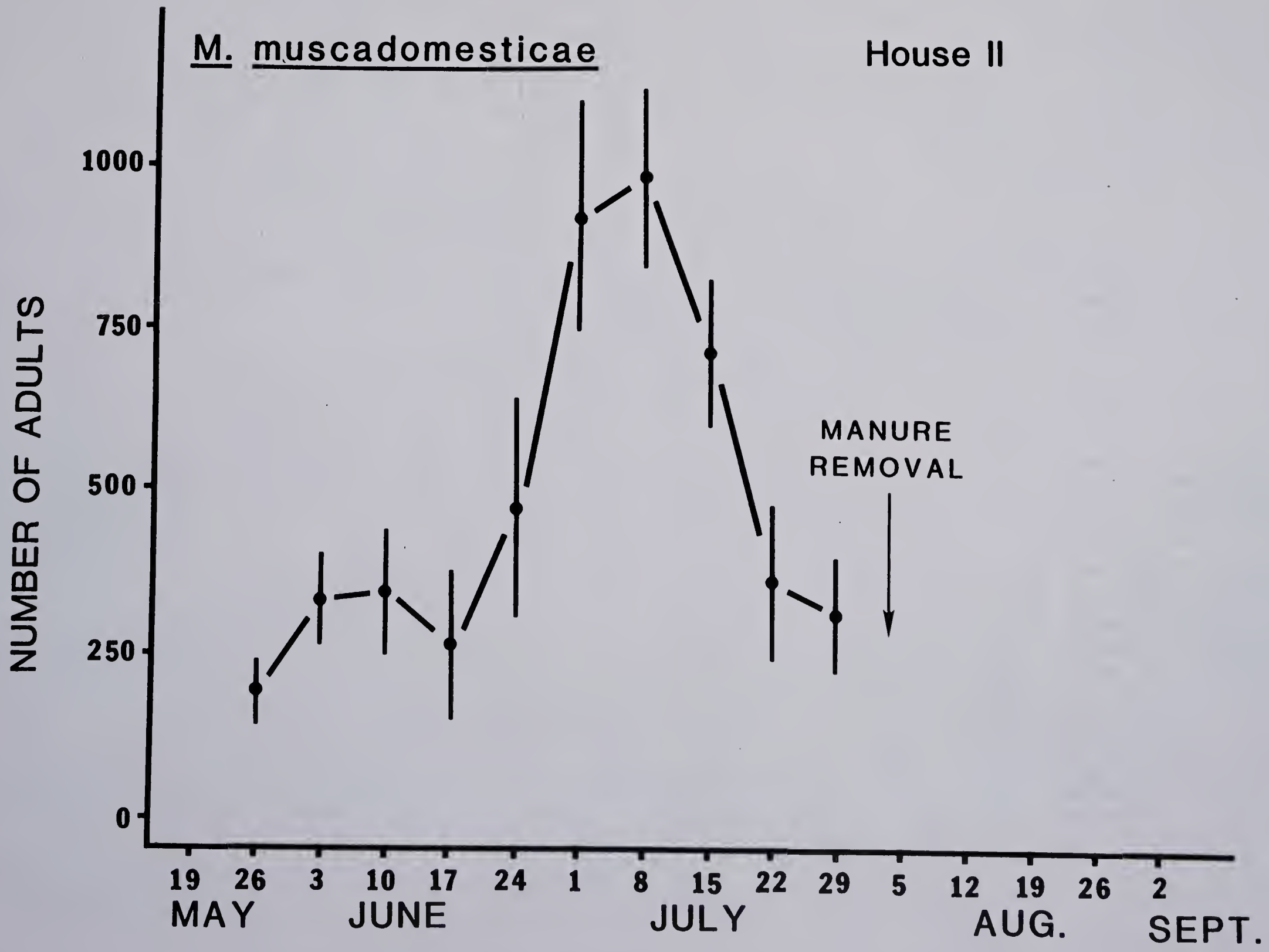

M. muscadomesticae
House I
NUMBER OF ADULTS
1000
750
500
250
0
MANURE REMOVAL
MANURE REMOVAL
19 26 3 10 17 24 1 8 15 22 29 5 12 19 26 2
MAY JUNE JULY AUG. SEPT.

Fig. 8. Mean number of M. muscadomesticae adults collected weekly from six 1.5-liter core samples of poultry manure from House II, where manure had accumulated for six weeks prior to sampling.


M. muscadomesticae
House II
NUMBER OF ADULTS
1000
750
500
250
0
MANURE
REMOVAL
19 26 3 10 17 24 1 8 15 22 29 5 12 19 26 2
MAY JUNE JULY AUG. SEPT.

per sample, for the rest of the month. In House II (Fig. 8), mite numbers were consistantly higher than in House I during the period from May 26 through July 1. As in House I, a sudden rise in Macrocheles abundance was observed on July 1 and July 8 (weeks 11 and 12 PC), and also peaked on the latter date at 970.5 ± 135.6/sample. Following this peak, mite numbers declined over the following three weeks prior to house cleanout.

Sphaerocerid (Coproica hirtula) adult populations were small (53.3 ± 12.6/sample) in House I prior to cleanout, then rose abruptly to 318.5 ± 51.0/sample on the following sampling date of May 26 and dropped slightly on June 3 to 277.8 ± 71.4/sample (Fig. 9). Over the next five weeks, fly numbers continued to rise, and peaked at over 1,500 flies per sample on July 1 (6 weeks PC). Flies were still abundant on July 8 (993.7 ± 306.6/sample), then dropped sharply to below 80 per sample for the remainder of the season. In contrast to the situation in House I, C. hirtula adults were present in numbers exceeding 100 flies per sample only on May 26 (6 weeks PC) in House II, then dropped to below 40 per sample for the balance of the sampling period. Because of the low, stable levels of this species in House II, except for the first sample, these data are not presented in a figure.

Larval sphaerocerid populations in House I (Fig. 10) showed a similar pattern to that of the adults. Following house cleanout, larval numbers increased from a pre-cleanout level of 41.1 ± 11.0 on May 19 to 351.0 ± 108.1/sample on May 26. On June 3, a slight drop

Fig. 9. Mean number of C. hirtula adults collected weekly from six 1.5-liter core samples of poultry manure throughout a complete manure accumulation cycle in House I.

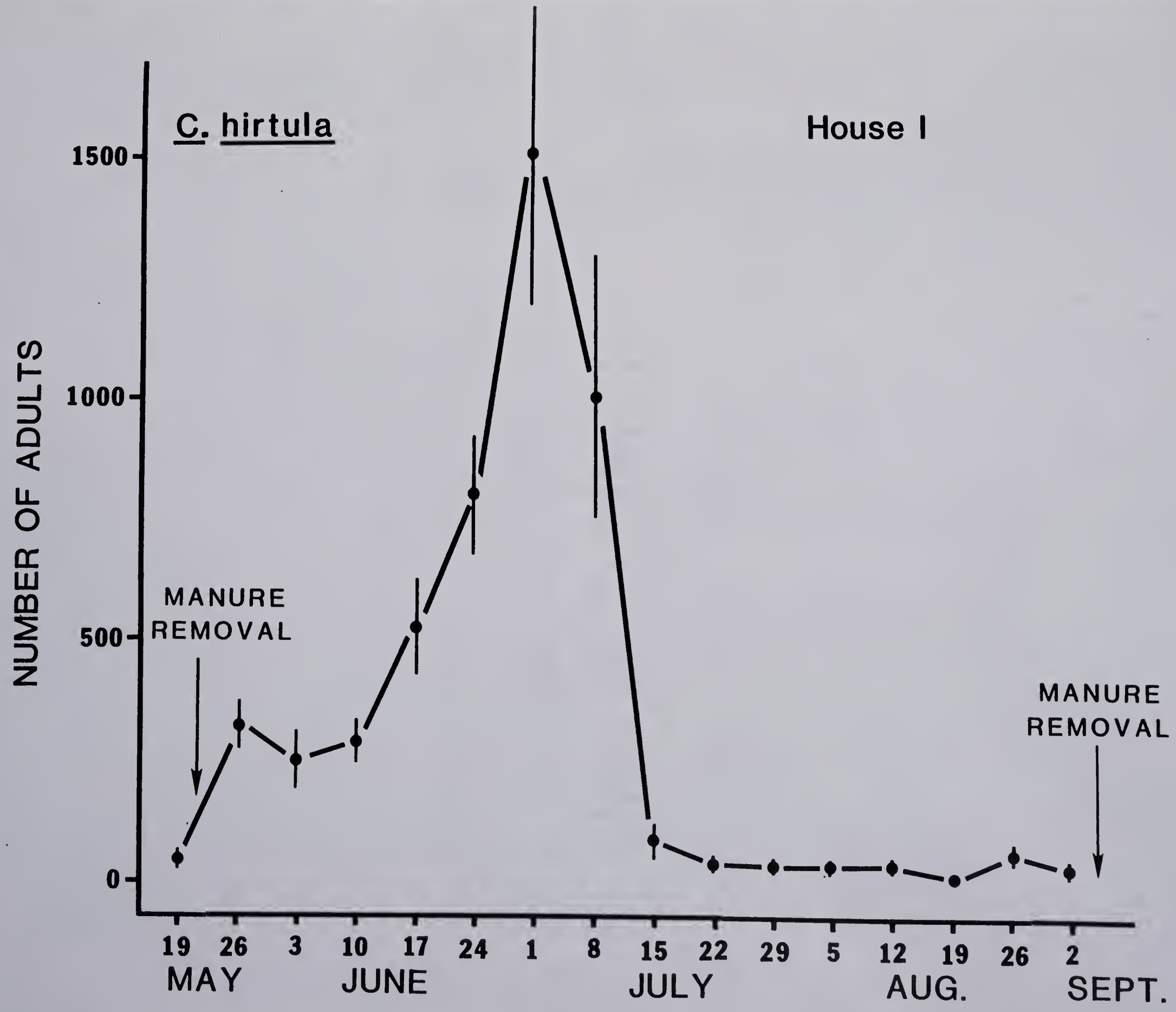
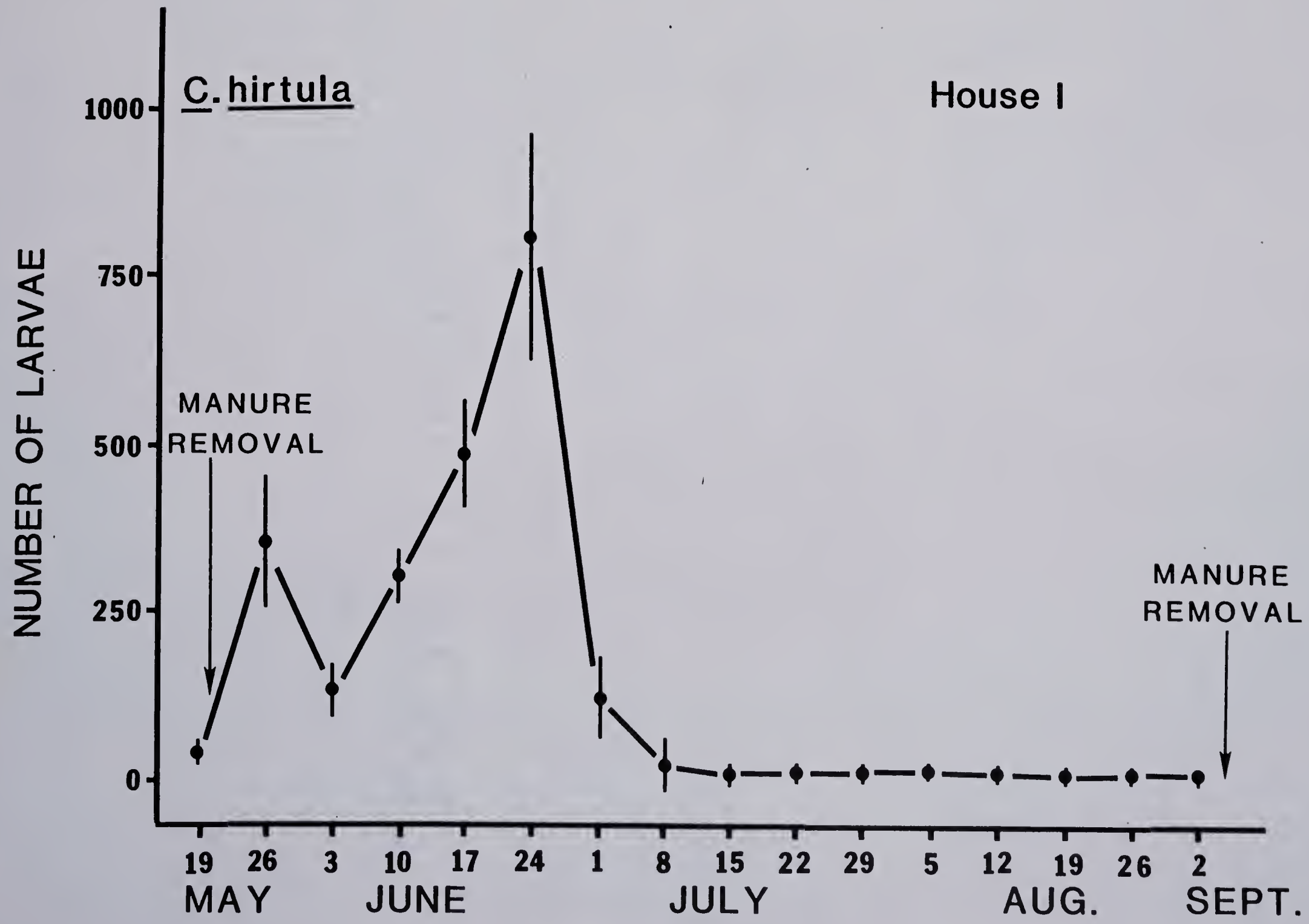

C. hirtula
House I
NUMBER OF ADULTS
1500
1000
500
0
MANURE REMOVAL
MANURE REMOVAL
19 26 3 10 17 24 1 8 15 22 29 5 12 19 26 2
MAY JUNE JULY AUG. SEPT.

Fig. 10. Mean number of C. hirtula larvae collected weekly from six 1.5-liter core samples of poultry manure throughout a complete manure accumulation cycle in House I.


C. hirtula
House I
NUMBER OF LARVAE
1000
750
500
250
0
MANURE
REMOVAL
MANURE
REMOVAL
19
26
3
10
17
24
1
8
15
22
29
5
12
19
26
2
MAY
JUNE
JULY
AUG.
SEPT.

was observed, followed by a steady increase over the next three weeks, with immature C. hirtula numbers peaking at 812.8 ± 79.4/sample on June 24 (5 weeks PC), 1 week prior to the peak of adults of this species in the same house. A precipitous drop in the number of immatures was observed on the following week (125.3 ± 47.0/sample) followed by a decline to below 10 larvae per sample, which persisted through the remainder of the season. As with the adults of this species, few larvae were found at any time in House II, with no more than 32 immatures present in any sample throughout the season. These data are not presented in a figure.

Counts of cereal mites and other non-predaceous acarines were highly variable throughout the sampling period, and are presented on a log scale in Figs. 11 and 12 for House I and House II, respectively. This variability was presumably due to the presence of several species in these pooled counts, each of which may have differed in their seasonal abundance patterns. In general, mite numbers in House I were low, between 10 and 1000 per sample during the first 6 weeks PC, then increased to levels of greater than 1000 for the rest of the sampling period. Peak numbers of mites were observed on Aug. 12 (12 weeks PC), when samples contained 79,000 ± 12,740 mites. In House II (Fig. 12), where sampling was initiated 6 weeks PC, mite numbers were consistently high, between 1000 and 100,000 per sample on every sampling date. Peak numbers were observed on July 15 (13 weeks PC), at 89,600 ± 1,620 mites per sample.

Fig. 11. Mean number of non-predaceous mites of all stages collected weekly from six 1.5-liter core samples of poultry manure throughout a complete manure accumulation cycle in House I.

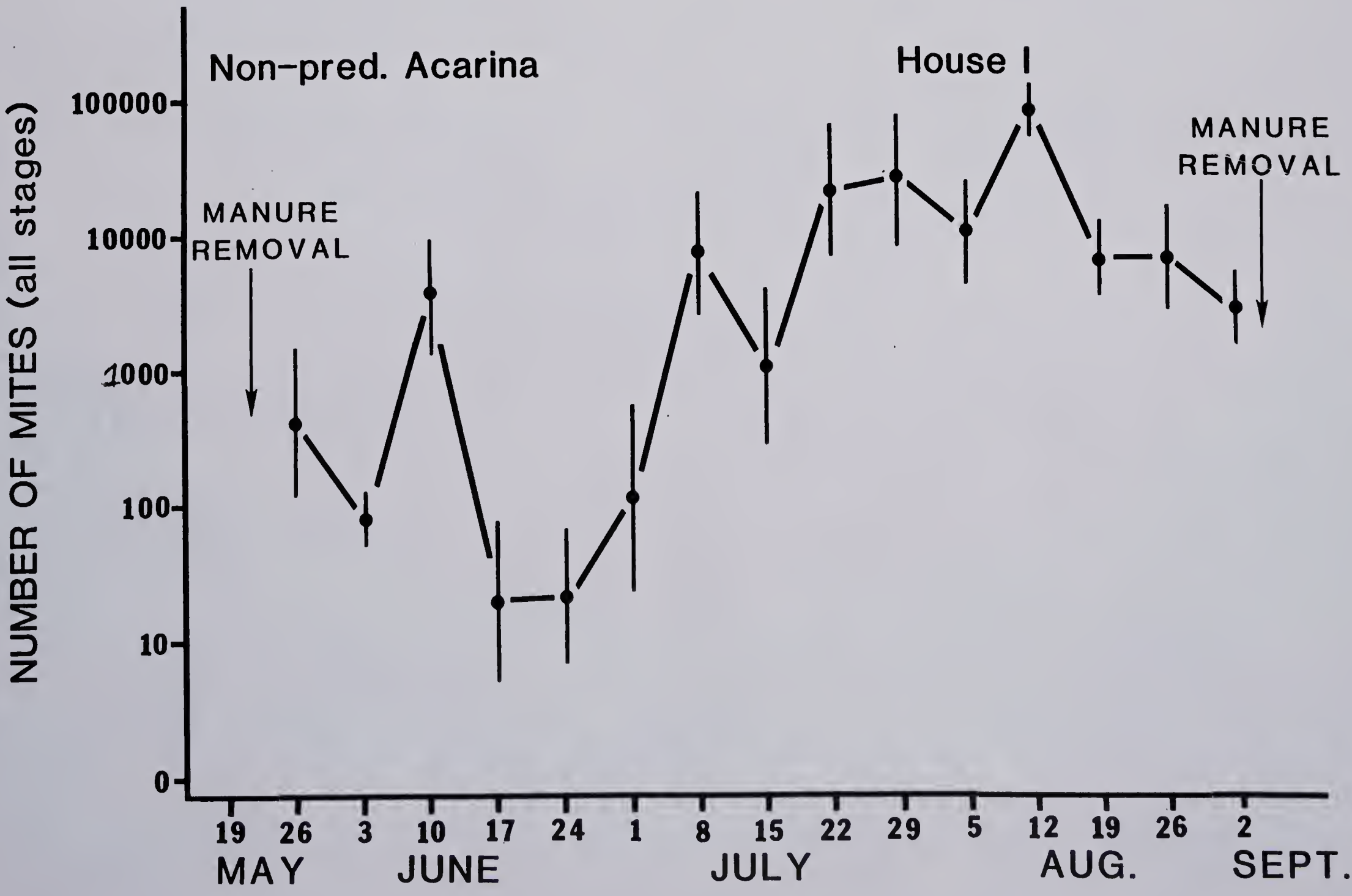
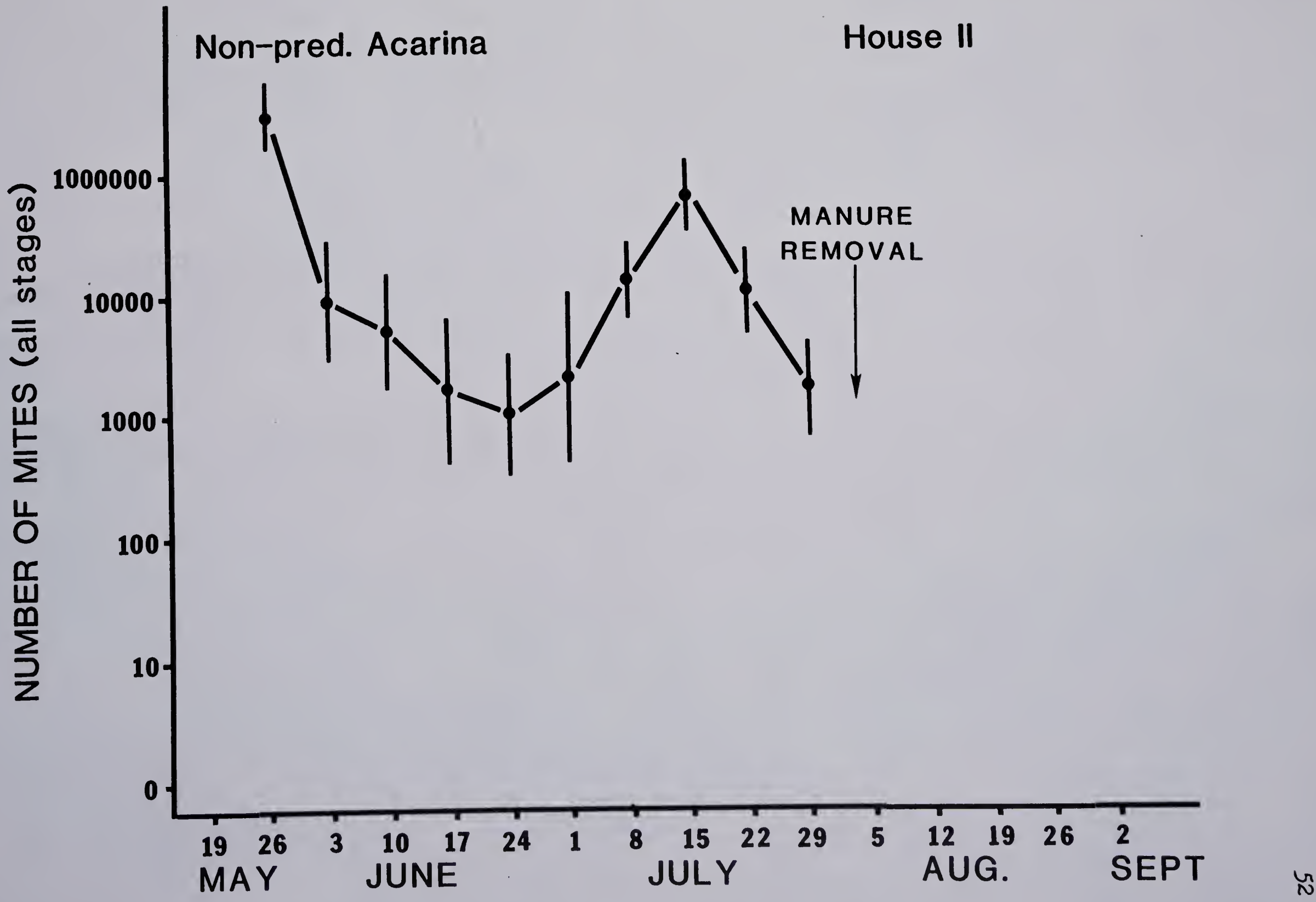

Non-pred. Acarina
House I
MANURE REMOVAL
MANURE REMOVAL
NUMBER OF MITES (all stages)
100000
10000
1000
100
10
0
19 26 3 10 17 24 1 8 15 22 29 5 12 19 26 2
MAY JUNE JULY AUG. SEPT.

Fig. 12. Mean number of non-predaceous mites of all stages collected weekly from six 1.5-liter core samples of poultry manure from House II, where manure had accumulated for six weeks prior to sampling.


Non-pred. Acarina
House II
MANURE
REMOVAL
NUMBER OF MITES (all stages)
1000000
10000
1000
100
10
0
19
26
3
10
17
24
1
8
15
22
29
5
12
19
26
2
MAY
JUNE
JULY
AUG.
SEPT

Other insects. In addition to Carcinops, Macrocheles, Coproica and cereal mites, the following insects were also found, at very low levels (fewer than 5 per week), at various times during the sampling period:

Diptera:

Musca domestica L.

Fannia canicularis (L.)

Sphaeroceridae (other than C. hirtula)

Psychodidae

Scatopsidae

Coleoptera:

Gnathoncus nanus (Scriba)

Alphitobius diaperinus (Panzer)

Tenebrio molitor L.

Tenebroides mauritanicus (L.)

Stegobium paniceum (L.)

Dermestes lardarius L.

Philonthus sp.

Lobrathium sp.

Lepidoptera:

Tinea sp.

Temperature data. Mean temperature readings 1 m above, 1 cm above and 6 cm below the manure surface at each sample position, plus the ambient outdoor temperature, are presented in Table 1. Examination of

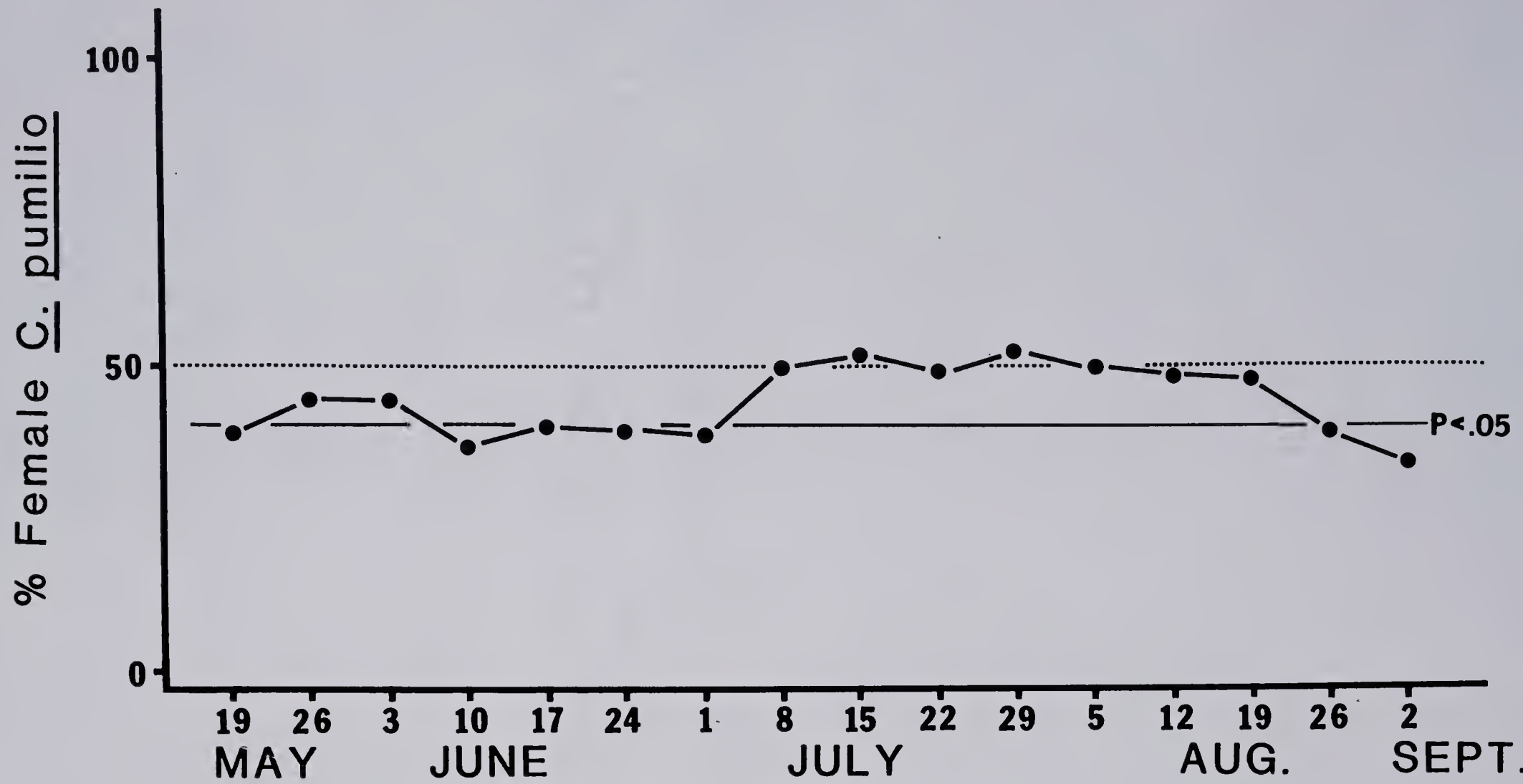
Table 1. Outside air temperature and mean temperature inside 2 poultry houses 1 m above, 1 cm above and 6 cm below the manure surface at six locations in each house. House I was monitored throughout a complete manure accumulation cycle starting one day before manure removal. In House II, manure had accumulated for 6 weeks by the first sampling date (May 26), and was removed on Aug. 3.

Date	Temperature (°C)						
	Outside	Inside poultry houses					
		House I			House II		
		Distance from manure surface			Distance from manure surface		
		1 m above	1 cm above	6 cm below	1 m above	1 cm above	6 cm below
May 19	21.5	23.7	21.4	26.2	---	---	---
26	21.5	22.0	21.0	19.5	23.5	21.6	25.8
June 3	27.0	26.0	23.7	22.5	27.0	24.5	29.8
10	31.0	33.0	31.4	27.1	33.5	31.5	33.6
17	22.0	26.5	24.5	23.5	28.0	23.6	29.6
24	31.5	32.5	31.5	33.1	32.0	30.7	36.7
July 1	28.2	27.5	27.0	28.5	27.5	26.5	33.5
8	20.5	24.7	23.2	28.8	24.2	23.8	33.3
15	32.5	33.2	30.1	36.3	32.0	30.5	32.3
22	33.0	32.0	29.8	36.2	31.5	30.2	34.5
29	22.0	23.1	21.4	33.7	24.7	22.9	31.6
Aug. 5	36.0	32.3	31.5	38.3	---	---	---
12	28.0	29.0	28.0	32.9	---	---	---
19	24.0	24.9	24.2	36.7	---	---	---
26	31.0	30.9	30.7	37.3	---	---	---
Sept. 2	30.0	29.0	26.1	32.7	---	---	---

this data reveals major differences in habitat temperature at these different locations. The manure appeared to have a buffering effect on the air temperature at the manure-air interface, which was less variable, and cooler than, that of the air 1 m from the manure surface on all sampling dates in both houses. Manure temperature 6 cm below the surface showed a trend towards increasing temperature with longer accumulation times. This trend appeared to be relatively independent of the air- and manure-air interface temperature. Thus, during the first four weeks PC in House I (May 26-June 17), within-manure temperature was relatively low (19.5-27.1°C), and was between 1.0 and 4.3°C cooler than that of the air just above the manure surface. In contrast, within-manure temperature in House II during the same calender period (but weeks 6-9 PC) was 2.1 to 6.0°C warmer than that of the surrounding air. On several occasions, within-manure temperature of droppings with long accumulation times was greater than 10°C warmer than that of the air at the manure-air interface.

Sex ratios and ovarian state of C. pumilio. Results of sex determinations of 100 beetles per week from House I are presented in Fig. 13. Male-biased sex ratios were observed from May 19, one day before house cleanout, through July 1 (6 weeks PC). The most skewed ratio was observed on June 10, when males outnumbered females by a factor of 63:37. On July 8, the proportion of males was nearly equal to that of females (51 ♂:49♀) and remained at ca. 50% males through Aug. 19. On Aug. 26 and Sep. 2 a male bias was again apparent, with

Fig. 13. Seasonal changes in proportions of male and female C. pumilio collected throughout a complete manure accumulation cycle in House I. Data are presented as percent females of 100 beetles which were collected and sexed each week. Significantly male-biased samples (≤40% females) are indicated by their position below the line labelled "P<.05", as determined by chi-square analysis,


% Female C. pumilio
100
50
0
P<.05
19
26
3
10
17
24
1
8
15
22
29
5
12
19
26
2
MAY
JUNE
JULY
AUG.
SEPT.

sex ratios of 61♂:39♀ and 66♂: 34♀, respectively.

The condition of the two most-developed oocytes from each of 20 females per week from House I during the period from May 26-Sept. 2 are presented in Table 2. No significant differences were found among beetles from the three time intervals (first, middle and last 5 weeks PC) with respect to the state of the most-developed oocyte, with a total average length of 0.65 ± 0.318 mm/oocyte. Completely developed, chorionated eggs ranged from 0.65 to 0.92 mm in length. The length of the second-most-developed oocyte per female was significantly smaller (0.31 ± 0.202 mm) in beetles collected during the last 5 weeks than in those from the first (0.41 ± 0.232 mm) or middle (0.43 ± 0.251 mm) five weeks PC. To determine whether this decrease in oocyte size in later samples was related to the smaller average body size of females collected during this time interval (see next section), correlation analyses were conducted for relationships between various morphometric characters and reproductive parameters (length of fully developed, chorionated eggs; lengths of most- and second-most-developed oocytes). No significant correlations were found between any body size measures and any of these indicators of ovarian condition.

Morphometric analysis of C. pumilio. Analysis of body size differences of Carcinops females over the season in House I are presented in Table 3. No significant differences were found with respect to the five characters which were examined (PWH,PWM,EWA,ELM,ELD) between beetles which were collected during the

Table 2. Length (mm) of most-developed and second-most-developed oocytes of female C. pumilio collected from House I during three time intervals corresponding to the first, middle and last five weeks of a manure accumulation cycle.

Time interval	Oocyte 1	Oocyte 2
May 26-June 24	0.68 ± 0.300 a	0.41 ± 0.232 a
July 1-July 29	0.63 ± 0.324 a	0.43 ± 0.251 a
Aug. 5-Sept. 2	0.64 ± 0.330 a	0.31 ± 0.202 b

Data are presented as mean oocyte length in mm ± SD. Means within columns which are not followed by the same letter are significantly different. (Student-Newman-Keuls Range Test, P = .05). N = 100 beetles per time interval (20/week).

Table 3. Size (mm) of five morphometric characters of female C. pumilio collected from House I during three time intervals corresponding to the first, middle and last five weeks of a manure accumulation cycle.

Character	Time interval		
	May 26–June 24	July 1–July 29	Aug. 5–Sept. 2
PWH	0.70 ± 0.031 a	0.70 ± 0.039 a	0.69 ± 0.030 a
PWM	1.39 ± 0.068 a	1.39 ± 0.077 a	1.36 ± 0.073 b
EWA	0.83 ± 0.039 a	0.84 ± 0.048 a	0.82 ± 0.049 b
ELM	1.39 ± 0.064 a	1.41 ± 0.075 a	1.37 ± 0.078 b
ELD	1.71 ± 0.079 a	1.72 ± 0.090 a	1.67 ± 0.095 b

Data are presented as mean character size in mm ± S.D. Means within rows which are not followed by the same letter are significantly different (Student-Newman-Keuls Range Test, P = .05). N = 100 beetles per time interval (20/week). (PWH = pronotal width at head, PWM = pronotal width at widest point, EWA = elytral width at anterior end, ELM = elytral length at longest point, ELD = elytral length along diagonal from inner anterior to outer posterior points).

first and middle five weeks PC. Females collected during the last five weeks (weeks 11-15 PC) were, however, significantly smaller than those collected earlier in the season, as indicated by smaller values for four of the five characters (PWM,EWA,ELM,ELD).

Results of analysis of 13 morphometric characters to locate sex differences are presented in Table 4. No significant differences between sexes were found with respect to head (HW), pronotal (PWH,PWM,PLM) or elytral (EWA,ELM,ELD) characters. The femora (FF,MF,HF) and tibiae (FT,MT,HT) of males were, however, significantly longer than those of females. Lengths of leg segments in themselves were not found to be reliable diagnostic characters for beetle sex due to variation in overall size within sexes. Analysis of character proportions revealed that the most exclusively diagnostic character ratio was that of the diagonal elytral length to the length of the hind tibia (ELD/HT). For the series of 100 males which were examined, this ratio ranged from 2.460-2.574, while for females the range was 2.610-2.810.

Discussion

Weekly survey of manure arthropods. Throughout the sampling period in both houses, immatures of the house fly and lesser house fly were virtually absent, except for occasional mature fly larvae which were seeking pupation sites after having developed in predator-free refugia (Chapter III). Sphaerocerids (C. hirtula), which were present in

Table 4. Size (mm) of 13 morphometric characters of 100 male and 100 female C. pumilio collected from House I.

Character	Males	Females
HW	0.60 ± 0.025	0.61 ± 0.027 ns
PWH	0.69 ± 0.030	0.70 ± 0.027 ns
PWM	1.37 ± 0.063	1.36 ± 0.074 ns
PLM	0.81 ± 0.037	0.81 ± 0.044 ns
EWA	0.82 ± 0.039	0.82 ± 0.047 ns
ELM	1.37 ± 0.066	1.38 ± 0.076 ns
ELD	1.67 ± 0.077	1.68 ± 0.094 ns
FF	0.63 ± 0.027	0.60 ± 0.030 **
FT	0.57 ± 0.025	0.55 ± 0.028 **
MF	0.58 ± 0.028	0.56 ± 0.033 **
MT	0.55 ± 0.028	0.52 ± 0.032 **
HF	0.68 ± 0.030	0.65 ± 0.037 **
HT	0.66 + 0.031	0.62 ± 0.035 **

Data are presented as mean character size in mm ± S.D. ns = not significant, * = P<.05, ** = P<.01 (Oneway ANOVA). (HW = head width, PWH = pronotal width at head, PWM = pronotal width at widest point, PLM = pronotal length at longest point, EWA = elytral width at anterior end, ELM = elytral length at longest point, ELD = elytral length along diagonal from inner anterior to outer exterior points, FF,MF and HF = lengths of the fore-, middle- and hind femora, FT,MT and HT = lengths of the fore-, middle- and hind tibiae).

small numbers in House II (not represented in a figure) at the time of the cleanout of House I, appeared to rapidly invade the freshly accumulating manure in the latter house and increased to extremely large population sizes in subsequent weeks. M. muscadomesticae appeared to be highly responsive to changes in fly densities, and peaked at over 1000 mites per sample one week following the peak of C. hirtula adults (7 weeks PC). Willis and Axtell (1968) found that Macrocheles populations peaked at ca. 20 days post-cleanout in a study of North Carolina poultry houses, then declined in subsequent weeks. Laboratory studies have established the suitability of C. hirtula as a prey source for this mite (Chapter V). Sphaerocerid populations then crashed and Macrocheles, apparently responding again to changes in dipteran prey availability, also declined and were subsequently maintained by the large populations of cereal mites and other non-predaceous acarines. It is more difficult to interpret the predator mite peak in House II, which occurred at the same time as that in House I but was not apparently related to changes in either dipteran or acarine prey abundance. Axtell (1970a) also reported large fluctuations in M. muscadomesticae population sizes in six poultry farms over two years in North Carolina, and stated that this variation "illustrates the difficulty in generalizing about the importance of predaceous mites in the natural control of flies".

A possible cause of the coincident peaks of Macrocheles numbers in both houses may have been phoretic transfer of mites by either sphaerocerid or Carcinops adults. This mite has frequently been

reported to be phoretically associated with flies from animal manure (Axtell 1964, Filipponi 1955, 1960, Petrova 1964, Steve 1959). Since C. hirtula did not appear in great numbers in House II during the explosive outbreak of this species in House I, it is an unlikely candidate as a vehicle for mite transport. Comparison of Figs. 3 and 4, however, suggests that there may have been considerable beetle movement between the houses, which were separated by a distance of ca. 30 meters. Following manure removal from House I, adult C. pumilio moved back into the house from the old manure which was piled outside, and were present in fairly large numbers at 2 weeks PC. Following this early peak, beetle numbers declined steadily over the next few weeks. Since Carcinops is a relatively long- lived species (Chapter V), sudden drops in the number of beetles in a given area is more likely to reflect movement out of the habitat than mortality. Other studies (Chapter III, Peck 1968, Peck and Anderson 1970) have suggested that newly accumulating manure is non-attractive or repellent to Carcinops adults, even when prey densities are high. Thus, in House I, there appeared to be an emigration of beetles from the house 3-5 weeks PC, which coincided with increasing numbers of beetles which appeared in House II. Similarly, beetle numbers in House I increased sharply in the weeks following the cleanout of House II. Further evidence for beetle transport of mites via phoresy comes from frequent personal observations of immature predator mites clinging to dispersing Carcinops collected in the field. (Dispersal behavior of C. pumilio is discussed in greater detail in Chapter IV).

Even after ethanol washings of field-collected beetles, viable immature mites are often found on protected regions of the cuticle, especially under the elytra (Chapter V). In Fiji, Bornemissza (1968) reported finding mites (including Macrocheles sp.) in phoretic association with the predaceous histerid Pachylister chinensis Queens.

In addition to beetle movement between the houses, Carcinops abundance over time was clearly influenced by the seasonal patterns of immatures of this species (Fig. 5). Beetle larvae, after a brief rise associated with the initial adult re-entry into House I, increased steadily from July 24 to July 15, reflecting a delayed response to sphaerocerid prey and increasing availability of non-predaceous mites. Peaks of beetle larvae in House I (June 17 and July 22) preceded adult peaks (July 8 and Aug. 12) by three weeks, which is the approximate developmental time of this species from adult to adult (Chapter V).

Later in the season, as adults became increasingly more numerous, larval populations declined and the ratio of adults to immatures became increasingly adult-biased. This drop in the number of immatures may have been due, at least in part, to intense competition between predatory species, life stages and individuals. Other evidence indicates that additional factors may have played a role as well, however. First, acarine prey densities remained high (10,000 to 100,000 mites/sample) throughout the crash in larval Carcinops numbers and thus were not limiting in themselves. Second, examination of the ovarian state of adults during this period showed that beetles were only slightly, albeit significantly, less fecund than were beetles

during peaks of larval numbers. It is possible that when beetle larvae are crowded above a certain threshold, feeding efficiency is drastically reduced due to mutual interference with foraging. In the lab, larvae are pugilistic and engage in protracted bouts of agonistic behavior when they contact one another, even in the presence of abundant prey (Chapter V). Hammer (1941) noted a similar behavior among immatures of Hister unicolor L. in Denmark. Other factors which may have contributed to the decline in beetle immatures are cannibalism and predation by Macrocheles on Carcinops eggs (Chapter V, Smith 1975). Under optimal conditions of temperature (30-31°C), space (<7 females/liter of medium) and prey availability, C. pumilio females are capable of producing and depositing over 10 eggs per day (Chapter V). Based on the relative numbers of beetle adults and immatures found in this and other studies (Peck and Anderson 1969, Pfeiffer 1978, Legner et al. 1975b, Smith 1975), it is clear that this reproductive potential is seldom realized under field conditions.

Overall, populations of Carcinops adults were found to be greatest later in the sampling period in House I, and were more numerous in House II than in House I during the first few weeks of sampling. These observations are in agreement with those of many other workers who have noted that large histerid populations are associated with long manure accumulation times (Anderson at al. 1968, Anon. 1975, Axtell 1981, Bills 1973, Dunning etal. 1978, Legner and Brydon 1966, Legner and Olton 1968, Legner et al. 1975b, Peck and Anderson 1969, 1970). On the basis of results presented here, as

well as other information on the life history (Chapter V, Smith 1975), ecology (Chapter III) and behavior (Chapter IV) of C. pumilio, this trend may be viewed as reflecting the combined influences of increasing habitat acceptability, emergence of new adults into the population, the long lifespan of adults of this species and immigration of beetles from neighboring houses.

Most of the research on arthropod predators and scavengers in poultry manure has been conducted in warmer regions of the U.S. such as California and North Carolina, where climatic factors and open-sided house design result in far greater manure community diversity. Because of the virtual lack of coleopteran competitors in this system in Massachusetts, C. pumilio was found at considerably higher population densities in the present study than in these latter areas. Legner et al. (1975b), in a study of seasonal abundance of manure arthropods on two farms in California, found that histerid adults (C. pumilio and G. nanus) were present at peak densities of only 27.9 beetles/liter. Peck and Anderson (1969), also working in California, reported maximum densities of 13.8 histerids/liter in manure which had accumulated for six months prior to sampling. In a monthly survey of the coleopteran fauna of 15 poultry farms in North Carolina, Pfeiffer (1978) found more than 140 Carcinops per liter on only one occasion on one farm. Of the 26 sampling dates at these 15 farms, a grand mean of ca. 20 beetles/liter was observed (calculated from data presented in Pfeiffer 1978). In contrast, samples taken during the present study contained an average of less than 33

beetles/liter on only four sampling dates in House I, all of which were within the first 6 weeks PC. In House II, where all sampling was conducted after 5 weeks PC, all samples contained at least 47 C. pumilio adults/liter.

Coproica hirtula was found to be the dominant dipteran present in poultry manure in this study, where large numbers were observed in the weeks following house cleanout. Richards (in Stone et al. 1965) reported this species to be widespread in its distribution in the U.S., however, there have been few habitat records noted for C. hirtula in North America (Ware 1966, Poorbaugh et al. 1968). Despite the scarcity of published habitat information for this species, it is apparently quite common in poultry houses in many areas of the Northeast, including Connecticut (J. Rock, pers. comm.), New York (D. Rutz, pers. comm.), Maryland (L. Hellman, pers. comm.) and Ontario (S. Marshall, pers. comm.). While Tenorio (1968) found C. hirtula breeding in cow dung in Hawaii, this species appears to develop primarily in avian manure, where it has been most commonly found in the U.S. (see above), the Netherlands (Rohacek, pers. comm.) and Czechoslovakia (Zuska and Lastovka 1969). Sphaerocerids are among the first colonizers of freshly accumulating manure in deep-pit poultry houses in England (Bills 1973), where they occasionally present nuisance problems to workers in the houses (Anon. 1975). Later in the accumulation cycle, populations of these flies decline due to predator pressure, and can quickly become re-established in areas where predator densities are low (Chapter III). Peck (1968) found

sphaerocerids to be present throughout the year in California poultry houses, with greater numbers occurring from June to September.

Although Coproica populations had greatly declined by the time of peak Carcinops numbers, these flies appeared to be important in the initial establishment of predators in newly accumulating manure, where cereal mite populations were still relatively small. Data which are presented in the next chapter (Chapter III) also suggest that C. hirtula larvae may in fact be more available to predators later in the season than is indicated by core sample data. The suitability of sphaerocerids as prey for Carcinops is further substantiated by the successful colonization of C. pumilio through seven generations in the lab using only Coproica (on CSMA fly medium) as a prey source (Chapter V). Since these dipterans are weak fliers which generally do not leave the poultry houses (Geden, pers. obs.), they do not pose a pest problem in themselves to neighboring communities. Therefore, given the potential role of C. hirtula in promoting natural enemies of other, pestiferous fly species and in the degradation and aeration of newly accumulating manure (S. Marshall, pers. comm.), producers should be discouraged from efforts to control them, even during "outbreaks".

Temperature data. In another study (Chapter III), arthropod predators and prey in poultry manure were found to be most abundant in the surface regions of the habitat. Based on information presented in Table 1, it appears that more mobile species in the community such as Macrocheles and Carcinops adults, which freely move on and below the

manure surface, are exposed to a wide range of temperatures within a small area. Thus, for example, predators which moved through the outer 6 cm of the manure on Aug. 19 in House I experienced a range of temperature from 24.2 to 36.7°C. In a similar study conducted in a deep-pit house in England, Bills (1973) also found that after the first few weeks PC, the manure temperature (8 cm below the surface) was always higher than that of the air immediately over the manure surface. He reported finding, on one occasion, large clusters of C. pumilio larvae in manure which had a temperature of 43°C, compared with a manure-air interface temperature of 14° C. In the present study, the highest manure temperature reading for any individual sample was 41.5° C, which was observed on Aug. 5 in House I. After extraction, this 1.5 liter sample was found to contain 246 C. pumilio adults, 69 and 42 first and second instar beetle larvae, respectively, 334 M. muscadomesticae adults, 26 C. hirtula adults and 188,000 cereal mites and other non-predaceous acarines. It is difficult to separate the relative thermal contributions of microbial and arthropodan activity from other chemical changes occurring in the manure. Nonetheless, it is apparent that those species which utilize this highly metabolically active substrate are tolerant of fairly high local habitat temperatures. Carcinops adults are also tolerant of rather low temperatures, and may be maintained for several months at 6° C with no apparent diminution of survival or fecundity (Geden, pers. obs.).

In Massachusetts, where poultry houses are environmentally

controlled to some extent throughout the year with respect to photoperiod and temperature, none of the members of the manure community appear to enter diapause. Even in February the manure-air interface temperature seldom falls below 15°C, and all life stages of the species or groups discussed in this study can be found in the relatively warmer surface regions of the manure, although in somewhat smaller numbers (Geden, pers. obs.).

Sex ratios of C. pumilio. Smith (1975) found an overall sex ratio of 60 ♂:40 ♀ based on 100 beetles collected from a Massachusetts-style poultry house in New Hampshire. In the present study, male Carcinops were found in proportionately greater numbers than females during the first seven weeks of sampling in House I, after which an approximately equal number of males and females was observed for the remainder of the season, except for the final two sampling dates (weeks 14 and 15 PC). Possible sources of this seasonal variation are between-sex differences in dispersal tendency, emergence success or post-emergence mortality. In another study (Chapter IV), no significant differences were found in the sex ratios of dispersing and foraging C. pumilio populations, with both showing similarly male-biased ratios. In laboratory colonies, pupal sex ratios are close to 1:1 and there are no major differences between the sexes with respect to adult emergence success and post-emergence survival (Chapter V). Under field conditions, however, other forces may act to reduce female longevity such that older populations of this long-lived species would have

proportionately more males than would younger populations. This would explain the observed change in sex ratios from male-biased to ca. 1:1 which occurred as increasingly more newly emerged adults entered the population in the period from July 15 to Aug. 12. Under crowded conditions in the lab, ovipositing females are frequently attacked by other adults, which tear at the exposed, membranous ovipositor (Geden, pers. obs.). If this behavior occurs in the field, it could partially account for the change back to male-skewed sex ratios which were observed on Aug. 26 and Sept. 2, several weeks after adult Carcinops were present at peak densities.

Ovarian state of C. pumilio. Because Carcinops females develop eggs singly and do not resorb oocyte nutrients unless they are subjected to prolonged periods of prey deprivation (Geden, pers. obs.), it is difficult to make a meaningful assessment of ovarian condition as it relates to prey availability and recent nutritional history. In all samples of females which were examined, a great deal of variability in ovarian state was observed, with some beetles showing no perceptible egg development and others, in a few rare cases, possessing more than two fully developed, chorionated eggs. Since beetles are capable of producing over 10 eggs per day (Chapter V), the condition of the most-developed oocyte in this species provides a "snapshot" impression of the immediate state of the ovaries but gives no information on the rate of egg development. Thus, for example, if a female is collected whose most-developed oocyte consists of a completely developed egg, it

is impossible to determine, from this information alone, whether that individual was about to lay its 10th egg in 24 h or its first in three days. It is therefore not surprising that no significant differences were found among beetles during different time intervals for this parameter of fecundity.

Examination of the second-most-developed oocyte, however, gives some insight into the nutrient reserves which are available for further egg maturation and is thus a more sensitive indicator of prey availability. During the last 5 weeks PC (weeks 11-15), when adult Carcinops population densities were at their peak and larval numbers were low, females had significantly smaller second-most-developed oocytes than did beetles from either of the two earlier age intervals, suggesting increased competition for prey or mutual interference with feeding behavior. This difference was small, however, and cannot entirely account for the crash in numbers of beetle immatures which was also observed during this period.

Little is known of the prey-specificity of C. pumilio or of the relative nutritional value of potential prey items with respect to reproductive output. Peck (1969) reported that C. pumilio would feed readily on house fly eggs and early instar larvae. Smith (1975) found that masses of house fly eggs elicited a stronger feeding response by adult beetles than did scattered fly eggs. He also observed that beetles quickly discovered and fed on cereal mites which had contaminated a mealworm colony, and concluded that "it is probable that acarids make up a portion of the natural diet of C. pumilio in

chicken manure, especially when flies are not abundant" (Smith 1975). In addition, I have also seen adult beetles attack house fly adults as they struggle to emerge from their puparia, and have often observed them feeding on a variety of dead arthropods as well as on broken chicken eggs. Based on these observations and the wide range of habitats from which this species has been recovered (Hicks 1959, Hinton 1945), it seems clear that C. pumilio is an opportunistic predator and scavenger which is capable of establishing and maintaining large populations in the absence of house fly. Further work is needed to determine the relative conversion efficiency of these various food items into beetle egg output, and to relate this information to the natural foraging behavior and feeding preferences of Carcinops in the field.

Morphometric analysis of C. pumilio. Overall, slightly smaller beetles were collected in the last 5 weeks PC than in either of the two earlier time intervals. Since there are no simple, reliable physiological age-grading techniques for this species (Chapter IV) and since there is continuous overlap in generations of these long-lived beetles, it is difficult to assess the proportion of newly emerged individuals in populations sampled from the field. Nonetheless, several lines of evidence strongly suggest that this observed decrease in average body size was the result of intense predator competition or interference which led to the production of undersized adults later in the season. First, the last five-week interval, when smaller adults

were noted, included the period when adult population densities were maximal (Aug. 5-Sept. 2). This peak in adult numbers was preceded by several weeks by similar peaks in the number of beetle immatures. Second, Macrocheles adults were still present at fairly high levels and dipteran prey were relatively scarce during the weeks when beetle larvae were present in greatest numbers. Finally, when beetle larvae are crowded in the laboratory or provided with suboptimal prey densities, they take longer to develop and produce smaller pupae and adults than larvae maintained on optimal regimes (Geden, pers. obs.). The fitness of these smaller-bodied adults remains to be investigated.

C H A P T E R III

INFLUENCE OF SPATIAL POSITION, LOCAL ENVIRONMENTAL CONDITIONS AND HABITAT MATURITY ON DISTRIBUTION PATTERNS OF ARTHROPODS ASSOCIATED WITH POULTRY MANURE.

Introduction

Interest in biological control of filth flies has increased in recent years, reflecting efforts to apply integrated pest management concepts and methodologies to the regulation of pests affecting man and animals (U.S.D.A. 1981). To date, much of the emphasis of this work has been on pteromalid parasites of fly pupae such as Spalangia and Muscidifurax spp. Under certain, highly controlled conditions over small areas, these parasites have been demonstrated to be capable of significantly reducing (Legner and Brydon 1966, Legner and Dietrick 1972,1974, Morgan et al. 1975a,b, Olton and Legner 1975, Rutz and Axtell 1979) house fly populations. Major successes have been achieved only through mass releases of parasites, which are available to cattle and poultry producers only through commercial insectaries, whose products have frequently been found to be deficient in quality control (Stage and Peterson 1981, Legner 1981).

In poultry houses in the Northeast, native predators of fly immatures are the most important filth fly biological agents.

Predators alone have been noted to maintain house fly populations at essentialy zero levels on some farms in Maryland (L. Hellman, pers. comm), Pennsylvania (C. Collison, pers. comm.), New York (D. Rutz, pers. comm.), Connecticut (J. Rock, pers. comm.), Ontario (G. Surgeoner, pers. comm.) and Massachusetts (Geden, Chapter II). In Massachusetts, the two principal predators are Macrocheles muscadomesticae (Scolopi), a mite which feeds on house fly eggs and newly hatched larvae (Axtell 1961, 1963a,b, 1969, 1970a,b) and Carcinops pumilio (Erichson), an histerid which also preys on fly eggs and immatures. Both adults and larvae of the latter species are predaceous, and it is viewed as being equally effective as M. muscadomesticae with respect to filth fly biocontrol (Peck 1969, Peck and Anderson 1969, Axtell 1981). C. pumilio, together with another histerid, Gnathoncus nanus (Scriba), are often the most abundant coleopterans in poultry manure throughout the United States (Legner 1971, Legner and Olton 1970, Peck and Anderson 1969, Pfeiffer and Axtell 1980) and Great Britain (Bills 1973).

Little is known of the environmental factors which promote and maintain predator populations in the absence of house flies. The objectives of the present study were to gather needed ecological data on distribution patterns of members of the poultry manure arthropod community under conditions of high, naturally occurring predator densities. These objectives were as follows: (1) to determine within-habitat distribution patterns of members of the manure community; (2) to examine the relative contributions of spatial

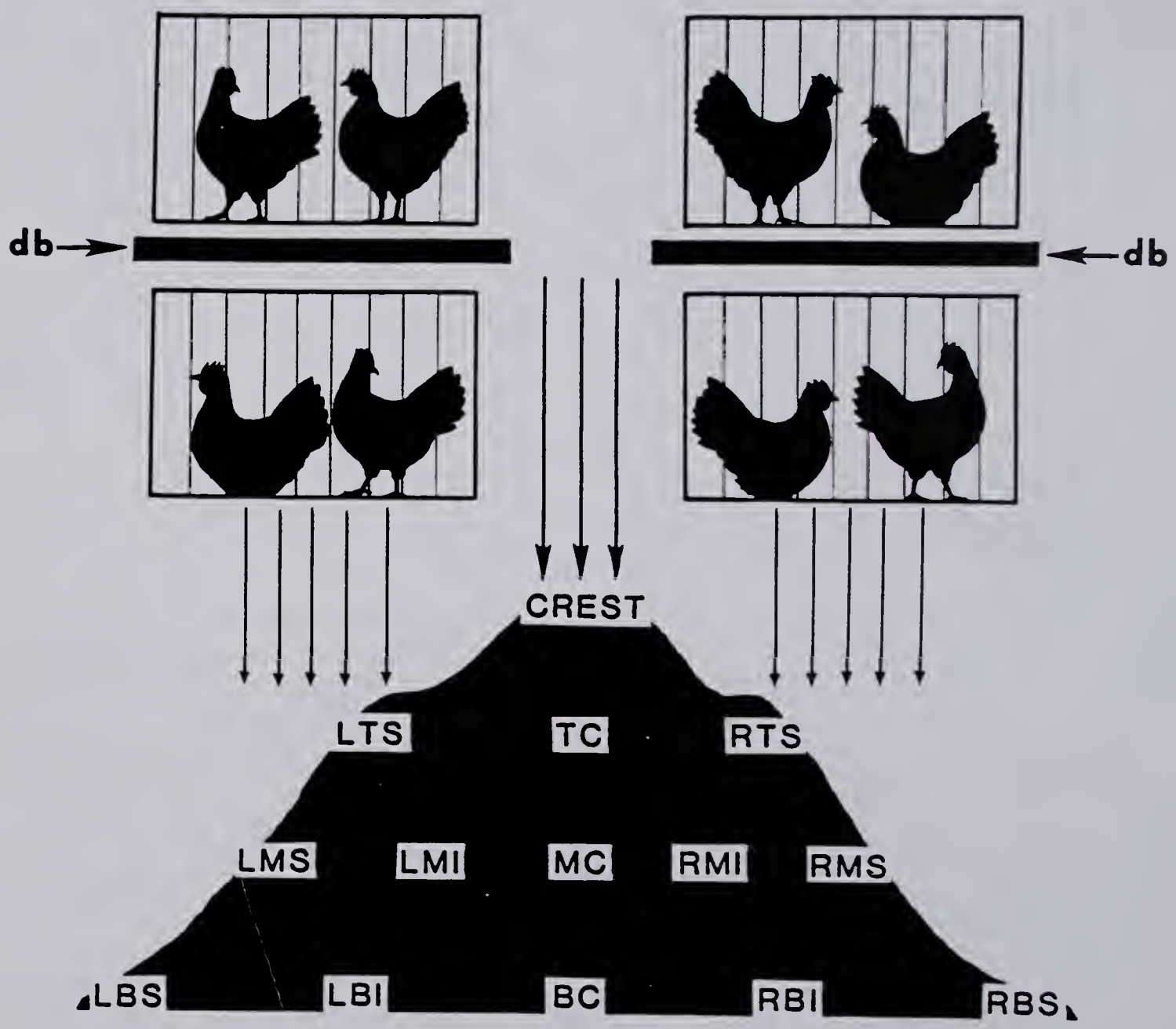
position, prey availability and local environmental conditions on predator distribution patterns; (3) to determine whether temporary, relatively predator-free manure accumulations serve as oviposition sites for flies; and, (4) to investigate the influence of habitat maturity on predator and prey distribution.

Materials and Methods

Study site and house design. All studies were conducted in 1981-1982 at a commercial egg production facility in Central Massachusetts (Hill's Farm, Hubbardston, MA) with an eight year history of natural house fly control (see Chapter II for details). House design was typical of Massachusetts' producers, with hens in paired, two-tiered rows of cages suspended ca. 1.2 m over a concrete floor. Manure from birds in the upper tiers dropped onto so-called "dropping boards", where it accumulated for 24 h before being scraped onto the main manure rows beneath the lower birds (Fig. 14). Manure was removed at 3-4 month intervals.

Cross-sectional profile samples. To determine within-habitat distribution patterns of manure arthropods, cross-sectional profile samples were taken from mature (3 mo accumulation time) manure on July 28, 1981. Profiles were examined at five equidistant locations along the central row of birds to minimize edge and side biases. At each location an area was first shovelled out to allow access to the

Fig. 14. Schematic illustration of manure accumulation in a typical Massachusetts poultry house, and positions of samples taken during a cross-sectional manure profile study in 1981. Light arrows indicate manure dropping continuously from lower tiers of birds. Manure fom upper tiers collects on dropping boards and is scraped every 24 hr onto the main manure row. Dark arrows represent this daily deposition of dropping board manure onto the crest of the main manure row below. (LTS = left top side, TC = top center, RTS = right top side, LMS = left middle side, LMI = left middle interior, MC = middle center, RMI = right middle interior, RMS = right middle side, LBS = left bottom side, LBI = left bottom interior, BC = bottom center, RBI = right bottom interior, RBS = right bottom side.)


db
db
CREST
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TC
RTS
LMS
LMI
MC
RMI
RMS
LBS
LBI
BC
RBI
RBS

profile. Fourteen sample positions were then determined and marked as follows: (1) four equidistant vertical positions were measured and marked at the center of the profile, with one at the crest (CREST), one at the base (BC), and two in between (TC,MC); (2) from the bottom two central positions (MC,BC), the distance to both edges of the profile were marked (LMS,RMS,LBS,RBS), as well as the midpoint of these distances (LMI,RMI,LBI,RBI); (3) from the the central position below the crest (TC), only edge positions were marked (LTS,RTS). This method resulted in seven surface positions and seven interior positions, which are illustrated schematically in Fig. 14.

From each of these 14 positions, half-liter samples were taken with a metal corer (diam = 12.5 cm, length = 4.0 cm), placed in paper containers with organdy cloth covers, returned to the lab and extracted through modified Tullgren funnels into 80% ethanol. Arthropods were separated from debris in the alcohol via water flotation and selective screening. All stages of C. pumilio and sphaerocerids (mostly Coproica hirtula Rondani) were counted individually. Counts of cereal mites and other non-predaceous acarines were determined volumetrically by first removing all other arthropods from the alcohol by hand and counting mite numbers in subsample aliquots of known dilution. Three mite subsamples were counted for each sample, the mean number per subsample was determined, and the total number in the original sample was estimated by multiplying this mean figure by the dilution factor. Immature Macrocheles were disregarded in the counting of these samples. For

the latter species, only adults were counted, since the generation time of M. muscadomesticae is less than three days (Axtell 1981). The large number of treatments (14 sample positions) precluded statistical treatment of the data.

Surface distribution and local environmental conditions. Results of the above study revealed strong clumping of all groups on or just below the manure surface. To examine this pattern more closely and to investigate the influence of local environmental conditions on predator-prey distribution, samples corresponding to the seven surface, or peripheral, positions cited above were taken at ten locations along the central row of manure on Aug. 14, 1981. The temperature of the manure 2 cm below the surface was taken for each of these 70 samples. Also, for each sample taken for extraction, an adjacent sample was taken for determination of manure moisture content. These latter samples were weighed immediately in the field to avoid initial water loss (Peck and Anderson 1969), returned to the lab, dried thoroughly in a microwave oven, and reweighed to determine the original water content. Samples for arthropod extraction were handled as described in the previous section. The abundance of arthropods and manure moisture content from the different sample locations were analyzed by Student-Newman-Keuls Range Test at P=.05 (Steel and Torrie 1960). Due to the highly contagious distribution patterns of all species or groups, within as well as between sample positions, animal counts were subjected to log (x + 1.5)

transformation prior to analysis of variance. Original, untransformed counts are used in the presentation of the data in tables. Finally, analyses were conducted to examine significance levels of correlations between predators and prey, and of all arthropods with manure moisture content.

Dropping board samples. To determine the possible role of manure accumulating on dropping boards in providing a relatively predator-free environment for fly oviposition, samples of this manure were taken on Aug. 21, 1981. Samples were taken by forming depressions along the crest of the manure in the early morning, lining these depressions with aluminum flashing collecting troughs, and taking samples from the troughs immediately after the boards were cleaned. Ten one-liter samples of this manure were collected in this manner, placed in paper containers with organdy cloth covers and incubated for an additional 24 h at 28° C under constant light to allow dipteran egg hatch. Samples were then counted and extracted as above.

Influence of habitat maturity on distribution. Casual observations made during another study in 1980 (Chapter II) suggested that newly accumulting manure is non-attractive to predators, even when prey densities are high. A similar observation had been reported by Peck and Anderson (1969, 1970) in California. To test this, I had initially intended to follow repopulation of a row of new manure

surrounded by older rows to simulate alternate row removal conditions. With the cooperation of the producer, the central row of manure was removed from a different layer house on May 26, 1981, leaving it flanked by manure of 9-wk accumulation time at the start of the repopulation experiment. For the next three weeks, five half-liter samples were taken from each side of the central row and five samples from the facing sides of the two adjacent rows (20 samples/week). Sampling was discontinued after three weeks due to the accidental destruction of the house by a tornado on June 22. Samples were handled and counted as described above. Due to large between-week variation in population densities of most arthropods, each week was treated as a separate experimental unit. Between-row (age treatment) differences within weeks were analyzed by one way ANOVA using transformed counts as described above.

In a separate study conducted in 1982, islands of different manure maturity were established within a row by sequential hand-removal of manure at different times. This removal program resulted in the establishment of three groups of ten islands of manure of 2, 6 and 10-wk accumulation time. Each age-treatment island of manure was flanked by islands of the other two age treaments. Two weeks was selected as the earliest age treatment in order to allow the development of a normal age structure for C. pumilio (Chapter V). Half-liter samples were taken from each of these 30 islands on July 10, 1982, and handled and counted as described above. Differences in numbers of arthropods among the three age-treatment groups of islands

were analyzed by Student-Newman-Keuls Range Test at P = .05 using transformed counts.

Results

Cross-sectional profile samples. Results of cross-sectional profile samples from July 28, 1981 are presented in Table 5. For each arthropod species or group, at least 85% of all individuals were found in the seven surface samples (CREST,LTS,RTS,LMS,RLS,LBS,RBS). Peripheral clumping was most pronounced in C. pumilio 2nd instar larvae (93.9% of the total), C. hirtula immatures (95.2%), M. muscadomesticae adults (97.9%) and other acarines (99.7%). Comparisons of within-stratum samples (eg. LMS,LMI,MC,RMI,RMS) indicate that this surface clumping is height-independent, with far greater numbers of individuals present in surface than interior samples in all three multi-sample strata. Further, the three uppermost peripheral positions (CREST,LTS,RTS) were favored by all groups, and accounted for 53.3% of all C. pumilio adults collected, 59.1% and 63.3% of C. pumilio 1st and 2nd instar larvae, respectively, 63.4% of non-predaceous mites, 67.4% of C. hirtula adults, 76.9% of M. muscadomesticae adults and 86.8% of C. hirtula immatures.

Surface distribution and local environmental conditions. Results of surface distribution samples from Aug. 14, 1981 are presented in Table 6. Because of the highly contagious distribution patterns of all

Table 5. Total numbers of arthropods collected from 5 half-liter samples of manure at each of 14 positions along cross-sectional profiles of 12-week-old poultry manure. Numbers in parentheses indicate percent of total found at the sample position.

Position	Species or group			
	C. pumilio			*M. muscadomesticae*
	1st instars	2nd instars	adults	adults
CREST*	260 (10.9)	119 (7.6)	405 (18.3)	2,750 (15.1)
LTS	587 (24.6)	470 (30.1)	385 (17.8)	4,707 (25.7)
RTS	562 (23.6)	400 (25.6)	379 (17.2)	6,530 (35.9)
TC	22 (0.9)	8 (0.5)	38 (1.7)	88 (0.5)
LMS	193 (8.1)	189 (12.1)	274 (12.4)	974 (5.4)
RMS	246 (10.3)	252 (16.1)	247 (11.2)	2,297 (12.6)
LMI	67 (2.8)	20 (1.3)	23 (1.0)	18 (<0.1)
RMI	88 (3.7)	34 (2.2)	117 (5.3)	125 (0.7)
MC	16 (0.6)	2 (0.1)	16 (0.7)	35 (0.2)
LBS	70 (2.9)	15 (0.9)	155 (7.0)	228 (1.2)
RBS	176 (7.4)	22 (1.4)	106 (4.8)	316 (1.7)
LBI	22 (0.9)	7 (0.4)	18 (0.8)	28 (1.3)
RBI	71 (3.0)	22 (1.4)	44 (2.0)	91 (0.5)
BC	3 (<0.1)	2 (0.1)	3 (0.1)	4 (<0.1)
TOTAL	2,383	1,562	2,208	18,195

	Other Acarina	*C. hirtula*	
	all stages	larvae	adults
CREST*	127,481 (6.4)	122 (73.1)	51 (36.2)
LTS	757,742 (38.1)	17 (10.3)	12 (8.5)
RTS	371,365 (18.7)	6 (3.6)	32 (22.7)
TC	1,246 (<0.1)	0 (0.0)	1 (0.7)
LMS	286,741 (14.4)	0 (0.0)	1 (0.7)
RMS	406,722 (20.4)	14 (8.4)	19 (13.4)
LMI	2,235 (<0.1)	1 (0.6)	3 (2.1)
RMI	893 (<0.1)	1 (0.6)	1 (0.7)
MC	74 (<0.1)	0 (0.0)	1 (0.7)
LBS	24,866 (1.3)	0 (0.0)	2 (1.4)
RBS	7,902 (0.4)	0 (0.0)	2 (1.4)
LBI	151 (<0.1)	0 (0.0)	8 (5.7)
RBI	765 (<0.1)	5 (3.0)	8 (5.7)
BC	15 (<0.1)	1 (0.6)	0 (0.0)
TOTAL	1,988,198	167	141

* See text and Fig. 14 for explanation of sample positions.

Table 6. Mean numbers of arthropods collected from 10 half-liter samples of manure at each of 7 positions along the surface of 12-week-old poultry manure.

Position	Species or group			
	C. pumilio			*M. muscadomesticae*
	1st instars	2nd instars	adults	adults
CREST	40.9 ± 8.72bc	26.8 ± 6.61b	84.8 ± 6.87c	681.6 ± 74.42c
LT	81.8 ± 12.48c	60.7 ± 12.79c	63.9 ± 7.23b	794.6 ± 106.05c
RT	84.5 ± 12.32c	66.7 ± 9.90c	68.9 ± 7.15b	1,044.0 ± 145.24c
LM	38.4 ± 9.47b	40.1 ± 11.61bc	51.6 ± 10.58b	254.4 ± 62.73b
RM	64.1 ± 8.95bc	52.4 ± 12.34bc	66.8 ± 7.79b	514.2 ± 98.29c
LB	11.4 ± 1.90a	3.0 ± 0.67a	32.6 ± 5.09a	94.3 ± 28.46a
RB	8.5 ± 5.32a	9.8 ± 2.48a	36.3 ± 4.24a	195.8 ± 54.44b

	Other Acarina	*C. hirtula*	
	all stages	larvae	adults
CREST	22,289.2 ± 10,490.4ab	33.4 ± 10.94c	9.3 ± 2.97b
LT	37,805.1 ± 13,402.7ab	4.8 ± 1.51b	2.8 ± 0.61ab
RT	127,949.3 ± 32,995.2c	5.4 ± 2.26b	6.9 ± 2.09b
LM	72,864.0 ± 15,879.9bc	0.8 ± 0.55a	1.0 ± 0.49a
RM	72,404.0 ± 33,301.2bc	4.8 ± 3.04b	3.1 ± 1.18ab
LB	5,404.8 ± 1,631.7a	0.0 ± 0.00a	0.8 ± 0.33a
RB	6,219.1 ± 2,330.6a	0.6 ± 0.34a	3.8 ± 1.24ab

Means within columns which are not followed by the same letter are significantly different (Student-Newman-Keuls Range Test, P=.05). Data are presented as $\bar{X}$ number/sample ± S.E. See text and Fig. 14 for explanation of sample positions.

groups, within-position variation was high. Nonetheless, certain patterns may be discerned. Significantly more Carcinops adults were found at the manure crest than at any other sample position, and significantly more were present in the upper four side positions (RT,LT,RM,LM) than the two basal positions (RB,LB)). Both 1st and 2nd instars of this species were significantly more abundant in the top five than the bottom two positions, however, clumping at the crest was not apparent. A slight, but not statistically significant, clumping trend was also evident on the right-hand positions (RT,RM) of the four upper positions.

With the exception of the middle-right position (RM), M. muscadomesticae were significantly more abundant in the upper three than the lower four sample positions. In addition, a right-hand side bias was clearly evident in this species and was statistically significant at the basal and middle positions. Other mites were found in greatest numbers in the middle positions and the top right sample sites. Pronounced side bias was apparent in the top side samples, with nearly 130,000 mites present on the right-hand side (RT) compared with the corresponding left-hand position (LT=ca. 30,000).

Sphaerocerid (C. hirtula) adults were present in low numbers and showed little clumping tendency, except for a right-hand side bias at most levels. Immatures, on the other hand were almost exclusively found in the crest position, with some larvae also present in the upper side (RT,LT) and the middle right (RM) positions.

Analysis of manure moisture content (Table 7) revealed the most

Table 7. Moisture content of manure at 7 surface positions corresponding to sample locations presented in Table 6.

Position	Moisture content (% water ± S.E.)
CREST	63.6 ± 1.99cd
LT	60.5 ± 2.83c
RT	67.9 ± 1.56d
LM	62.1 ± 2.72cd
RM	68.6 ± 2.29d
LB	25.8 ± 3.44a
RB	41.1 ± 3.94b

N=10 for each position. Means which are not followed by the same letter are significantly different (Student-Newman-Keuls Range Test, P=.05). Data are presented as mean percent water ± S.E. See text and Fig. 14 for explanation of sample positions.

moist regions to be the upper five positions. Also, the left-hand side of the row was significantly drier than the right-hand side, which was closer to the wall housing the large exhaust fans. This may seem paradoxical, however, Smith (1975) examined air flow patterns and manure moisture in houses of similar design in New Hampshire, and found that air flows more quickly over the row sides distal to the wall fans, with the result that manure on these distal sides is drier than that on the proximal sides, except for the row immediately adjacent to the fans. Distribution of all arthropods with respect to manure moisture is presented in Figs. 15-18. Because considerably more moist (>50% water) samples were collected than drier samples, data in these figures have been converted to mean numbers of individuals per moisture interval rather than total numbers. Both C. pumilio and C. hirtula adults were found to forage over a broad range of manure moisture content. C. pumilio larvae were mainly found in manure with greater than 50% moisture, as were M. muscadomesticae adults. A small number of C. hirtula larvae were found in manure with a moisture content of 41-50%, but never below 41%. The majority of these larvae were found in samples with greater than 51% water. Non-predaceous mites were also present in greatest numbers in wetter manure, and appeared to be most abundant in the 61-70% moisture range. Correlation coefficients and significance levels of correlations between all groups and manure moisture are presented in Table 8. C. pumilio and C. hirtula larvae, and M. muscadomesticae adults were strongly and significantly correlated with manure moisture ($P<.01$).

Fig. 15. Distribution of C. pumilio adults and immatures in poultry manure with respect to manure moisture content. Bars represent mean numbers of individuals per moisture content interval.

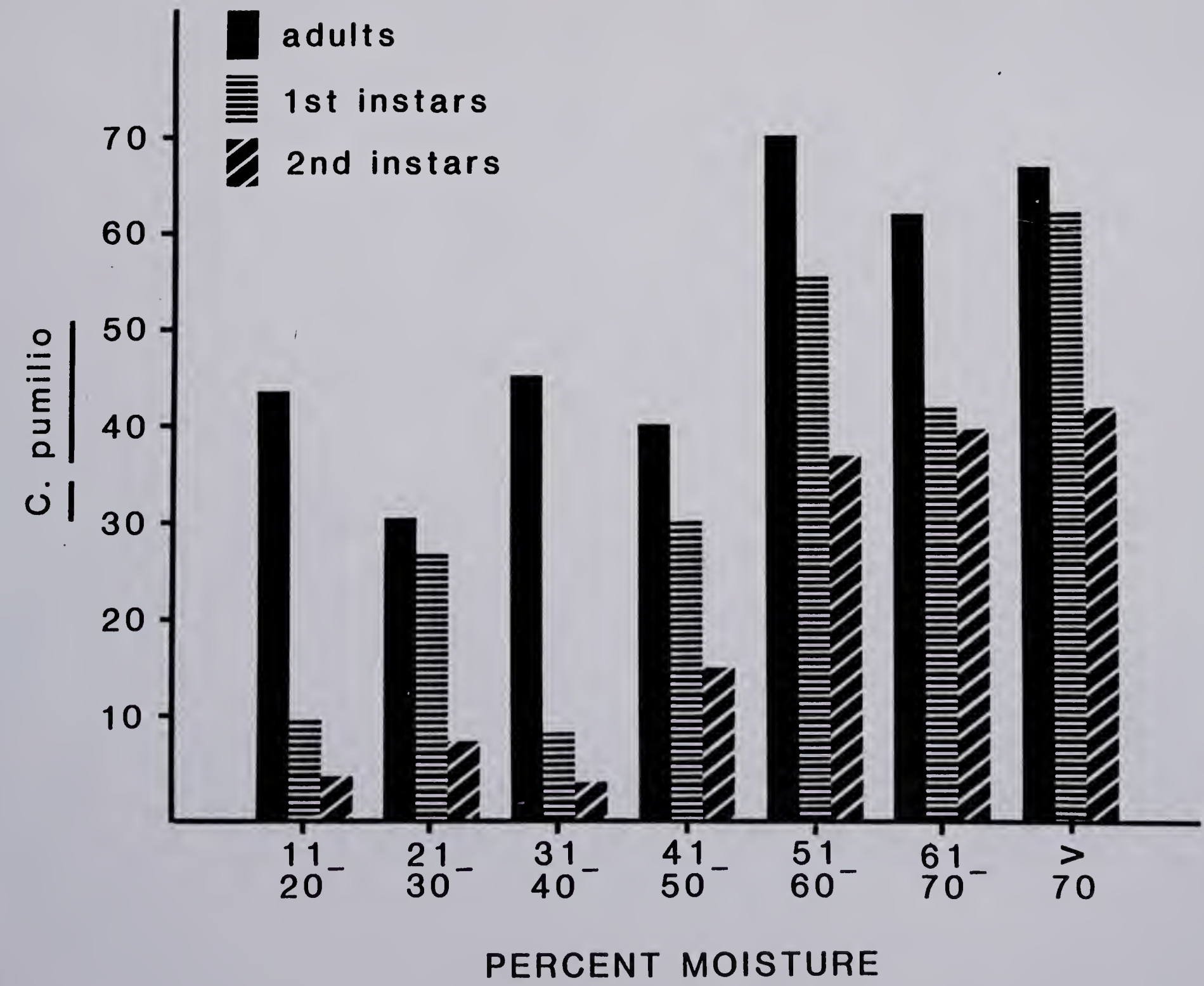

adults
1st instars
2nd instars
C. pumilio
70
60
50
40
30
20
10
11-20
21-30
31-40
41-50
51-60
61-70
>70
PERCENT MOISTURE

Fig. 16. Distribution of C. hirtula adults and immatures in poultry manure with respect to manure moisture content. Bars represent mean numbers of individuals per moisture content interval.

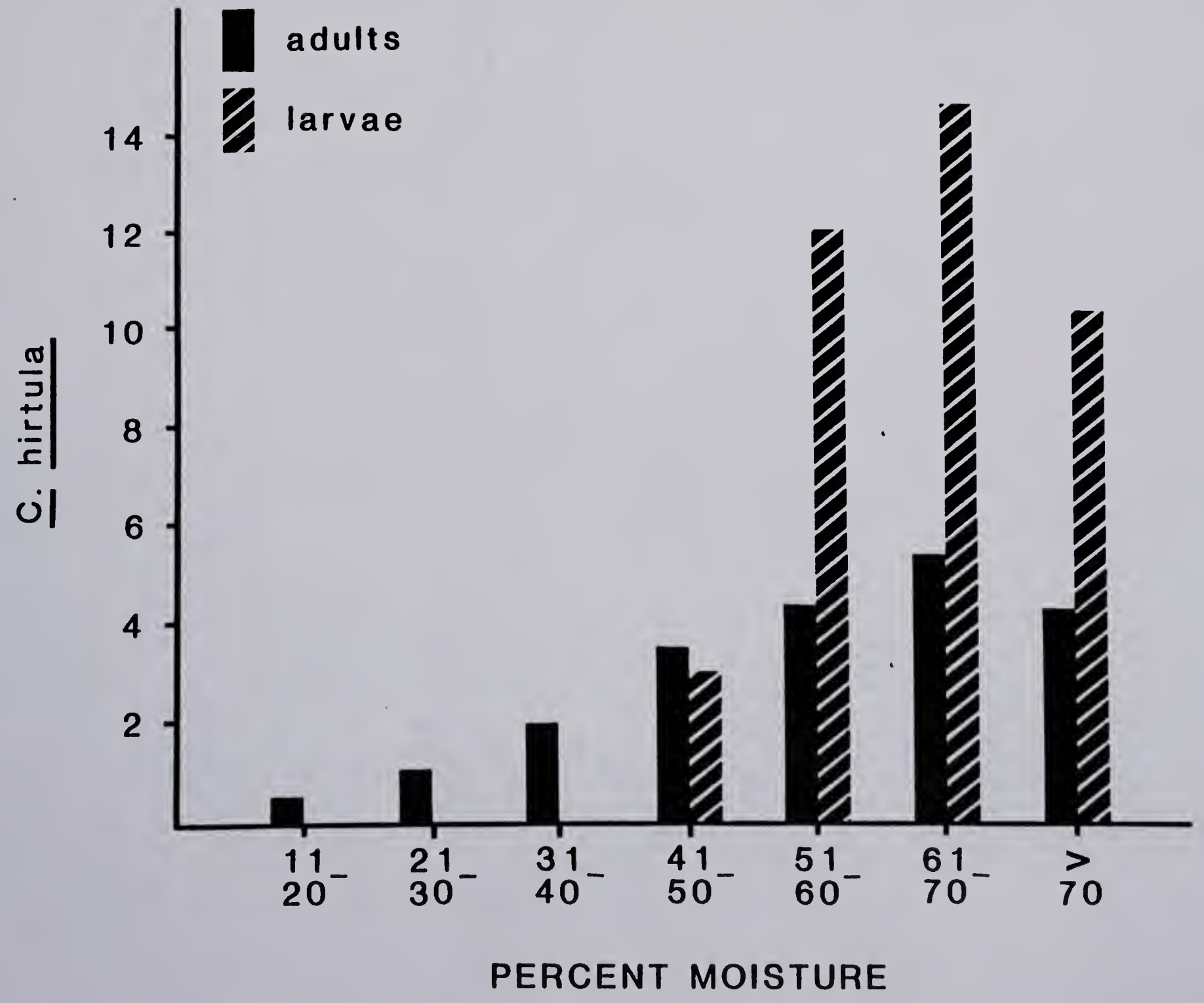

adults
larvae
14
12
10
8
6
4
2
C. hirtula
11-20
21-30
31-40
41-50
51-60
61-70
>70
PERCENT MOISTURE

Fig. 17. Distribution of M. muscadomesticae adults in poultry manure with respect to manure moisture content. Bars represent mean numbers of individuals per moisture content interval.

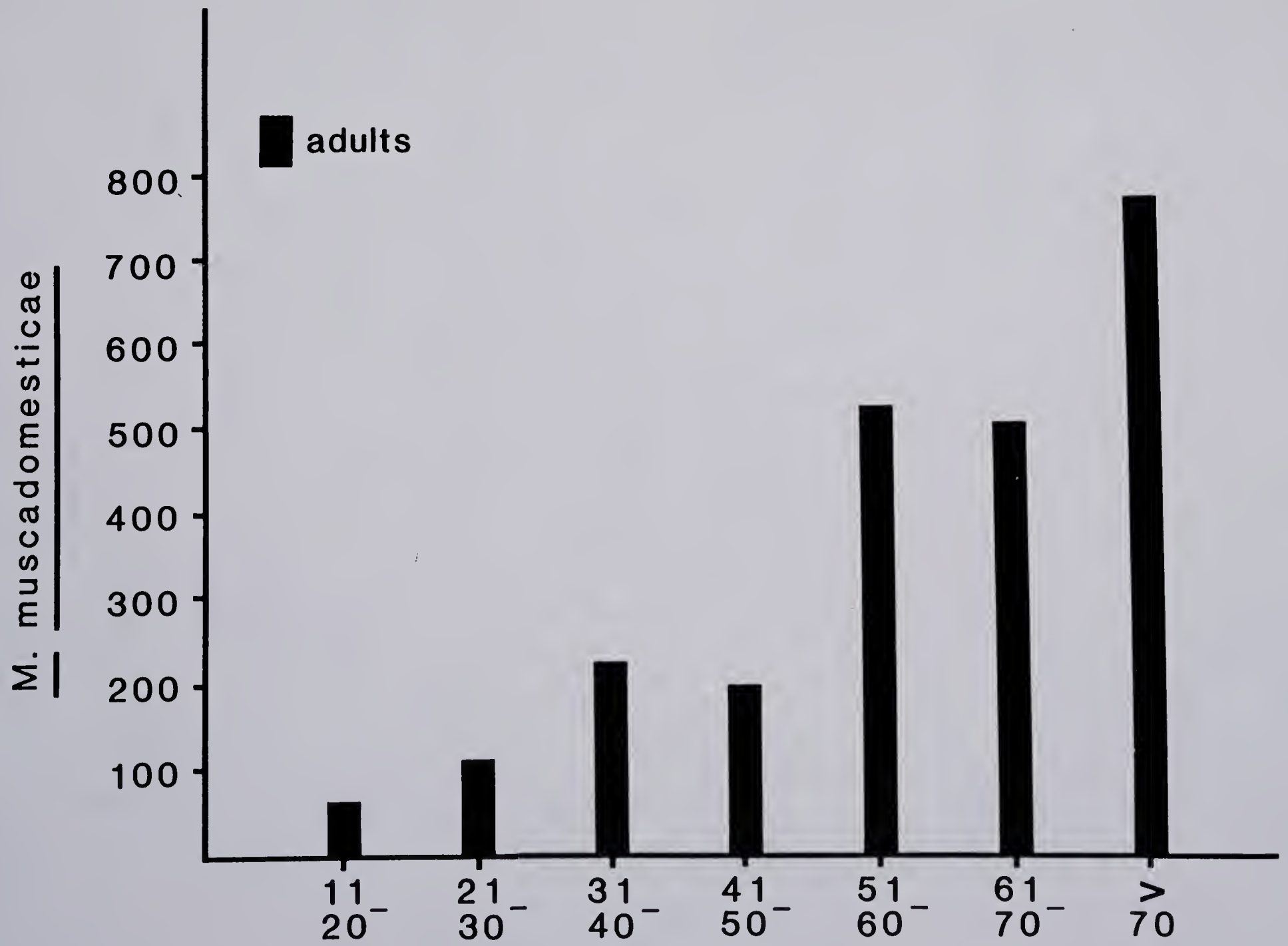
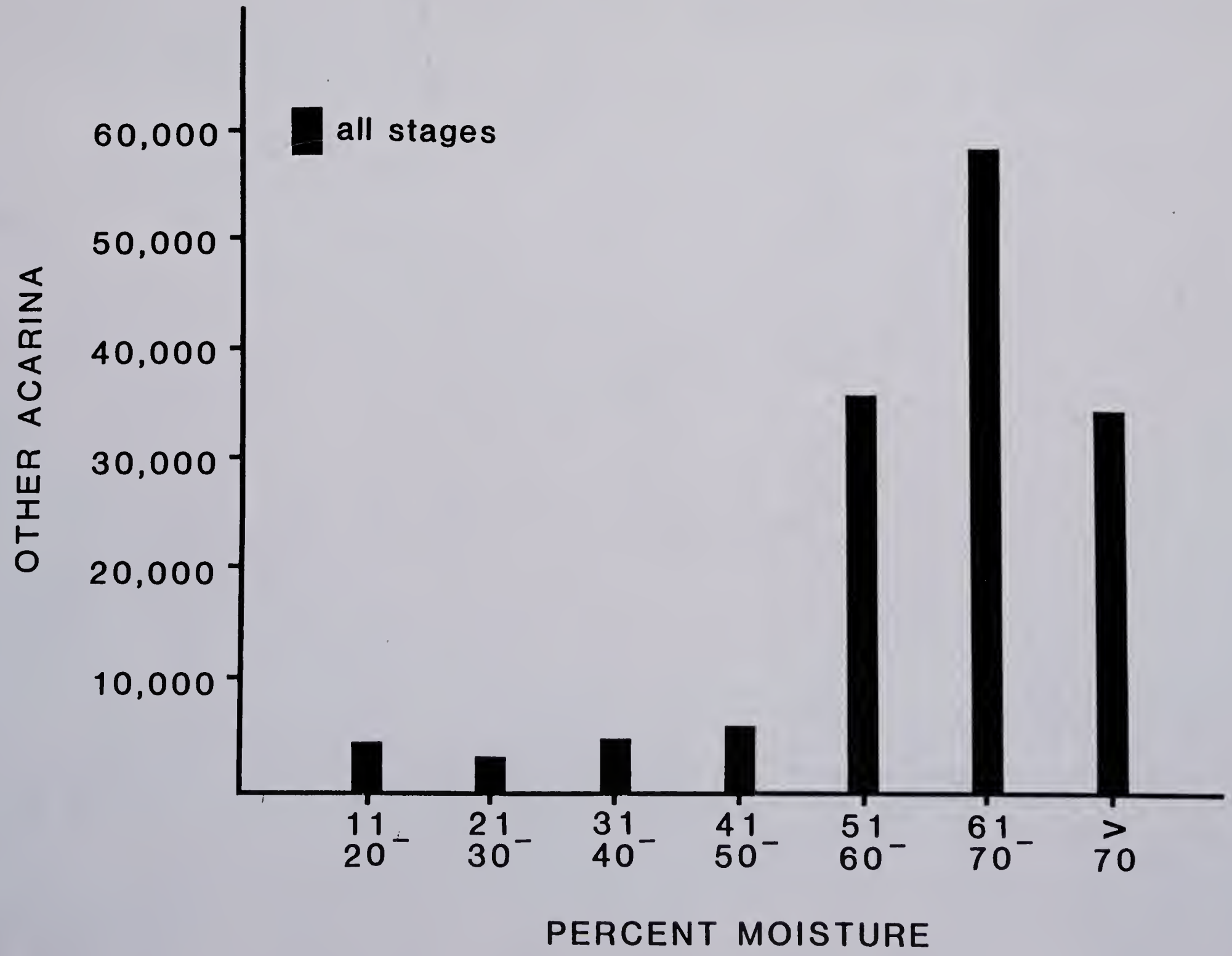

adults
800
700
600
500
400
300
200
100
M. muscadomesticae
11
20
21
30
31
40
41
50
51
60
61
70
>
70
PERCENT MOISTURE

Fig. 18. Distribution of Acarina other than M. muscadomesticae in poultry manure with respect to manure moisture content. Bars represent mean numbers of individuals of all stages per moisture content interval.


all stages
60,000
50,000
40,000
30,000
20,000
10,000
OTHER ACARINA
11 - 20
21 - 30
31 - 40
41 - 50
51 - 60
61 - 70
> 70
PERCENT MOISTURE

Neither adults of C. pumilio and C. hirtula nor all stages of non-predaceous mites were significantly correlated with moisture at the 5% level, however, the latter correlation approached significance (P=.053).

Correlation coefficients and significance levels of correlations between predators and potential prey are also presented in Table 8. All stages of C. pumilio and adult M. muscadomesticae were strongly (R>0.45) and significantly (P<.001) correlated with non-predaceous mites. C. hirtula larvae contributed significantly (P<.05), but weakly, to adult C. pumilio (R=0.24) and M. muscadomesticae (R=0.21) distribution, and were not significantly correlated with C. pumilio immatures. Results which are presented in the following section suggest that sphaerocerid larvae are actually more available to predators than is apparent from the preceding core sample data.

Dropping board samples. Numbers of arthropods present in manure which had accumulated for 24 h on dropping boards on Aug. 21, 1981, are presented in Table 9. Since these samples were incubated for an additional 24 h prior to extraction, counts of early instar dipteran larvae may be viewed as reflecting fly eggs and newly hatched larvae which are available to predators on the three upper surface positions discussed above (CREST,LT,RT). With the exception of the highly mobile adults of M. muscadomesticae, predators were present in low numbers in this isolated and temporary habitat. Counts of C. hirtula larvae were fairly high (69.5 larvae/sample). Early instar house fly

Table 8. Correlation coefficients and significance levels of correlations between arthropod predators and prey, and all arthropod numbers with manure moisture content. Data from surface dispersion samples presented in Tables 6 and 7. Arthropod counts subjected to log (x + 1.5) transformation prior to analysis.

Independent variable	Dependent variable	Correlation coefficient (R)	Significance level
C. pumilio (imm.)	manure moisture	0.635	<0.001
C. pumilio (ad.)	manure moisture	0.226	0.078
C. hirtula (imm.)	manure moisture	0.462	0.003
C. hirtula (ad.)	manure moisture	0.210	0.113
M. muscadomesticae (ad.)	manure moisture	0.694	<0.001
Other Acarina*	manure moisture	0.232	0.053
C. pumilio (imm.)	C. hirtula (imm.)	-0.081	0.252
	other Acarina*	0.673	<0.001
C. pumilio (ad.)	C. hirtula (imm.)	0.241	0.018
	other Acarina*	0.545	<0.001
M. muscadomesticae (ad.)	C. hirtula (imm.)	0.213	0.038
	other Acarina*	0.461	<0.001

ad.=adults, imm.=immatures
* Acarina other than M. muscadomesticae (all stages).

Table 9. Mean numbers of arthropods collected from 10 one-liter samples of manure which had accumulated on dropping boards for 24 h prior to sampling.

Species	$\bar{X} \pm$ S.E.
C. pumilio - 1st instars	3.0 ± 0.41
C. pumilio - 2nd instars	4.9 ± 1.65
C. pumilio - adults	7.5 ± 0.90
M. muscadomesticae - adults	39.3 ± 11.56
C. hirtula - larvae	69.5 ± 8.56
C. hirtula - adults	6.7 ± 0.85
M. domestica - 1st and 2nd instars	104.4 ± 25.84
M. domestica - mature larvae	13.9 ± 8.61

larvae, which had not been detected in any samples from the main manure rows below, were present in high numbers also (104.4 larvae/sample). Mature house fly larvae and 2nd instar C. pumilio immatures were also found in these samples, and are presumed to have been developing in clumps of manure around support beams along the boards which had not been reached during previous board cleanings.

Influence of habitat maturity on distribution. Results of repopulation of newly accumulating manure under alternate row removal conditions are presented in Table 10. One week following removal of the manure from the central row, numbers of predators present in fresh manure were significantly lower than in more mature (10-wk-old) manure in adjacent rows. C. hirtula adults were present in equal numbers in both age classes of manure, while larvae of this species were far more abundant in newly accumulating (377 larvae/sample) than in older (41.7 larvae/sample) manure. At two weeks post-removal, predators had still not significantly repopulated the fresher manure, while immatures of C. hirtula averaged over 3,000 larvae per sample in this newer manure, compared with 6.0 larvae per sample in more mature manure (11-wk old). By three weeks post-removal, M. muscadomesticae had reached numbers that were significantly higher in fresher than more mature manure, presumably due to a combination of manure composting and high prey-densities. C. pumilio adults on newer manure had increased over the previous week but were still significantly less numerous than on more mature manure (12-wk-old). C. pumilio larvae showed no increase

Table 10. Mean numbers of arthropods collected from half-liter samples of manure under conditions simulating alternate row removal for three weeks following removal of the central row.

Weeks since removal	Species or group					
	C. pumilio			*M. muscadomesticae*		
	1st instars	2nd instars	adults	adults		
1	1.0 ± 0.52	1.7 ± 0.56	7.3 ± 2.78	59.0 ± 17.61		
10	24.5 ± 7.12**	32.9 ± 7.28**	20.2 ± 8.98*	172.0 ± 38.39*		
2	0.5 ± 0.34	0.5 ± 0.22	4.0 ± 1.88	82.8 ± 15.03		
11	72.0 ± 14.92**	75.7 ± 14.45**	43.3 ± 10.43**	188.8 ± 42.62**		
3	1.2 ± 0.52	0.2 ± 0.17	21.0 ± 6.18	454.3 ± 101.44		
12	109.3 ± 17.90**	91.7 ± 8.35**	74.8 ± 19.83*	229.7 ± 35.71*		
	Other Acarina	*C. hirtula*				
	all stages	larvae	adults			
1	347.0 ± 128.6	377.0 ± 128.61	423.5 ± 152.02			
10	14,449.6 ± 7,207.8*	41.7 ± 23.40*	582.8 ± 143.12ns			
2	2,472.7 ± 1,585.7	3,229.5 ± 1,185.28	383.3 ± 106.87			
11	18,259.3 ± 14,315.9ns	6.0 ± 1.41**	273.7 ± 72.15ns			
3	11,359.5 ± 3,625.7	1,207.3 ± 371.08	191.3 ± 32.16			
12	71,292.2 ± 46,830.2ns	6.2 ± 2.77**	74.7 ± 28.83**			

For each of three weeks following removal of the central row of manure, 10 half-liter samples were collected from both newly accumulating (weeks 1, 2 and 3) and older (weeks 10, 11 and 12) manure. Data were analyzed by pairwise comparisons of numbers of individuals in fresh vs. older manure on each of these three sampling dates (one way ANOVA). Data are presented as $\bar{X}$ number/sample ± S.E. (* = $P<.05$, ** = $P<.01$, ns = not signifigant).

and were still present in negligible numbers (<2.0) in fresher manure, compared with the numbers of first (109.3/sample) and second (91.7/sample) instars in more mature manure. Non-predaceous mites were present in equivalent numbers in both 3- and 12-wk-old manure. C. hirtula adults and larvae were significantly more abundant on less mature manure and had declined since the previous week.

Results of samples taken in 1982 from artificially established islands of manure of varying maturity are presented in Table 11. C. pumilio adults were present in significantly greater numbers in 10-wk-old than 6-wk-old manure, and in significantly greater numbers in the latter than in 2-wk-old manure. Both larval instars of Carcinops were significantly more abundant in 10-wk-old manure than either of the two younger age classes. Adults of M. muscadomesticae were significantly more abundant in manure of the two older age classes than in 2-wk-old manure. Other acarines were present in greatest numbers in 6-wk-old manure. C. hirtula adults showed little preference for any manure age class, while significantly more immatures of this species were found in the two younger manure age classes than in 10-wk-old manure. House fly larvae were found in appreciable numbers only in manure which had accumulated for two weeks.

Discussion

Cross-sectional profiles, surface distribution and local environmental

Table 11. Mean numbers of arthropods collected from 10 half-liter samples of manure from each of three groups of manure "islands" of different accumumulation times.

Manure age (wk)	Species or group							
	C. pumilio			*M. muscadomesticae*	Other Acarina	*C. hirtula*		*M. domestica*
	1st instars	2nd instars	adults	adults	all stages	larvae	adults	larvae
2	0.3 ± 0.21a	0.1 ± 0.10a	6.1 ± 2.19a	580.6 ± 122.73a	46,924.7 ± 7,987.2a	537.3 ± 163.28b	35.7 ± 5.59ab	41.1 ± 19.03b
6	2.4 ± 1.23a	16.7 ± 6.91a	20.9 ± 3.25b	1,237.6 ± 223.79b	288,310.0 ± 25,269.0c	284.2 ± 76.32b	90.7 ± 41.02b	4.2 ± 3.35a
10	32.0 ± 5.56b	57.9 ± 9.89b	54.7 ± 5.85c	810.7 ± 128.26b	146,661.0 ± 20,115.1b	21.1 ± 5.69a	21.4 ± 4.63a	0.0 ± 0.00a

Means within columns which are not followed by the same letter are significantly different (Student-Newman-Keuls Range Test, P=05). Data are presented as $\bar{X}$ number/sample ± S.E.

conditions. In this study of distribution of arthropod predators and prey within mature manure, nearly all individuals of all species and life stages were found within a narrow band on or just below the manure surface. At the time when these samples were taken, the manure rows were ca. 6 ft wide by 4 ft high. From these results it can be seen that only a small proportion of the available habitat is utilized by predators and prey alike. Willis and Axtell (1968) noted a similar distribution pattern for M. muscadomesticae and Fuscuropoda vegetans (DeGeer) in poultry manure in North Carolina, although no details were given. The reasons for this apparent restriction of manure arthropods to the surface layers are not clear. More interior regions may not be optimal for dipteran and acarine prey development due to prior over-exploitation of the resource or to changes in the abundance, activity or species composition of the associated microflora. Alternatively, physicochemical properties of these interior zones may render the original substrate unsuitable for further utilization by arthropods. For example, the greater density of manure from interior regions may restrict foraging movements of both predators and their prey. Also, gas exchange may well become limiting for arthropods as they move further from the surface and encounter decreasing oxygen tensions and increased levels of ammonia and other noxious gases.

Legner (1971) suggested partial removal of upper portions of manure as a fly management strategy. The results presented here demonstrate that, at least for the type of house design typical of Massachusetts, quite the opposite should be recommended; the manure

surface with its predators should be conserved and the relatively arthropod-free interior discarded during house cleanouts. Such an approach would pose tactical difficulties, however, and may not be practical under field conditions. These results also indicate that the position at which core samples are taken have a profound influence on perceived predator and prey abundance. Thus, samples taken half-way up the pile in this type of house give a misleadingly low impression of Carcinops, Macrocheles and dipteran abundance compared with samples taken from the crest. Crest samples, on the other hand, mask non-predaceous mite availability to mobile predator life stages and do not accurately reflect C. pumilio larval population sizes. Similar distribution information is needed for deep-pit and high-rise house designs, where manure accumulation times are considerably longer and predator populations are frequently very high (Bills 1973, Dunning et al. 1978, Anon. 1975).

Peck and Anderson (1969) reported that Carcinops favored drier regions (ca. 50% water) of manure in open-sided poultry houses in California. Smith (1976), working in New Hampshire, found the greatest proportion of beetles at ca. 40% moisture content, however the total number collected was low. In addition, there is a general feeling among poultrymen and researchers that predators are more abundant in dry manure. Since beetle adults aid in the process of manure aeration by their movements through the substrate, it is likely that drier manure is often a consequence, rather than a cause, of large predator populations. In the present study, most manure samples

were fairly moist (>50% water). This was partially due to the fact that sampling was conducted in the approximate geometric center of the house, where relative humidity is maximal (Geden, pers. obs.). Despite the overall higher moisture levels found in most of these samples, predators were quite abundant. C. pumilio adults appeared to forage across a broad range of manure moisture conditions (11 - 70% water) and were not significantly correlated with either wetter or drier manure. Rather, beetles seemed to select regions of the habitat which were rich in prey.

In addition to bird manure, which appears to be the natural habitat for this species (Hicks 1959), C. pumilio has been recovered from numerous and varied habitats associated with human activity, including cut grass, stored grain, stale yeast, glue factories, bone works and carrion (Hinton 1945). I have also found adults in an experimental composting toilet at an Audobon nature center which had developed phorid and sphaerocerid fly problems (unpub. obs.). Thus, it may be concluded that Carcinops has a wide range of tolerance for moisture conditions and forages wherever prey and other food items are found in the local environment.

Immatures, on the other hand, were significantly and positively correlated with moisture content. This may reflect adult choice with respect to oviposition sites higher larval mortality under drier conditions, or movement of immatures into regions of higher moisture, where dipteran prey are more abundant. Since the optimum manure moisture content for M. domestica larvae is 60-75% (Miller et al.

1974), Carcinops shows considerable ecological overlap with this pest from the standpoint of this environmental parameter.

Dropping board samples. Temporary manure deposits on dropping boards clearly provide a relatively predator-free environment for house fly and sphaerocerid oviposition. During times of high adult fly populations or immigrations from neighboring houses, the number of dipteran eggs and newly hatched larvae in this short-lived habitat must be considerable. Cleaning of these boards onto the main rows of manure beneath the lower tiers of birds provides substantial prey input to foraging predators on the surface of these rows, and probably accounts in part for predator clumping on and near the crest although other factors may play a role as well (Willis and Axtell 1968). Many of these prey items are consumed shortly after their deposition on the main rows' surface, since sphaerocerid larvae are found in much lower numbers in crest samples taken in the afternoon than are present in dropping board manure at the time of board cleaning (compare Tables 6 and 9). House fly larvae were not detected in any core samples taken from the main manure rows, but were present in high numbers in dropping board manure which was held for 24 hr, suggesting predator preference for house fly eggs over those of sphaerocerids. On the other hand, house fly eggs may simply be more apparent to predators. House fly eggs are deposited in batches by female flies, which frequently oviposit in groups. In contrast, sphaerocerid eggs are much smaller than those of house fly and are deposited singly in

crevices under the manure surface (Chapter V).

Influence of habitat maturity on distribution. Several workers have suggested alternate row manure removal as a strategy in filth fly IPM programs (Legner and Brydon 1966, Legner and Olton 1968, Anderson at al. 1968, Dunning et al. 1978) since predator populations are generally higher and more stable after longer accumulation times (Legner et al. 1973, 1975, Peck and Anderson 1969). Peck and Anderson (1970) examined the impact of several manure removal schedules on predator and prey repopulation. Since histerid populations were very low under all schedules which they examined, and since C. pumilio and G. nanus were not counted seperately in that study, I decided to look at manure age preferences in houses which contained large populations of both Carcinops and M. muscadomesticae. Under simulated alternate row removal conditions, Carcinops adults were present at much lower levels in newly accumulating manure after three weeks than in older (12 week) manure from the adjacent rows, even though dipteran prey were 200 times more abundant in the former (Table 10). In a complimentary study, employing contiguous manure islands of varying accumulation times, beetle adults were again more abundant in older than fresher manure, even though the latter contained far more fly larvae (Table 11). Since the distance between the islands was very small, this distribution pattern may be viewed as a reflection of active choice by the highly mobile adults of Carcinops and Macrocheles.

From this study, as well as others (Chapter II, Peck 1968, Peck and Anderson 1970), it appears that fresh manure is non-attractive to adults of both predator species. Data which are presented in Chapter II indicate that, at least for Carcinops, newly accumulating manure has a repellent effect as well. This repellency occurs at a time when prey densities are at their peak (Legner et al. 1973) and when manure is best able to support fly larval development (Miller et al. 1974). Further work is needed to determine the specific olfactory, gustatory or tactile factors involved in this effect, and to identify the biotic and physicochemical changes which occur over the following weeks which render older manure more attractive to predators. From an applied standpoint, these results indicate that while alternate row removal may assist in long-term predator repopulation of newly accumulating droppings, there remains a critical period of several weeks following removal when fresh manure is highly susceptible to fly invasion and establishment. A management program incorporating predator conservation and selective use of pesticides which are compatable with natural enemies during this "window of vulnerability" has the greatest potential for success. Further, it appears that sphaerocerids are important alternative prey items in the diet of Carcinops (Chapters II, IV and V) and other histerid predators (Bornemissza 1968). Since these flies do not appear to pose a nuisance problem to communities adjacent to farms, producers should be discouraged from efforts to control them.

C H A P T E R IV

PREY-MEDIATED DISPERSAL BEHAVIOR OF THE PREDACEOUS HISTERID, CARCINOPS PUMILIO (ERICHSON)

Introduction

Carcinops pumilio (Erichson) is an histerid predator which is most commonly found in commercial egg production facilities where large, stable deposits of poultry manure accumulate (Legner and Olton 1970). Adult and immature beetles inhabit the surface layers of the manure and forage for dipteran and acarine prey (Chapter II), making this species an object of interest from the standpoint of filth fly pest management. Now cosmopolitan, C. pumilio is believed to have originated in Africa (Fauvel 1889) and, prior to man's domestication of fowl, lived in the nests of wild avian species (Hicks 1959).

Despite the widespread distribution of this beetle in nature and the very high population densities achieved in poultry houses, little is known of the means of transport from one farm to another, a distance which frequently spans many kilometers. Under normal circumstances, Carcinops is repelled by strong light and is rarely observed to fly (Geden, pers. obs.). During a larger study of the

poultry manure arthropod community conducted in central Massachusetts (Chapters II and III), I occasionally observed large numbers of adult beetles climbing the inside walls of poultry houses, flying about the overhead lights and initiating flight from windows.

During this 3-year observation period, dispersal was not found to be correlated with calender date, but occurred at varying levels from May to September. Times of peak dispersal coincided with long manure accumulation times (3-4 mo.), when adult C. pumilio populations are most abundant and immatures of this species are present in relatively low numbers (Chapters II and III). Since flight is an uncommon event in this species, these observations raised the possibility that C. pumilio may undergo a migratory, or adaptive dispersal phase (Johnson 1969).

The objectives of the present study were therefore to investigate causal aspects of dispersal in C. pumilio with respect to the following: 1. sex ratios of dispersers compared with non-dispersers; 2. physiological age (mating condition, parity and ovarian state) of dispersers and non-dispersers; 3. morphometric analysis of dispersers and non-dispersers; and, 4. potential for reversal and induction of dispersal under experimental conditions.

Materials and Methods

Study site and beetle collection methods. All beetles were collected from a commercial egg production facility with a long history of

natural house fly suppression (Hill's farm, Hubbardston, MA) in 1980-1982. For comparisons of "dispersing" and "foraging" C. pumilio, "dispersers" are defined here as those beetles which were actively climbing the walls of the poultry houses and orienting towards the narrow windows near the ceilings of the houses. Such beetles were most commonly found near large exhaust fans in the walls, where the greatest amount of incident daylight reaches the interior of the houses. Dispersers were collected by gently scraping beetles off the walls into plastic bags with a putty knife. "Foraging" beetles are defined as those which were found moving about immediately beneath the manure surface. These were collected by taking large samples of sub-surface manure and mechanically removing beetles with a moistened camel's hair paint brush.

Phototactic response of field-collected dispersing and foraging C. pumilio. To make initial determinations of whether there was in fact a behavioral difference between dispersing and foraging C. pumilio as defined above, beetles were first tested for phototactic response. This test was suggested by field observations that wall-climbing (dispersing) beetles would reverse their upward direction of travel when illuminated from below with a bright flashlight. Beetles from the manure sub-surface (foragers), on the other hand, were observed to burrow down into manure when exposed and illuminated from above with the same light.

To examine this response in greater detail, dispersers and

foragers were collected on July 1, 1980, and tested in a simple light-dark choice chamber. This chamber consisted of a 30 cm length of clear plastic tubing (diam.=20mm) with clear plastic 1 oz collecting cups affixed to either end. Half the length of the tubing and one of the collecting cups were wrapped in black electrical tape, the other half and its cup were left clear. The light end of the chamber was oriented towards a south-facing window in a room with no artificial lighting. All tests were run between 2:00 and 4:00 PM, within 4 hours of beetle collections. A replicate consisted of 50 beetles, introduced one at a time, into the middle of the chamber through a hole at its midpoint. Five minutes following the introduction of the 50th beetle, the number found in the light end of the chamber was counted and scored as photopositive.

Flight initiation by field-collected dispersers and foragers. To determine whether positive phototaxis was a prelude to flight, flight initiation was investigated in the lab, using field-collected dispersers and foragers. This behavior was assayed by the use of take-off chambers. Each chamber consisted of a 1 oz plastic cup filled two-thirds full with fine river sand, with a dental wick (Absorbal*) bridge arching across the surface of the sand. This small cup was then placed inside a 16 oz paper container with a clear plastic lid. The dental wick bridge was found to be essential for monitoring flight initiation, since beetles were reluctant to take-off from the flat surface which the sand provided, but flew readily from

the Absorbal wick when sufficiently motivated to fly.

Beetles were introduced, in replicates of 20 beetles per chamber, onto the surface of the sand in the inner containers. All containers were then placed near a south-facing window in a room with no artificial lighting for a 1 hr observation period commencing at 2:00 PM on May 28, 1981, several hours after beetles were collected. Beetles were unable to climb the surface of the inner container; therefore, any which were found in the outer container after 1 hr were scored as positive for flight initiation.

Morphometric analysis of dispersers and foragers. To test the possibility that dispersal was a delayed response to intense larval competition, resulting in the production of smaller adults, morphometric measurements of field-collected dispersers and foragers were made. Since there is a slight size difference in certain characters between sexes (Chapter II), only females were measured. Measurements were made of 25 dispersing and foraging C. pumilio which were collected on May 19, 1981, using an ocular micrometer under a dissecting microscope. The following characters were measured for each individual: head width across eyes (HW), maximum pronotal width (PWM), pronotal width across points at head (PWH), maximum pronotal length (PLM), right elytral width at anterior end (EWA), maximum right elytral length (ELM), diagonal length of right elytron from inner left (anterior) to outer right (posterior) points (ELD), and the lengths of the fore, middle and hind femora (FF,MF,HF) and tibiae (FT,MT,HT).

Sex ratios, mating condition, parity and ovarian states of dispersers and foragers. Sex ratios of dispersers and foragers were determined from beetles collected on July 1 and Aug. 14, 1980, and May 28, 1981. Beetles were collected as before, preserved in 70% ethanol, and dissected for sex determinations, as there are no reliable external diagnostic characters for separating the sexes of this species (Chapter II). One hundred dispersing and foraging C. pumilio were sexed from each of these 3 sampling dates, for a total of 600 beetles.

Additional beetles were collected on June 21, 1982, for determinations of mating condition, parity and ovarian state. One hundred live dispersing and foraging C. pumilio females were dissected in physiological saline for determination of parity as evidenced by the presence of follicular relics (yellow bodies) at the bases of the lateral oviducts (Chapter V). In addition, the spermathecae of 25 beetles from each group were examined under a compound microscope for the presence of sperm. Finally, the ovarian state of 25 female dispersers and foragers was determined. These beetles were preserved in 70% ethanol prior to inspection, since alcohol preservation allows discrimination of chorionated from non-chorionated eggs via differential tissue shrinkage. C. pumilio has four ovarioles per ovary and develops and deposits eggs singly. At any one time, one rarely finds more than one fully developed, chorionated egg per female, and seldom more than 2 oocytes with substantial yolk deposition (Chapter V). The condition of the four most-developed

oocytes (2/ovariole) was therefore determined visually and ascribed an index value ranging from 0 to 5 according to the following criteria: 0= undeveloped oocyte, no visible yolk deposition; 1= early developed oocyte, some yolk, length up to ca. 0.35mm; 2= oocyte length ca. 0.35-0.50mm; 3= oocyte length ca. 0.50-0.65mm; 4= nearly completely developed egg, chorion lacking, length ca. 0.65-0.80mm; 5= completely developed egg, chorion present, length generally greater than 0.80mm.

Effects of feeding treatments on dispersing C. pumilio. Results of the above work indicated that dispersal was not related to sex, physiological age or long-term nutritional history (ovarian state), raising the possibility that this behavior is appetetive and driven by hunger. To test this, dispersers were collected from the field, subjected to pre-treatment phototactic and flight assays as described above, then held for 24 h on 4 different feeding treatments. These were as follows: 1. water only (saturated dental wick); 2. water plus granulated sucrose; 3. "prey-free" manure, which had been collected in the field, baked in a drying oven, and remoistened to ca. 60% water; and, 4. water plus house fly eggs and newly hatched larvae. After 24 hr on these feeding treatments, beetles were assayed again for phototaxis and flight initiation. Phototaxis tests were run on July 5 and 6, 1980, with 50 beetles/replicate and five replicates/treatment. Flight assays were conducted on Aug. 11 and 12, 1982, with 25 beetles/replicate and five replicates/treatment.

Induction of dispersal in prey-deprived beetles. Since administration of prey was found to reverse dispersal in field-collected beetles, prey-deprivation was strongly suggested as the releasing cue for this behavior. To examine this and to determine the amount of time required for the expression of dispersal, colony beetles were subjected to prey-deprived conditions and assayed for flight initiation daily. Beetles used in this study were from the F4 generation reared in the lab and were approximately four weeks old at the start of the experiment. For the first four weeks of life, beetles were maintained in CSMA house fly medium, with high densities of larvae of the small dung fly, Coproica hirtula (Rondani), in a rearing room maintained at 30-31° C, 24 hr light and 60-70% RH. C. hirtula is a natural prey item in the diet of C. pumilio in the field (Chapter II and III), and is more easily manipulated for beetle colony maintenance than is the house fly (Chapter V). After four weeks on this prey-rich diet, beetles were transferred to containers with moistened dental wick only and assayed daily for flight initiation. Assays were conducted as described above at 20 beetles/relicate, 15 replicates/day. Between assays, beetles were returned to and held in the above-mentioned rearing room.

Results

Phototactic response and flight initiation of dispersing and foraging C. pumilio. Results of phototactic and flight initiation assays of

field-collected dispersers and foragers are presented in Table 12. Data have been converted to percentages for ease of comparisons between tests, in which the number of beetles per replicate varied. Of the dispersers, 94.0% oriented towards the light end of the light-dark choice chamber, and 90.4% initiated flight during a 1 hr test period. In contrast, 28.8% of the foraging C. pumilio were positively phototactic and only 2.2% initiated flight. Observation of the flight chambers confirmed that beetles found in the outer containers at the end of the observation period had indeed initiated flight. Beetles displayed a characterictic behavior of crossing and re-crossing the dental wick bridge prior to take-off, apparently in search of the highest available point in the local environment. After several such crossings, individual beetles stopped at the peak of the bridge, extended the forelegs so as to raise the anterior part of the body, tucked the head under the pronotum, and opened the elytra. Between <1 to 3 sec. later, either the hind wings opened and the beetles would jump to initiate flight, or the elytra closed again. Those beetles which did not fly after assuming the pre-flight posture generally walked a short distance and repeated the behavioral sequence. It was not uncommon for an individual to "prepare" for flight in this manner five or six times before finally taking off. Those beetles which did fly struck the walls and fell to the bottom of the outer container. Subsequently, they generally walked up the walls of this container and circled about the upper rim, which was covered with a clear plastic lid. Flight was rarely attempted from the smooth

Table 12. Comparisons of phototactic response and flight initiation of dispersing and foraging C. pumilio collected from poultry houses in 1980 and 1982, respectively.

	Dispersers	Foragers
% positively phototactic (X ± S.D.)	94.0 ± 0.98	28.8 ± 4.14 **
% initiating flight (X ± S.D.)	90.4 ± 3.06	2.2 ± 0.82 **

** P<.01, Oneway ANOVA

surface of the container bottom, although such documented flyers would readily reinitiate flight when placed in the inner container a second time.

Foraging beetles, on the other hand, generally did not climb the arched wick, but burrowed into the sand at its base. Most foragers which did climb the wick did not display the crossing and recrossing behavior of the dispersers, except for the small percentage (2.2%) which flew.

During the handling of these field-collected beetles, another behavioral difference was noted that was of some interest. Foragers, when touched by the paint brush, frequently exhibited thanatosis (Hinton 1945), retracting the head and legs for as long as one minute. Dispersers, on the other hand, did not show this behavior, but continued to move actively when contacted.

Sex ratios, mating condition, parity and ovarian state of dispersers and foragers. Results of sex ratio determinations of 3 dispersing and foraging C. pumilio populations in 1980-1981 are presented in Table 13. No significant differences were found on any of the sampling dates, with a total, male- biased, sex ratio of 348♂:252♀.

Of 25 dispersing and foraging females collected June 21, 1982, all were found to have mated (Table 13). Similarly, no significant differences were found with respect to parity, with 94% and 98% of 100 dispersers and foragers having yellow bodies, respectively. Also, no significant differences were found between 25 dispersers and foragers

Table 13. Comparisons of sex ratios, mating condition, parity and ovarian state of dispersing and foraging C. pumilio collected from poultry houses in 1980-1982.

	Dispersers	Foragers	
Sex ratio (♂:♀)	59:41	57:43	
% mated	100	100	
% parous	94	98	
Oocyte 1	3.8 ± 1.51[1]	4.1 ± 1.63	ns[2]
Oocyte 2	2.4 ± 1.54	0.3 ± 1.37	ns
Oocyte 3	1.5 ± 1.21	1.7 ± 1.37	ns
Oocyte 4	0.6 ± 0.89	0.9 ± 0.77	ns

1. Mean oocyte index ± S.D. See text for index criteria.
2. Not significant at P= .05.

with respect to the condition of the four most-developed oocytes (Table 13).

Morphometric analysis of dispersers and foragers. Results of measurements of 13 characters from 25 dispersing and foraging females are presented in Table 14. No significant differences were found between the two groups for any of the characters which were examined.

Effects of feeding treatments on dispersing C. pumilio. Results of the tests for the effect of diet on the behavior of field-collected dispersers are presented in Table 15. Pre-treatment assays on the day of collection confirmed that beetles were in dispersal mode, with 89.6% showing a positive phototactic response and 91.6% initiating flight. Maintaining these beetles for 24 hr on water only had no significant effect on either dispersal-related behavior, with 87.3% still attracted to light and 93.6% initiating flight. Administration of sucrose as well as water had a slight, but not statistically significant, dampening effect on both behaviors. Those beetles which were allowed to feed on prey showed a profound reversal in dispersal behavior, with only 3.7% attracted to light and 4.8% initiating flight. "Prey-free" manure appeared to have a dampening effect as well, however, this effect was not significant at the 5% level.

Induction of dispersal in prey-deprived C. pumilio. The effect of prey-deprivation on colony beetles with a previous prey-rich feeding

Table 14. Comparisons of morphometric characters of dispersing and foraging C. pumilio females collected from poultry houses on May 19, 1981. All values are expressed as mean distance in mm ± S.D.

	Dispersers	Foragers
HW	0.59 ± 0.023	0.60 ± 0.029 ns
PWM	0.69 ± 0.026	0.68 ± 0.031 ns
PWH	1.36 ± 0.071	1.33 ± 0.073 ns
PLM	0.82 ± 0.039	0.79 ± 0.057 ns
EWA	0.80 ± 0.042	0.78 ± 0.044 ns
ELM	1.36 ± 0.094	1.34 ± 0.107 ns
ELD	1.67 ± 0.070	1.72 ± 0.073 ns
FF	0.60 ± 0.022	0.59 ± 0.029 ns
FT	0.55 ± 0.028	0.54 ± 0.031 ns
MF	0.56 ± 0.026	0.55 ± 0.025 ns
MT	0.52 ± 0.029	0.51 ± 0.029 ns
HF	0.64 ± 0.030	0.63 ± 0.027 ns
HT	0.62 ± 0.026	0.61 ± 0.028 ns

ns = not significant (Oneway ANOVA, $P \geq .05$). (HW = head width at eyes, PWM = pronotal width at widest point, PWH = pronotal width at head, PLM = pronotal length at longest point, EWA = elytral width at widest point, ELM = elytral length at longest point, ELD = elytral length along diagonal from inner anterior to outer exterior points, FF, MF and HF = lengths of the fore-, middle- and hind femora, FT, MT and HT = lengths of the fore-, middle- and hind tibiae.)

Table 15. Phototactic response and flight initiation of field-collected dispersing C. pumilio before and after being maintained for 24 h on four different feeding treatments.

	% positively phototactic (X ± S.D.)	% initiating flight (X ± S.D.)
Pre-treatment	89.6 ± 4.88 a	91.6 ± 9.17 a
After 24 h on:		
water only	87.3 ± 4.16 a	93.6 ± 4.56 a
water and sucrose	82.0 ± 10.58 a	77.2 ± 9.55 a
"prey-free" manure	68.6 ± 6.11 ab	54.4 ± 22.40 ab
water and prey	3.7 ± 2.52 b	4.8 ± 1.94 b

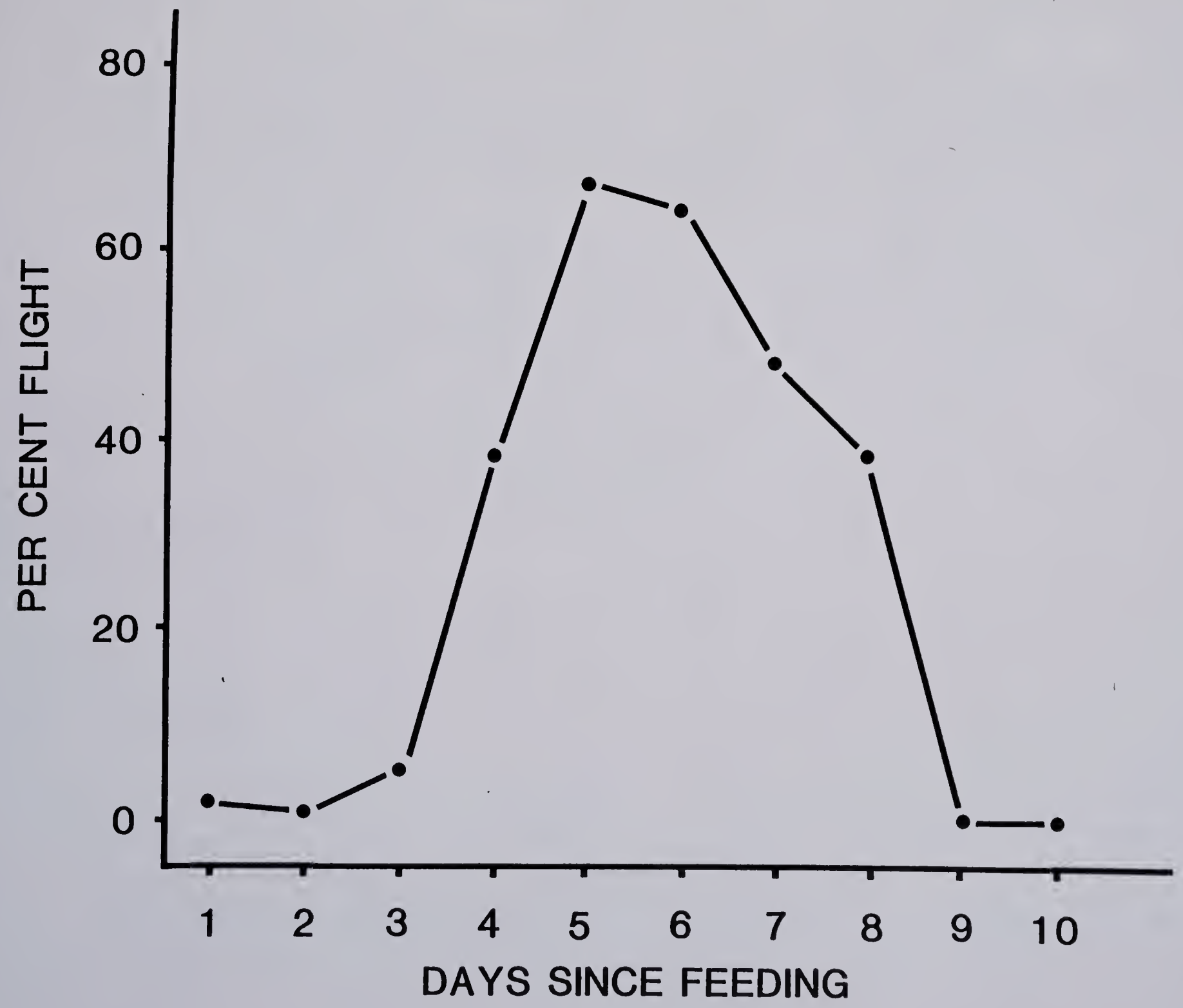
Means within columns which are not followed by the same letter are significantly different ($P<.05$, Student-Newman-Keuls Range Test).

history is illustrated in Fig. 19. On the first day of starvation, virtually none of the beetles initiated flight (1.7%). Flight initiation remained infrequent on the following two days, with 0.8% and 5.0% flying on days 2 and 3, respectively. On day 4, a sudden increase in flight propensity was observed (38.6%), which increased further on day 5 (67.2%) and remained high on day 6 (64.7%). Flight initiation then dropped on day 7 (47.0%) and day 8 (38.0%). On days 9 and 10, no flight was observed at all.

Discussion

Dispersal versus migration- general considerations. Various authors have attempted to clarify the distinction between dispersal, which is generally characterized by short flights between patches within habitats, and migration, which consists of longer flights between habitats (Johnson 1969, Kennedy 1961, Southwood 1962, Stinner et al. 1983). Johnson (1969) further suggested that the term "migration" be restricted to those flights which are non-appetitive (Thorpe 1951) and ontogenic. He also stated, however, that "no category is ever completely satisfactory", and pointed to examples of species which both feed and mate during true migrations (eg. locusts). Since Carcinops does not engage in trivial flight, but rather walks between patches within the habitat (poultry houses), flight in this species is reserved for movements between habitats, which may be separated by very long distances. The fact that flight may be shut down by

Fig. 19. Flight initiation response of C. pumilio which were placed on water-only regimes after being maintained for four weeks on a diet rich in dipteran prey.


80
60
40
20
0
PER CENT FLIGHT
1
2
3
4
5
6
7
8
9
10
DAYS SINCE FEEDING

administration of prey and induced by starvation indicates that such movements are appetitive. Thus, flight in C. pumilio appears to share certain characteristics of both dispersal and migration, suggesting that this species is a facultative migrant in the sense of Dingle and Arora (1973).

Adaptive dispersal and migration are mechanisms of escape from the site of development either as an obligatory syndrome occurring shortly after adult eclosion or in response to environmental cues indicative of declining habitat quality (Davis 1980, Johnson 1966, 1969, Messina 1982, Meyer 1982). Since emigration from the native habitat entails some risk of mortality, these behaviors are more common in species which utilize temporary, or patchily distributed, resources (Dingle 1978, Roff 1975, 1977, Southwood 1962, Vepsalainen 1978). In such habitats, a behavioral polymorphism with respect to emigration often evolves, reflecting a balance between the opposing selection pressures against the risks of dispersal with those of remaining in a deteriorating environment (Derr et al. 1981, Dingle 1965, Parker and Stuart 1976, Taylor and Taylor 1977). In the present study, the percentage of dispersers under experimental conditions never exceded 68%, even though all beetles were raised under similar conditions and were the same physiological age. These results suggest that certain individuals within the population are either not preadapted for flight (Young 1965) or are unresponsive to cues which trigger it in others, as has been found in the the milkweed bug (Dingle 1965, Rainkin 1978) and the alfafa weevil (Meyer 1982).

Sex ratios of dispersers and foragers. Males and female of C. pumilio were found to be present in equal proportions in dispersing and foraging populations, with a slight male bias in both, although the sex ratio at emergence is approximately 1:1 (Chapter V). Relatively little is known of the sexual composition of migrants of most species, although females have been shown to predominate in some (Johnson 1969, Messina 1982). In others, females have been noted to fly longer or travel farther than males (Cook 1967, Dingle 1966), however, males may have greater migratory potential when the entire lifespan of individuals is taken into account (Dingle and Arora 1973, Rose 1972, Solbreck and Pehrson 1979).

Physiological age of dispersers and foragers. No significant differences were found between dispersing and foraging C. pumilio with respect to mating condition, parity or ovarian development. Females mate repeatedly throughout life and are first inseminated within several hours of emergence, generally before the cuticle has fully hardened (Chapter V). It was therefore not surprising that 100% of both foraging and dispersing beetles collected from the field were found to have mated. Given the risks involved in emigration and the potential for individuals to be the first or only arrivals at a new breeding site, selection would be against virgin dispersers (Johnson 1969), although unmated insects have been reported to disperse more readily than mated individuals (Dingle 1966, Solbreck and Pehrson

1979).

The majority of migrating species which have been studied do so as post-teneral adults prior to the development or deposition of the first egg batch (Dingle 1965, 1966, Johnson 1969, Messina 1982, Meyer 1982). In the present study, no evidence for this "oogenesis flight syndrome" was found in C. pumilio, with most dispersing beetles having at least one nearly fully developed oocyte and having undergone at least one oviposition. In this species, the use of follicular relics as an indicator of age may, however, mask real age differences between the two groups. Mated, parous females may be as young as 8 or as old as 380 days post-eclosion (Chapter V). It is therefore possible that dispersal is a characteristic of younger beetles, with older beetles either histolizing the flight muscles or being unresponsive to stimuli inducing younger beetles to fly (Dingle 1972, Dingle and Arora 1973, Johnson 1969, Kennedy 1961, Solbreck and Pehrson 1979). Further experimental work with individuals of known age is needed to determine whether such is the case for this species.

Morphometric comparisons of dispersers and foragers. In addition to the behavioral polymorphism displayed by some migrant species, many others are composed of morphologically distinct forms, with some morphs adapted for flight relative to the population at large (Johnson 1969). Production of migratory morphs may be either genetically or environmentally determined (Harrison 1980). Wing polymorphism is perhaps the best documented example of this

phenomenon, and has been demonstrated to occur in many species, including aphids (Lamb and MacKay 1979), planthoppers (Denno and Grissell 1979), locusts (Kennedy 1956), carabids (Lindroth 1949), crickets (McFarlane 1964) and water striders (Andersen 1973, Vepsalainen 1978). In other species, overall body size has been found to be positively correlated with either proclivity for flight (Roff 1977) or its duration (Dingle et al. 1980). Rose (1972), on the other hand, noted that smaller bodied Cicadulina spp. were stronger flyers than larger-bodied individuals. In the present study, no evidence was found for wing or body size polymorphism, although smaller beetles occur in greater numbers following peaks of larval numbers, apparently reflecting competition for prey in the immature stages (Chapter II). Since times of such adult population peaks are also the times when greatest dispersal is evident, there may be some correlation between flight potential and body size which is not apparent in dispersing and foraging beetles sampled from the same population at the same time.

Prey-mediated induction and reversal of dispersal behavior. Administration of prey in the form of house fly eggs and larvae was found to reverse both parameters of dispersal measured in this study, phototaxis and flight initiation. Water-only and water-plus-sucrose had no significant effect on these behaviors, indicating that if dispersal in this species is appetitive, it is not driven and maintained by water or carbohydrate stress. "Prey-free" manure had a

dampening effect on dispersal, which may at first seem paradoxical. This manure, however, may have contained dead potential prey items. Since Carcinops is a scavenger as well as an opportunistic predator, it is likely that some beetles consumed sufficient dead arthropods in the manure to switch-off the dispersal behaviors. Dissections of prey-administered and water/sucrose-administered beetles also revealed differences in the condition of the digestive tract. Prey-fed beetles had greatly distended midguts with a yellow-brownish appearance. Those of water/sucrose-fed beetles, on the other hand, were not distended, clear and possessed many air bubbles, which presumably could aid in bouyancy during flight. Casual examination of field-collected dispersers and foragers confirmed this observation, with dispersers having bubbles in the gut and foragers having at least partially filled, bubble-free alimentary tracts.

The observation that flight could be induced by starvation in Carcinops has several parallels, although most examples of this phenomenon are from phytophagous species. Meyer (1982) has shown that the alfalfa weevil exhibits two flight periods, one of which is a post-teneral, pre-reproductive, pre-diapause syndrome. A second, post-diapause period of flight may be induced by witholding fresh alfalfa from the beetles (Meyer 1982). Dingle and Arora (1973) found that female Dysdercus spp. histolyze the flight muscles and develop eggs when fed continuously after eclosion, but undergo flight if starved for several days following emergence. The bugs continue to fly and do not histolyze the flight muscles until they are presented

with food. Males have the potential for flight throughout life. These authors concluded that Dysdercus spp. are "facultative migrants using starvation as a releasing cue". Solbreck and Pehrson (1979) found similar results with another seed bug, Neacoryphus bicrucis (Say), and noted a critical balance between food density, egg production, diapause-inducing conditions, and migration.

Rankin (1978) has investigated hormonal regulation of flight in Oncopeltus fasciatus (Say) and reviewed the literature available on other species. In Oncopeltus, starvation or feeding on suboptimal food items causes recently emerged females to delay reproduction and undergo long flights. Juvenile hormone (JH) was found to play a dual role in modulating reproductive and migratory efforts. High JH titres are present during periods of intense feeding and are associated with ovarian development, which in turn inhibits flight. Bugs placed on starvation regimes maintain high levels of JH in the absence of further oogenesis for several days, and respond to this high hormone titre with increased flight activity. As starvation continues, CA activity declines until the JH levels in the hemolymph fall below the threshold required for flight, with flight showing a marked decrease on day 9 post-starvation, after having peaked on day 2 (Rankin 1978). Stengel (1974) has found that JH plays a role in the direction, as well as the expression, of flight in the migratory cockchafer Melolontha melolontha L. In the present study, Carcinops also showed a delayed response to starvation, with virtually no flight being noted until day 4 of deprivation. JH may play a role in the flight of this

species as well, although perhaps in a different manner. Since ovarian state appears to have no effect on flight, it is possible that high JH titres associated with feeding and subsequent ovarian development inhibit flight, with this behavior being released in response to lower titres. Since males appear to disperse as readily as females, other hemolymph-borne factors associated with feeding may be involved as well. The observed decline in flight after day 6 is more difficult to interpret. Beetles which have had a prey-rich feeding history can survive on water alone for 30 days before significant mortality is observed (Chapter V). Thus, beetles on days 7-10, when flight declined, clearly had not exhausted their nutrient reserves, but appeared to have responded to internal cues which shut off flight. A similar rise and fall in flight behavior in response to starvation has been observed in the stilt bug Jalysus spinosus (Say) (Elsey 1974), and represents one of the only documented cases of this phenomenon in a generally flightless predator. J. spinosus, when deprived of its usual prey (tobacco hornworm eggs), did not show significant flight activity until day 4 post-deprivation. Flight continued to increase and peaked on day 7, followed by a gradual decline to the level of fed controls on day 12. In contrast with Carcinops, however, the decline in Jalysus flight appeared to be associated with decreasing fuel reserves, since mortality was much higher towards the end of the starvation period than at the beginning, and higher than the fed controls at the same time (Elsey 1974).

Conclusions

Prior to the domestication of fowl and the ensuing artificial accumulation of large and stable deposits of poultry manure, Carcinops pumilio was presumably associated with the nests of wild birds, where it fed on dipterans and other prey. Given the temporary nature of these early, natural habitats, selection for migratory potential appears to have been strong. A delayed, rather than immediate, response to declining habitat quality (insufficient prey) would serve to prevent beetles from making highly risky emigrations on the basis of a short-lived dearth of prey. Since Carcinops populations under natural conditions can be assumed to be small, selection has not favored a population-wide migration strategy which ensures dispersal from the breeding site, as is seen in many herbivorous migrants. Rather, prey availability is a more conservative cue which permits each individual to assess resource abundance and behave accordingly. Further, dispersal by adults in prey-scarce situations would enhance the fitness of their own progeny, with whom they would otherwise compete for rare prey items.

C H A P T E R V

SUCCESSFUL COLONIZATION OF THE PREDACEOUS HISTERID, CARCINOPS PUMILIO, WITH OBSERVATIONS OF DEVELOPMENT TIME, OVARIAN MATURATION, MATING READINESS, LONGEVITY, MORTALITY AND FECUNDITY

Introduction

Histerid predators of filth fly immatures in accumulating animal manure are frequently the most numerous coleopterans in this habitat (Bai and Sankaran 1977, Legner and Olton 1970, Peck 1968, Peck and Anderson 1969, Pfeiffer and Axtell 1980), and are thought to be among the most important natural enemies of synanthropic and zoophilous flies (Peck 1969). At least some of these predators appear to have shifted from natural associations with solitary mammals and birds into modern animal agriculture facilities, where large, stable deposits of manure are typically present (Hicks 1959, Kryzaovskij 1977).

Aside from invaluable observations by early workers in the field (Hammer 1941, Laurence 1943, Mohr 1943), relatively little is known of the biology of predatory histerids. Bornemissza (1968) conducted an exhaustive study of the life history and ecology of Pachylister chinensis Quenstedt, a predator which was introduced from Java into various areas of the South Pacific to regulate populations of flies breeding in cattle droppings. Several workers have investigated the

biology, seasonal abundance and predatory potential of histerids associated with cattle droppings in Texas (Summerlin 1980, Summerlin et al. 1981, 1982a, 1982b). The predatory potential of Carcinops pumilio, which is most common in poultry houses, was studied in the lab by Peck (1968, 1969), and some life history information on this species was provided by Smith (1975).

C. pumilio is viewed as a predator of major significance in the suppression of filth flies in poultry houses in the U.S. (Axtell 1981, Legner 1971, Peck 1969, Pfeiffer 1978), England (Anon. 1975, Bills 1974) and Denmark (Anon. 1982). Further efforts to study and manipulate this beetle have, until now, been hampered by the lack of a rearing system capable of producing large, self-sustaining colonies of Carcinops. Observations which were made by the author during a larger study of the population dynamics (Chapter II) and dispersion patterns (Chapter III) of this species in the field demonstrated that sphaerocerids, especially Coproica hirtula (Rondani), frequently represent the sole dipteran components of the diet of C. pumilio in Massachusetts poultry houses. The small size of these flies, plus their apparently high reproductive potential (Chapter II), suggested that they could be exploited as a prey base for Carcinops colonization.

The objectives of the present study were therefore as follows: 1. to colonize and mass-rear Coproica hirtula on a medium other than poultry manure; 2. using the latter as prey, to develop a rearing method for C. pumilio; and, 3. to gather essential life history

information on Carcinops, including development time, ovarian maturation, mating competence, longevity, fecundity, and stage-specific mortality.

Materials and Methods

Initial colonization of Coproica hirtula. Approximately 500 adult flies were collected on Sept. 24, 1981, in a poultry house at a farm in central Massachusetts (see Chapter II for farm description). On the date of collection, the manure in the house had accumulated for three weeks and was supporting outbreak level populations of sphaerocerids. Flies were collected with a canvas sweep net from the manure surface and from the inside walls of the house. After returning to the lab, roughly half of the flies were placed in small cages and provided with distilled water and granulated sucrose; none of these flies survived for more than 24 h. The other half were also placed in small cages and were provided with 250 cc of poultry manure which had been thoroughly dried in a microwave oven and remoistened to ca. 70% moisture (by mass) several days before fly introduction. Cages were placed in a rearing room maintained at 30-31°C, 60-70% RH and 24-h photoperiod.

Within 24 h of fly introduction, eggs were visible and had been deposited singly into crevices and folds under the surface of the manure. After this initial 24 h period, manure was removed and replaced with similarly prepared, "reconstituted" manure. Manure

which was removed was added to an equal volume (total vol. = 500 cc) of freshly prepared manure, and checked daily for fly development. The moisture level of the breeding material was maintained at 60-70% by the daily addition of small volumes of water.

Larvae were first noted on dav 2 post-adult-introduction, and pupae were first seen on day 5. Most larvae pupated by day 6. Newly emerged adults were first observed on day 9 and were present in greatest numbers on day 10. Males emerged earlier than females and were capable of mating within three hours of emergence. Females were receptive to mating immediately following eclosion; all copulating pairs which were observed consisted of older, fully-darkened males and newly emerged, incompletely-tanned females. After mating and "resting" for several hours after emergence, flies became positively phototactic, and climbed the walls of the cage to the underside of the cage top. (If geotaxis played a role, it was secondary to the light response; flies would track a moving illumination source to the bottom as well as the top of the cage.) Within 24 h of emergence this behavior was reversed, with flies showing negative phototaxis and starting to feed under the surface of the manure.

Most males died within 2 days of emergence. The mean adult lifespan of females was ca. 4 davs, with some living as long as 10 days. Dissection of females revealed the presence of 11 ovarioles per ovary. Eggs were developed in synchrony and flies began to oviposit within 48 hours of emergence. Females were capable of undergoing at least two gonotropic cycles, however, no record was kept of the total

number of eggs produced by individual flies throughout life.

Flies were reared through five generations in the manner described above, using prepared poultry manure as a substrate. Beginning with the F-6 generation, increasing proportions of CSMA* house fly diet were mixed in with the manure. By the F-12 generation, flies were maintained solely on the latter medium. Adult and larval survival and development time appeared to be unaffected by the transition from manure to house fly diet however, a dampening effect on fecundity was observed (Fredeen and Glen 1964). Inhibitors of fungi (NaOH, methyl parahydroxybenzoate) which become established in this medium were found to have profound deleterious effects on Coproica larval survival. On the other hand, larvae and adults were found to be unable to move through the dense fungal mats which developed 2-3 days following media preparation if no corrective action were taken. This technical problem was resolved by preparing the media four days in advance of use (at 3 parts dry diet: 1 part water by volume) and manually agitating the diet on days 2 and 3 post-preparation to disrupt the mycelial mats and aerate the medium. This four-day time lag also permitted the establishment of high levels of bacteria and other microorganisms on which the larvae feed.

Technique for mass-rearing C. hirtula. After considerable experimentation, the following method was developed for rearing large numbers of C. hirtula in the laboratory:

General considerations. Wide-mouthed 1-gallon jars (diam. at mouth=11.5 cm; diam. at mid-point=13.5 cm; height=24.8 cm) with organdy cloth covers were found to serve as ideal rearing vessels. Jars with narrower openings proved to be unsatisfactory due to problems with gas exchange and condensation on the inner walls. For maximum fly yield, minimum development time and greatest ease of adult extraction, optimal environmental conditions were found to be 30-31°C, 24 h photoperiod and at least 60% RH. Under these conditions, development from adult to adult took 9-10 days, with peaks of available new adults on days 10-11 following "seeding" of jars with flies. At temperatures below 28°C, development was slower and adults were sluggish and difficult to extract from rearing jars.

Adult extraction. Flies were extracted during the first 24 hours of adult life, when the flies were positively phototactic. As indicated above, this occurred 10-11 days following seeding in synchronous cultures. Flies were first tapped down from the undersurface of the cloth cover of the jar. The cloth was then removed and quickly replaced with a large plastic funnel with the wide end of the funnel overlapping the mouth of the jar. A 1 oz plastic cup with a parafilm cover was then pressed over the tapered, upper end of the funnel, and illuminated from above with a 60-watt light source. Recently-emerged flies were attracted to the light and would walk or fly up the funnel and become trapped in the plastic collecting cup. These cups were changed every five minutes during peaks of fly numbers

and closed with plastic snap-on lids. After most flies had been collected in this manner, the funnel was removed from the rearing jar and again replaced with an organdy cloth cover. Collecting cups which contained flies were then placed in a refrigerater (5°C) and chilled until flies ceased movement. Flies were either pooled and used immediately to seed new jars (see next section) or held at a slightly warmer temperature in the "egg keeper" section of the refrigerater (10°C) for up to 48 h until they were needed. Holding flies at this temperature for greater than 2 days resulted in substantial mortality.

"Seeding" new rearing jars with adult flies. Chilled flies were pooled and measured out into seeding lots on a volumetric basis. On average, 5 cc of flies was found to be the equivalent of ca. 8500-9500 individuals, depending on mean body size (smaller adults were produced under conditions where larvae were crowded). For routine colony maintenance, lots of 5-cc "fly equivalents" were introduced into 1 gallon jars containing an initial volume of 1 liter of 4-day-old premixed CSMA diet. Chilling of the flies, even for a very short time, was found to reverse phototaxis and dispersal behavior. Following revival, flies became negatively phototactic and commenced foraging on the medium. For each of the next four days, a small volume of water (ca. 20 ml) was sprinkled over the surface of the medium with a squeeze bottle to maintain moisture levels. On day 4 post-seeding, large numbers of larvae were seen crawling through the medium. At this time, a second liter of 3- to 4-day-old diet was

added to the surface of the medium in the jar.

Pupation and adult emergence. If left undisturbed, most larvae from the first gonotropic cycle would pupate on day 5 throughout the medium in relatively dry, protected locations among bits of plant debris. To enhance adult emergence success and to gain access to large numbers of pupae of known age, prepupae were driven to the surface layer of the medium by slowly adding ca. 250 ml of water to the rearing jars early in the day on day 5. When this was done, thousands of pupae were evident along the sides of the jar at the medium surface on day 6. This method had the additional advantage of synchronizing development, although younger larvae, which were not seeking pupation sites at the time of flooding, were lost in the process. Adults began to emerge on day 9, and peak numbers were available for extraction and seeding on days 10 and 11.

Using the method described above, each rearing jar was capable of producing sufficient flies for the seeding of four new jars (ca. 45,000 flies/emergence). With a labor investment of 20 hours per week, 350,000 flies were easily raised on a weekly basis.

Colonization of Carcinops pumilio.

Collection of beetles. Adult C. pumilio were collected from poultry manure on Feb. 12, 1982, at the farm where sphaerocerids were initially collected. At this time, manure had accumulated for four and a half months. All of the arthropods normally collected in summer

months at this farm (Chapters II and III) were also present on this collection date, although in somewhat smaller numbers. Inspection of the manure revealed considerable numbers of foraging Carcinops larvae, indicating that beetles were not in reproductive diapause. Beetles were removed from manure with a camel's hair brush and held in quarantine, on water only, for one week prior to introduction to Coproica rearing jars in an effort to avoid contamination of cultures with the predaceous mite, Macrocheles muscadomesticae. (Macrocheles readily discover and feed on Carcinops eggs (Smith 1975)). Despite this precaution, predator mites were found in these rearing jars within several days of beetle introduction, and soon developed into populations sufficiently large to prevent beetle population increases. Beetles were removed, quarantined a second time, and re-introduced into prey jars. Once again, mites contaminated the rearing containers. Close inspection of beetles from the contaminated media revealed predator mite immatures clinging to the intersegmental membranes under the elytra. After several additional attempts to "de-mite" the beetles, the following method was found to be effective: beetles were first shaken in a container filled with talc (Sweet Life* baby powder) for one minute, transferred to a beaker containing 70% ethanol for 30 sec, then allowed to dry. After two additional talc-alcohol treatments, beetles were placed in containers with water-saturated dental wick (Absorbal*) and held for three days. Mortality among beetles was high following this demiting procedure (>40%), however, it had the desired effect of eliminating all mite

contaminants from beetle cuticle.

Rearing method. One hundred beetle adults were placed, unsexed, in a day-5 Coproica rearing jar which had not been flooded with water (volume of medium = 2 liters). On the third and sixth day post-beetle-introduction, additional "pulses" of prey were added in the form of day-4 C. hirtula cultures which had been established on half the normal volume of medium (250 cc). By day 9 post-beetle-introduction, large numbers of second instar predator larvae were visible in the rearing jar, including many prepupae (large, sluggish, light-colored L2's with no food visible in the gut). The contents of the jar were then emptied into a live-beetle extractor. This extractor consisted of a rectangular pine box (175 cm long x 24 cm wide x 30 cm deep) with a hardware cloth bottom and a hinged top, on the underside of which 9 75-watt light bulbs were fastened. Because of its shape and appearance, the extractor was referred to as a "Berlese coffin". Heat and light from the bulbs drove beetle adults and immatures to the bottom of the box, where they fell through the hardware cloth into teflon-lined rectangular flower boxes.

Beetle adults and first and second instar larvae were separated by hand from debris in the flower boxes, counted into plastic holding cups, and placed separately in day-5 C. hirtula culture jars. Adults were frequently held for several days on moistened Absorbal prior to reintroduction to prey jars. Cannibalism and fighting among larvae

made it imperative that they be moved back into prey jars within several hours of extraction. Even when provided with large numbers of house fly eggs and larvae, beetle immatures which were crowded in plastic cups declined feeding and spent most of the time in protracted conflicts. This was especially true of the L2's. Whenever two larvae made contact, they would twist around to face each other and engage one another's mandibles. Once so engaged, pairs of larvae would twist and thrash about for periods of up to 20 minutes before uncoupling.

L2's, once transferred to day-5 Coproica jars, required no additional prey input to complete development to the adult stage. Jars containing L1's were provisioned with additional pulses of Coproica larvae four days following introduction. All jars containing larvae were subsequently monitored for adult emergence. Ten days following the appearance of the first adult, these jars were extracted as above and adult beetles were collected and counted. Beetles were sexed by gently squeezing the abdomen between the thumb and forefinger under a dissecting microscope and examining the everted genitalia (Smith 1975). With practice, this method proved to be faster and more reliable than examination of morphometric characters for proportional differences (see Chapter II). Chilling beetles prior to sexing was found to facilitate handling and genital extrusion.

After emergence of the first F-1's, routine colony maintenance consisted of introducing 50 female and 50 male beetles into 2 liters of day-4 C. hirtula cultures and following the schedule outlined above. When this protocol was followed, each 9-day feeding and

re-roductive bout by adults resulted in the production of sufficient larvae to give rise to over 400 new beetle adults.

Obtaining beetles of known age and sex. For various aspects of the life history studies described below, it was often necessary to obtain beetles of known, precise age, and to maintain the sexes separately from the time of emergence. In addition, it was felt that the risk of possible trauma caused by mechanical sex deteminations made this an unacce-table method for use in mating and survival studies. These problems were resolved by first separating prepupae from other L2's following extraction of beetle colony jars. Prepupae were then placed on sheets of moistened filter paper and returned to the rearing room. After an initial wandering period, these larvae would tear at the filter paper and, over the next few days, construct pupal cells of paper and silk. Cell construction appeared to be essential for pupation, since prepupae which were deprived of suitable cell-forming material would continue to wander until dead. After completion, cells were teased from the surrounding filter paper with forceps and placed in individual 1-oz containers with moistened Absorbal. Following pupation, the cells were gently opened and the sexes of the pupae were determined. Sex determinations were easily made in the pupal stage by examination of the abdominal terminalia. (Smith (1975) has provided line drawings of male and female Carcinops pupae, however, it should be cautioned that these figures were improperly labelled with the wrong sex designations.) Using this

method, virgin adults of known age and sex were obtained and maintained in individual containers.

Life history of C. pumilio.

Adult longevity. A cohort of 100 female and 100 male F-2 beetles which emerged between April 1 and April 15, 1981, were monitored throughout life for mortality, starting on the latter date. Since the precise emergence date of individuals in the cohort was not known, this date was assumed, for purposes of analysis, to have been April 5, such that all beetles were regarded as being 10 days old at the start of surveillance. Although the schedule occasionally deviated from plan, beetles were generally subjected to 9- or 10-day feeding bouts which were followed by 1- or 2-day periods in which beetles were extracted, sexed and counted. Because beetles were occasionally killed during sexing, percent mortality since the last count was determined for each interval and converted to represent the fate of a hypothetical cohort of 1000 adults at ten days post-emergence. Real mortality of males and females during the first 10 days of adult life was later determined by direct daily observation of 50 males and 50 females of known emergence dates which were fed ad lib. on house fly eggs.

Ovarian development of prey-fed beetles. Ovarian development of prey-fed beetles was observed by the daily dissection and examination of 10 females per day, starting on the day of emergence and ending

with the deposition of the first egg. Each female was paired, on the day of emergence, with a virgin male which had emerged at least 15 days earlier and had been allowed to feed ad lib. on fresh or frozen house fly eggs prior to pairing. Older males were used to insure that females would be mated at a natural post-emergence date and not be artificially delayed by the development of male mating competence. These observations were carrried out over a period of several weeks and were made on a number of F2 and F3 cohorts, depending on the availability of individually reared, newly emerged females. Pairs of beetles were maintained in 1 oz plastic cups with moistened dental wick and were provided with 100-300 fresh or frozen house fly eggs on each day. Casual observations were also made of the condition of the alimentary tract and the degree of hardness of the cuticle during the first few days post-emergence (henceforth referred to as PE).

Development of mating readiness by prey-fed beetles. To determine age- and sex-specific readiness for mating, three groups of paired beetles of different age compositions were fed on house fly eggs and checked daily for the presence of sperm in the spermathecae of females from 10 pairs from each group. In one group, newly-emerged females were paired with newly-emerged males. In the second group, newly-emerged females were paired with 10-day PE virgin males with a prey-rich feeding history. In the third group, newly-emerged males were paired with 10-day PE virgin females with a pre-rich feeding history. No assessment was made of the number of females which

individual males could inseminate in a given amount of time. As above, observations were conducted with beetles from more than one cohort and generation, depending on availability.

Effect of prey de~rivation on survival and reproduction. Casual observations which were made during other aspects of this project indicated that beetles with a prey-rich feeding history could withstand relatively long periods of prey deprivation. To quantify this, 50 male and 50 female F3 beetles which had been maintained on sphaerocerid prey throughout adult life were transferred to plastic containers and provided with moistened dental wick only. Beetles were ca. 30 days old at the start of prey deprivation. Containers were checked daily for mortality and the time to 50% mortality was determined. Dead beetles were removed from the containers on a daily basis. For comparison, 26 male and 26 female newly-emerged F4's were placed immediately on moistened dental wick and were never administered prey. As above, mortality was determined and dead beetles were removed on a daily basis.

To determine the effect of witholding prey from newly-emerged beetles on mating and ovarian development, beetles were paired at emergence with a member of the opposite sex and maintained, as separate pairs, on moistened dental wick only. Initially, 10 females per day were dissected and examined for mating condition and ovarian state. After 8 days PE, mortality was so high that smaller numbers were inspected. At least two females per day were examined until all

beetles were dead.

Development time of immature stages. Because of practical difficulties with respect to egg location and handling of young beetle larvae under observable conditions, no direct observations were made of egg, L1 and early L2 development times. Approximate development times for these stages were estimated by methods described more fully in the Results section. Briefly, development time for the egg stage was estimated by determining the amount of time between adult introduction to prey jars and the first appearance of newly-eclosed L1's. L1 development time was estimated by subtracting this figure from the observed time between adult introduction and the appearance of recently-molted L2's. Similarly, the development time from the L1/L2 molt to the prepupal phase was approximated by subtracting egg and L1 development times from the observed time between adult introduction and the appearance of prepupae. Direct, twice daily observations of varying numbers ($50<n<200$) of individuals of known age were used to determine development time for the life stage intervals prepupa-to-cell-formation, cell-formation-to-pupation and pupation-to-adult-emergence.

Mortality rates of immature stages. Again, because of difficulties in locating sufficient numbers of eggs to work with, no data were obtained on mortality for this stage L1 and L2 (to prepupa) mortalities were estimated by methods which parallelled those

used for development time. These are described in greater detail in the Results section. Briefly, L1 mortality was estimated by subtracting observed L2 (pre-prepupal)-to-adult mortality from observed L1-to-adult mortality. L2 (pre-prepupal) mortality was estimated by subtracting observed prepupa-to-adult mortality from observed L2 (pre-prepupal)-to-adult mortality. Mortalities for L1-to-adult, L2 (pre-prepupa)-to-adult, and prepupa-to-adult were based on actual observations of mortalities of 21 cohorts of L1's, L2's (pre-prepupae) and prepupae which were placed in Coproica rearing jars and extracted after adult emergence. Mortality rates for prepupa-to-cell-formation, cell-formation-to-pupation, and pupation-to-adult-emergence were determined by direct, daily observation of mortalities of individual immatures.

Apparent fecundity of beetles under various levels of crowding. Observations of ratios of Carcinops adults to immatures in poultry manure (Chapters II and III) indicated that, under field conditions, where crowding levels frequently exceed those employed in laboratory cultures (100 beetles/2 liters), factors act to dampen the fecundity of this species. To quantify this apparent crowding effect and to gain insight into the reproductive potential of this species under optimal conditions, varying numbers of beetles were introduced into an equal volume (2 liters) of CSMA containing C. hirtula larvae. On days 3, 5 and 8 following adult introduction, additional prey were added to the rearing jars to assure an overabundance of prey under the most

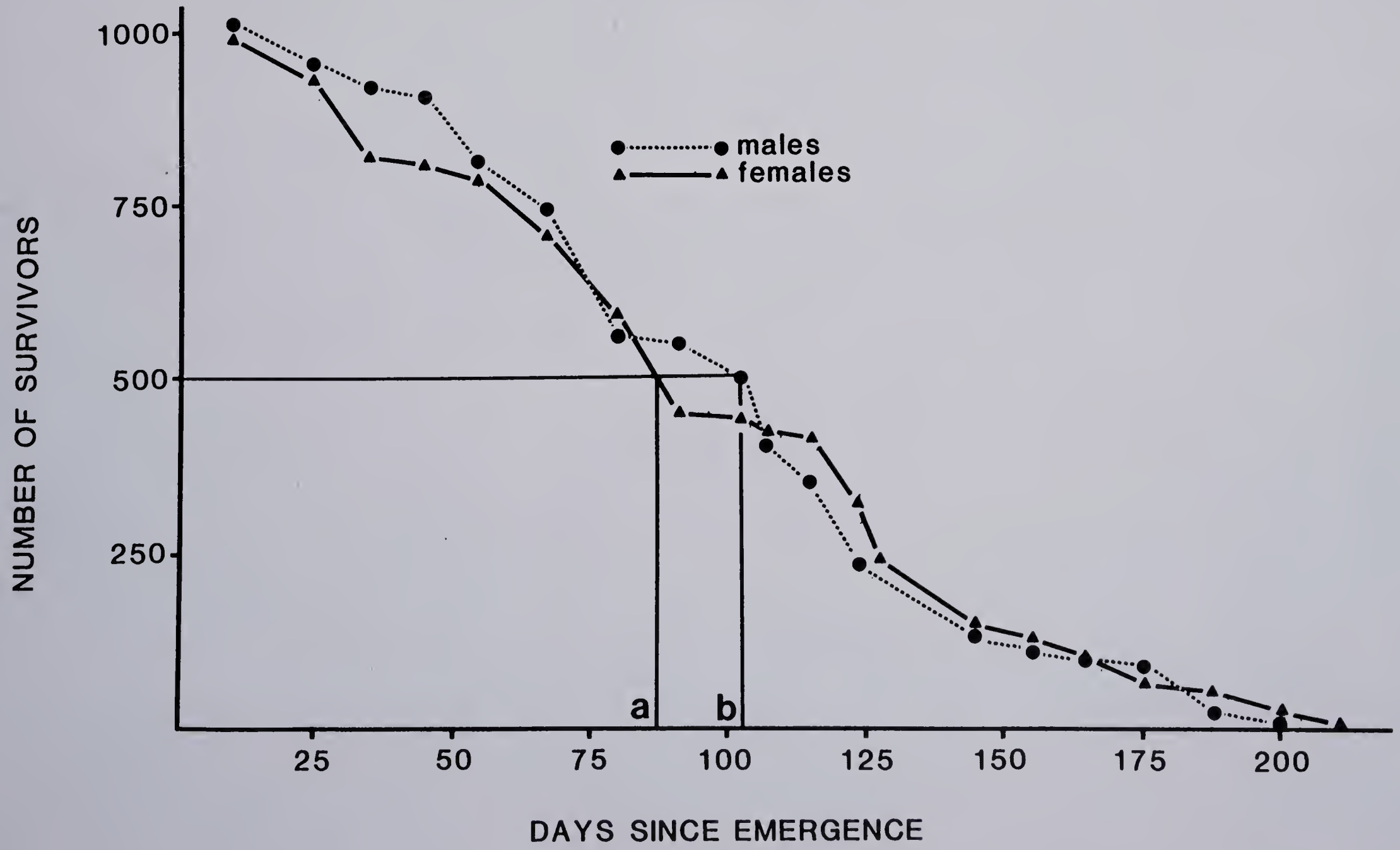
crowded predator conditions. Coproica larvae were live-extracted from the media prior to introduction during these supplemental prey pulses to minimize changes in the volume of the foraging area available to the predators. On day 9 post-adult-introduction, jars containing beetles were extracted and the numbers of surviving adults, L1's and L2's were counted. A minimum daily fecundity index based on ratios of immatures to females over time was then computed.

Using the method outlined above, observations of apparent beetle fecundity were made over a range of initial crowding conditions from 4 to 100 females per 2 liters of diet. In each test, an equal number of males was included as well to eliminate the potentially confounding factor of reduced fertility. In total, 31 observations were made over several months' time, using beetles of varying ages, generations and cohorts.

Results

Adult longevity. Survivorship curves for a cohort of F2 male and female C. pumilio are presented in Fig. 20. No major differences were observed between the sexes with respect to the slope or shape of the curves, with both males and females showing mortalities intermediate between Type II and Type III in the sense of Slobodkin (1962). The longest-lived females lived slightly longer (200-210 days) than the longest lived males (188-200 days), however, the time to 50% mortality was shorter for females (88 days) than for males (125 days).

Fig. 20. Survivorship of a hypothetical cohort of 1000 male and 1000 female Carcinops pumilio adults. Data based on observations of 100 male and 100 female F2 colony beetles which were maintained on a prey-rich diet continuously throughout adult life.


1000
750
500
250
NUMBER OF SURVIVORS
males
females
a
b
25
50
75
100
125
150
175
200
DAYS SINCE EMERGENCE

Similarly, mean adult longevity was 90.6 days for females and 104.3 days for males. These observations must viewed with caution, however, since the number of beetles actually monitored was fairly small (ni=100 males and 100 females).

Daily mortality rates at various times throughout adult life are presented in Table 16. Data for the interval 0-10 days PE were obtained by direct daily observation of 50 males and 50 females for the first 10 days of adult life. Other interval mortalities were based on data obtained during the above-mentioned study of adult survivorship. In both males and females, mortality was low (0.3 to 0.6% per day) for the first 45 days of life, then increased in later intervals.

In this surveillance of adult mortality, beetles were maintained continuously throughout life (except for periods of extraction and counting) in a highly prey-rich environment. Where prey is somewhat less abundant, beetles seem to live longer. In casual observations of another F2 cohort which was alternated between 10- to 12-day feeding bouts and longer (10- to 21-day) "holding" periods on CSMA only, beetles lived at least twice as long as those which were fed continuously. At this writing, 12 females and 8 males of this intermittently fed cohort (ni=121 females and 103 males) were still alive at ca. 380 days PE.

Ovarian development of prey-fed beetles. The ovaries of Carcinops were found to possess 4 ovarioles each, with the ovarioles showing the

Table 16. Daily mortality rates of female and male C. pumilio adults throughout life under colony conditions (30-31°C) where prey was never limiting.

Days since emergence	Daily mortality rate	
	Females	Males
0 - 10*	0.53	0.41
10 - 45**	0.56	0.29
45 - 81	0.70	0.98
81 - 113	0.91	1.23
113 - 144	2.03	1.93
144 - 176	1.89	1.17
176 - 210	4.25	4.76

* Based on laboratory observations of 50 and 50 F_3 beetles which were maintained on water and house fly eggs.

** Other mortalities were based on observations of an initial cohort of 100 and 100 F_2 beetles which were maintained in Coproica hirtula rearing jars throughout life.

polytrophic condition typical of the Polyphaga (Crowson 1981). Development of the ovaries for the first eight days of adult life are illustrated in Figs. 21-27, and may be summarized as follows:

Days 0-2. The ovaries were relatively undifferentiated (Fig. 21). Distinct oocytes were not visible, nor was any sign of yolk deposition apparent. For the first two days of adult life, females did not appear to feed. The alimentary tracts of beetles on those days were filled with a white, fluffy material which did not appear to be of prey origin, and the regenerative crypts of the midgut (Crowson 1981) were undeveloped, indicating that digestive enzymes were not being produced at this time. On day 2 PE, the midguts were at least partially filled with a yellowish material indicative of prey-feeding. The crypts were fully developed and everted, and were as long as the width of the midgut at its widest point. The cuticle at this time was still not fully hardened (a subjective observation based on the amount of resistance which the cuticle presented during dissections).

Day 3. In each ovary, the germinal vessicle was plainly visible at the base of the follicle of one of the four ovarioles, with some apparent yolk deposition (Fig 22). Smaller oocyte nuclei with no associated yolk could be seen in some other ovarioles as well.

Day 4. In each ovary, one follicle showed greater yolk

deposition than on the previous day, and was also more developed than the other three ovarioles (Figs. 23 and 24). Also, in most females, a size difference between the two most-developed oocytes (1/ovary) was apparent, with one showing significantly more yolk deposition than the other.

Day 5. Follicle size of the most-developed oocyte had at least doubled in size since day 4 (Fig. 25), while the second-most-developed follicle in the opposite ovary had increased by a smaller amount.

Day 6. Follicle sizes of the two most-developed oocytes had increased by at least a factor of two (Fig. 26). Considerable volk deposition was now visible in two additional (third- and fourth-most-developed) oocytes. In most females, the size difference between the two most-developed oocytes was less pronounced.

Day 7. By day 7, most females appeared to have undergone at leat one oviposition, as indicated by distension of the lateral oviducts and the faint presence of corpora lutea (yellow bodies) (Fig. 27). Large amounts of yolk were now apparent in the third- and fourth-most-developed oocytes.

From day 7 on, beetles which were supplied with over-abundant prey were capable of producing and depositing over 10 eggs per day (see fecundity section below). In general, beetles developed and deposited eggs sequentially and singly, with females rarely possessing more than four follicles with substantial yolk deposition. If denied

Fig. 21. Ovary of a newly emerged (<1 day old) female C. pumilio adult. (1 in = 0.196 mm)

Fig. 22. Ovary of a female C. pumilio on day 3 post-emergence, showing developing follicle in one ovariole. (1 in = 0.196 mm)

gv = germinal vessicle

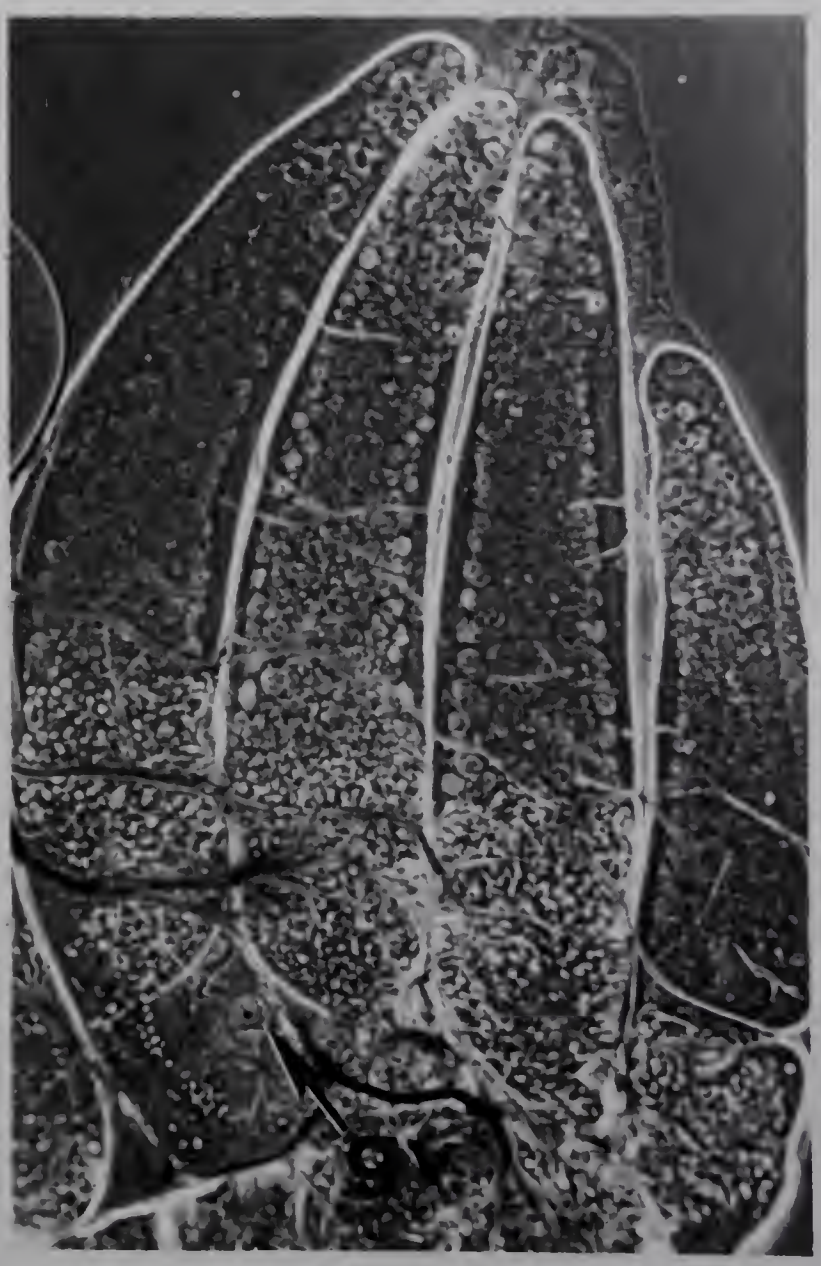
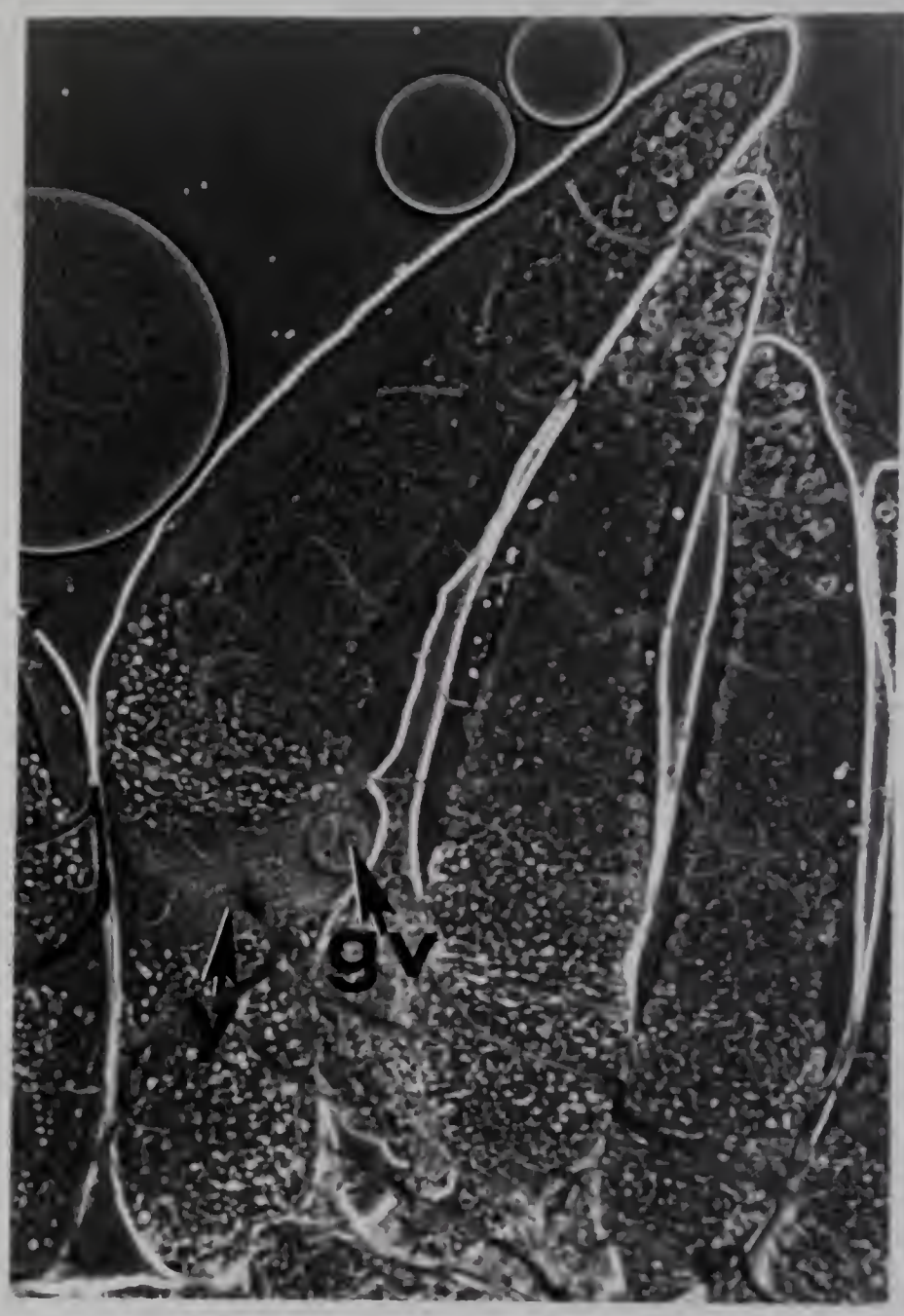


Fig. 23. Ovary of a female C. pumilio on day 4 post-emergence, showing most-developed oocyte. (1 in = 0.196 mm).

Fig. 24. Ovary of a female C. pumilio on day 4 post-emergence, showing second-most developed oocyte and the appearance of germinal vessicles in less-developed oocytes. (1 in = 0.196 mm)

gv = germinal vessicle, y = yolk


gv

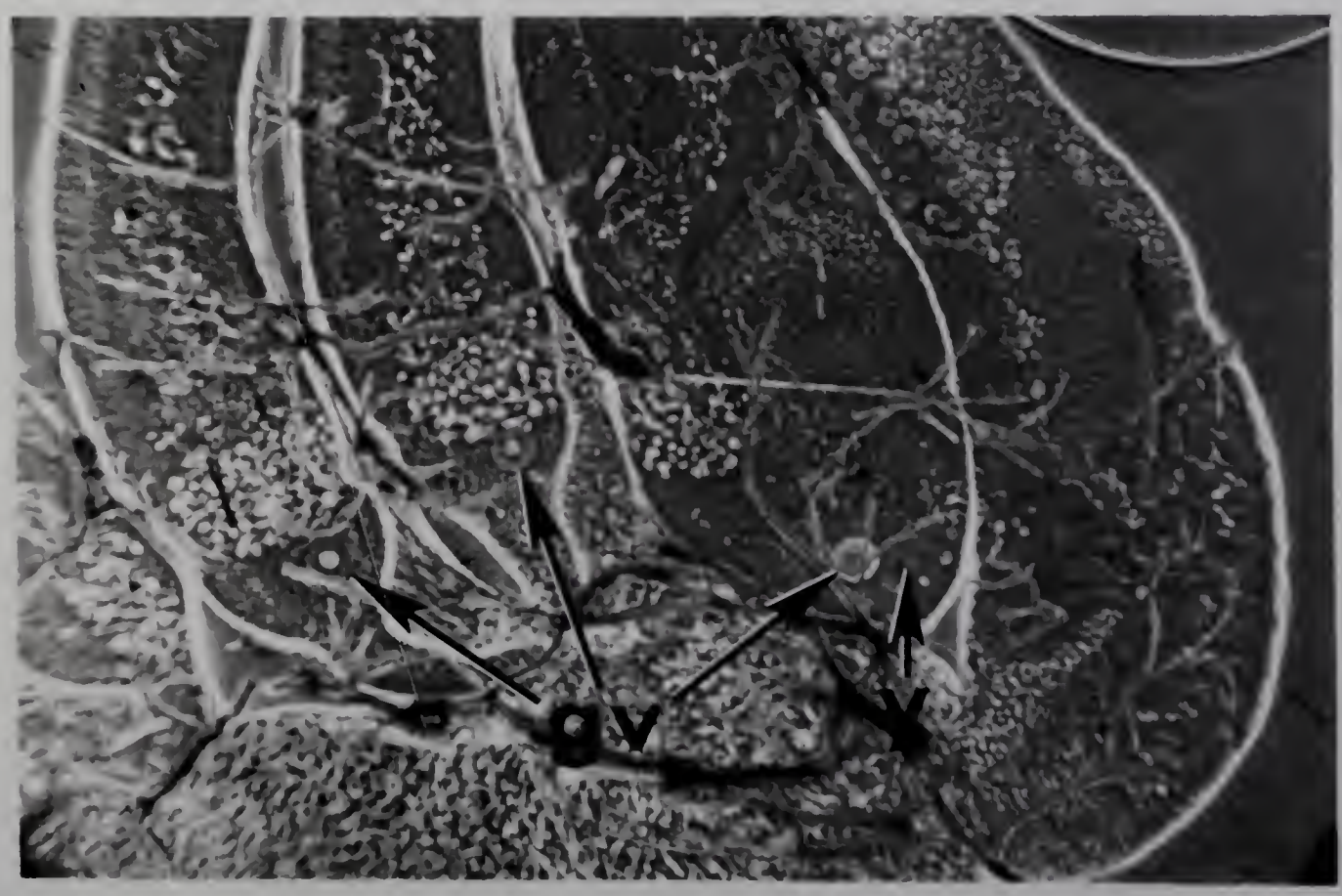

gv

Fig. 25. Ovary of a female C. pumilio on day 5 post-emergence, showing most-developed oocyte. (1 in = 0.196 mm).

Fig. 26. Ovary of a female C. pumilio on day 6 post-emergence, showing yolk deposition in 4 oocytes. (1 in = 0.49 mm).

gv = germinal vessicle, y = yolk

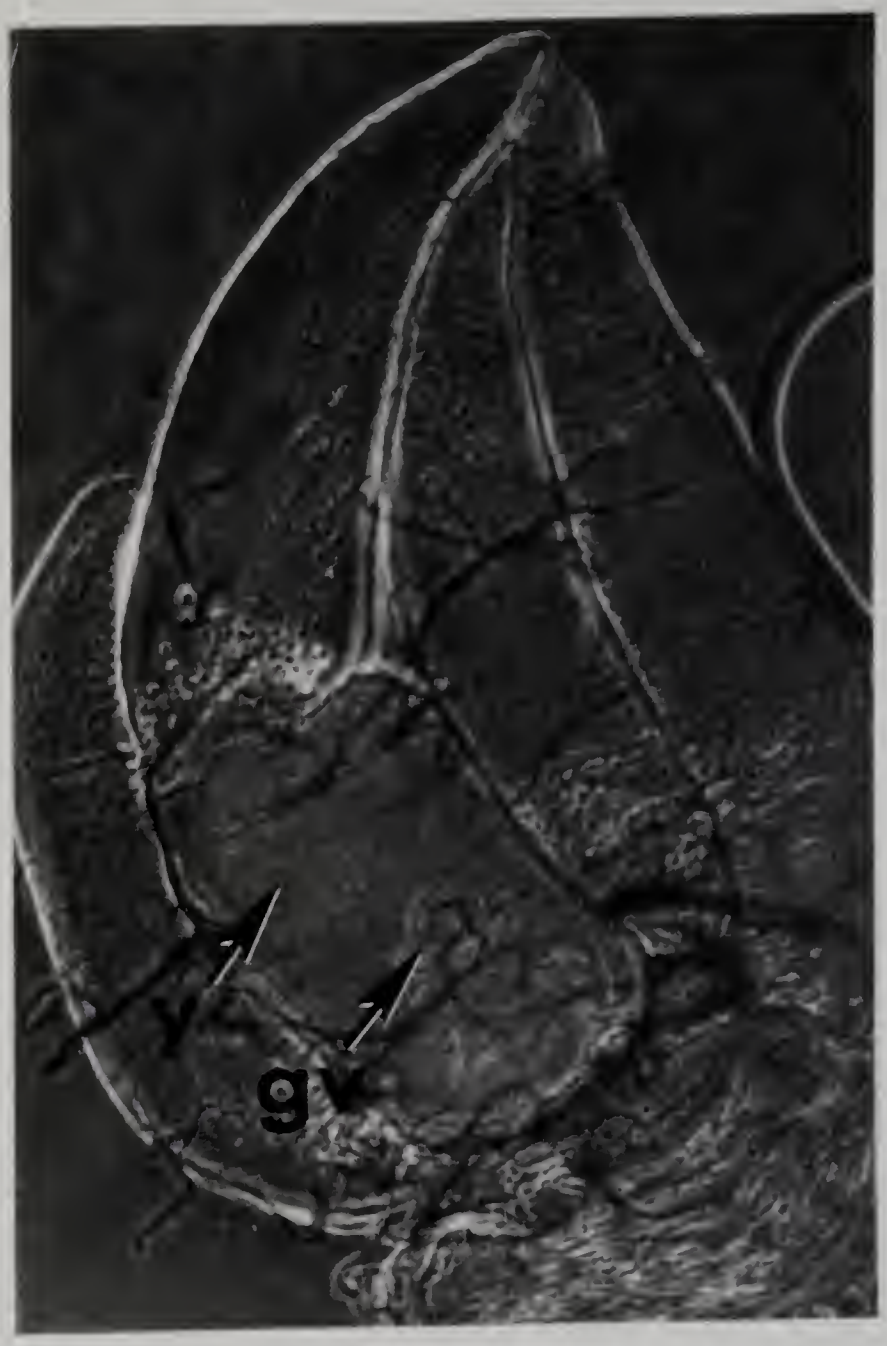

g

Fig. 27. Ovaries of a female C. pumilio on day 7 post-emergence. (1 in = 0.98 mm)

Fig. 28. Ovaries of a female C. pumilio which was fed on prey and deprived of a suitable oviposition site, showing development of additional ovarioles. (1 in = 0.98 mm)

a suitable oviposition site, however (eg. by holding them in a plastic petri dish with nothing but prey), females would continue to feed and begin to develop additional oocytes (Fig. 28).

Development of mating readiness by prey-fed beetles. Results of daily inspection of paired, fed beetles with respect to mating condition are presented in Table 17. When newly-emerged beetles were paired with newly-emerged males, no mated females were observed until day 5 PE. On day 6, all females were found to have mated. When newly emerged males were paired with older (10-day old) females, similar results were observed; none were found to have mated until day 5, and all were mated by day 7. When newly emerged females were paired with older males, however, all females were found to have mated within one day.

The actual event of copulation was rarely observed, since this nearly always occurred underneath objects in the local environment (dental wick, manure, CSMA, etc). Males displayed little discretion in their choices of potential mates and readily attempted copulation with other males and with mated females. In general, courtship appeared to consist of males climbing onto the backs of other beetles, everting the aedeagus and probing the terminal abdominal segments of the beetle below. On several occasions, however, when single virgin males and females were paired in containers with no objects to crawl beneath, a sequence of hind leg "pumping" behavior was observed. On these occasions, the two prospective mates faced each other, separated by a distance of less than 10 mm, and rapidly contracted and relaxed

Table 17. Time to first mating by C. pumilio males and females which were paired, at emergence, with either older beetles (10 days old) or other newly emerged individuals.

Days since emergence of younger member of pair	Number mated on each day among pairs of:		
	young ♀/older ♂	older ♀/young ♂	young ♀/young ♂
1	10	0	0
2	10	0	0
3	10	0	0
4	10	0	0
5	10	1	2
6	10	9	10
7	10	10	10
8	10	10	10

the muscles of the hind legs, giving the appearance of beetles doing "push-ups". This behavior persisted for at least five minutes before the male attempted copulation. Such attempts were successful on all six occasions when this behavior was observed. No record was kept of the duration of the copulatory period.

Following copulation, the spermatophore was found lodged in the common oviduct, and was connected to the small, single spermatheca of the female via the spermathecal duct (Fig 29.). The fate of the spermatophore following sperm transfer was not determined.

Effect of prey-deprivation on survival, mating and ovarian development. Survivorship of adult beetles which were placed on prey-deprivation regimes either at emergence or after a 30 day feeding period are presented in Table 18. The median survival time of previously-fed beetles was over three times greater than that of beetles which were deprived since emergence. Further, for the first ca. 31 days of prey-deprivation in the former group, daily mortality occurred at rates approximating those of continuously fed beetles (0.6-1.5% per day), with a sharp drop in survivorship starting on days 33-36. In the deprived-since-emergence group, no mortality was observed until day 8 post-deprivation, and all beetles were dead by day 13 (males) or 14 (females).

Among beetles from the latter group, ovarian development never proceeded beyond the appearance of oocyte nuclei, and no females were found to have mated.

Fig. 29. Reproductive system of newly emerged, recently mated female C. pumilio, indicating the spermatheca, spermathecal duct, spermathecal gland, and spermatophore. (1 in = 0.98 mm)

sc = spermatheca, sd = spermathecal duct, sg = spermathecal gland, sp = spermatophore.

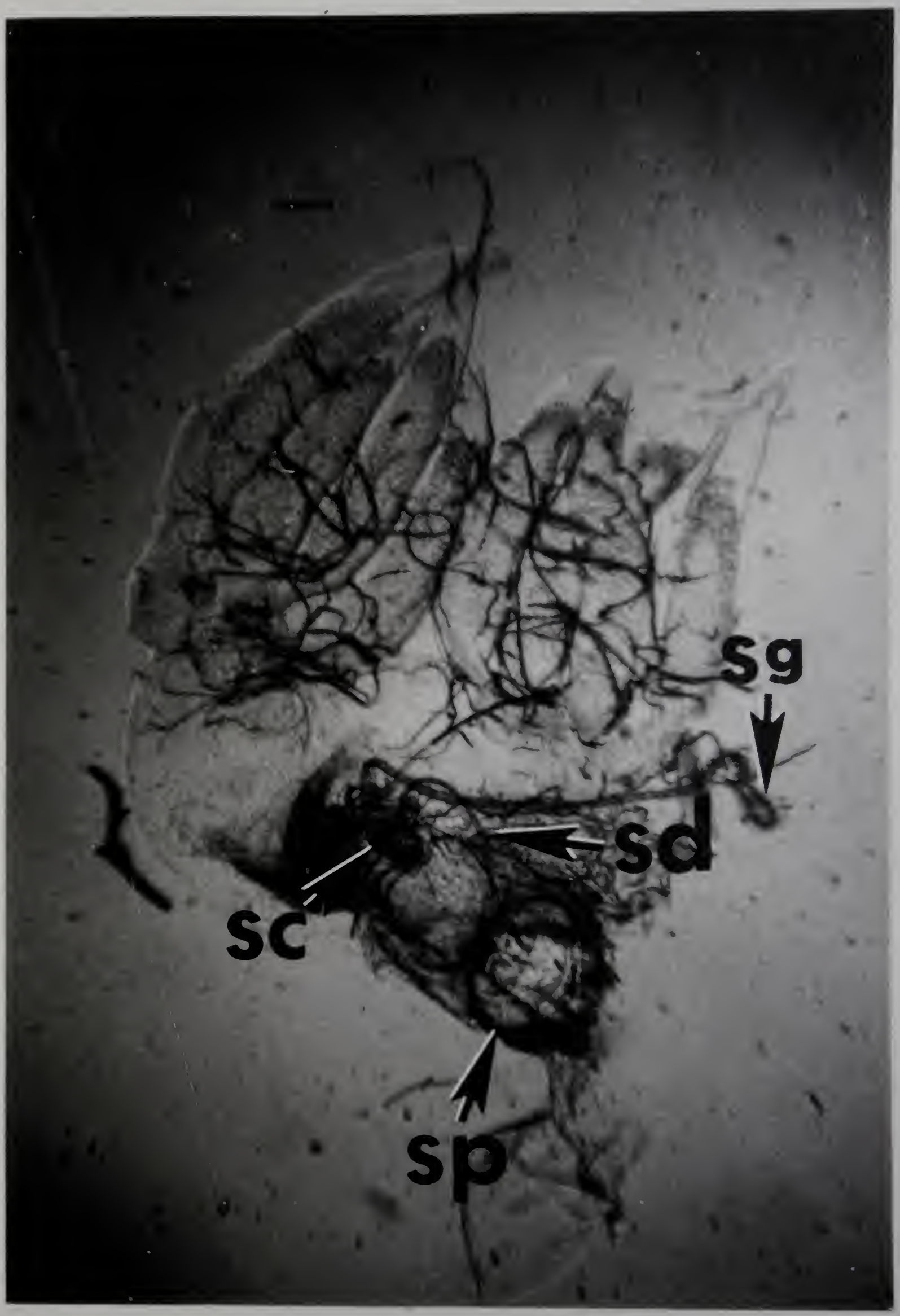

sg
sd
sc
sp

Table 18. Survival of prey-deprived Carcinops adults with a prey-rich prior feeding history and adults which never fed on prey.

Feeding history	Time to 50% mortality in days	
	females	males
never fed on prey*	11.4	10.8
fed on prey**	37.6	32.7

* 1 day post-emergence at start of study.

** ca. 30 days post-emergence at start of study.

Development time of immatures. Development times for Carcinops immature stages are presented in Table 19. As mentioned above, estimation methods were used to determine egg, L1 and L2 (to prepupa) development times. This was accomplished for the egg stage by introducing small numbers of females with a prey-rich feeding history into Coproica rearing jars, removing them 5 hours later, and searching through the medium every 12 h following for the presence of newly hatched L1's. Of 137 L1's which were recovered in this manner, 22 were found in 60 h post-adult-introduction, 100 were found at 72 h, and 5 were located at 84 h. Assuming that adults commenced ovipositing soon after introduction to the prey jars, these observations yield a rough estimate of egg stage development time of 72 h, or three days. A similar method was used to compute L1 development time by first determining the approximate time from adult introduction to the appearance of large numbers of newly-molted L2's (5.5 days). The egg stage estimate was subtracted from this figure to give an estimated L1 development time of 2.5 days. Numerous observations associated with routine colony maintenance procedures established that 9 days was the average time for the interval from adult introduction to the appearance of large numbers of prepupae. Thus, the L2 stage from the L1/L2 molt through the onset of the prepupal phase may estimated to be 9 - 2.5 - 3.0 = 3.5 days.

Development times for other stages (prepupa to cell formation, cell formation to pupation, duration of the pupal stage) were

Table 19. Estimated and observed development times of immature stages of C. pumilio under colony conditions (30-31°C) where prey was never limiting.

Stage	Development time in days	Percent of total development time
Egg	3.0	13.8
L_1	2.5	11.6
L_2:		
(L_1-L_2 molt to prepupa)	3.5	16.2
(prepupa to cell formation)	3.3	15.3
(cell formation to pupation)	2.9	13.4
L_2 total	9.7	44.9
Pupa	6.4	29.7
Total	21.6	100.0

Egg, L_1 and first interval of L_2 development times were estimated according to methods described in the text. Other times were determined by direct, twice-daily observations of individuals.

determined by direct observation of individual immatures. These observations are also summarized in Table 19. Summing of the estimated and observed development times for all stages gives an egg-to-adult development time of 21.6 days. This figure is in agreement with actual observed adult-to-adult development times, which ranged from 20 to 24 days under normal colony maintenance conditions.

Mortality rates of immature stages. Using methods paralleling those outlined ablove, L1 and L2 (to prepupa) apparent mortalities were estimated. For L1's, this was done by subtracting observed mortality from L2 (pre-prepupa) to adult (44.55%) from observed mortality from L1 to adult (51.82%), for an estimated L1 mortality of 7.27%. Similarly, L2(pre-prepupal)-to-prepupal mortality was obtained by subtracting observed prepupa-to-adult mortality (28.12%) from L2 (pre-prepupa)-to-adult mortality (44.55%), providing an estimated L2 (to prepupa) apparent mortality of 16.43%.

These data, along with observed apparent (within-stage) mortality information for other immature stages and F2 adult survivorship data, have been used to construct a partial life for this species under colony conditions (Table 20). These data may be viewed as reflecting mortality rates under conditions which approach optimality, since prey was never limiting and hazardous life events such as cell formation and the pupal stage were protected from predation and disruption by conspecifics. For example, when mortalities were directly observed from L1 to adult (51.82%), L2 to adult (44.55%) and prepupa to adult

Table 20. A partial life table for C. pumilio under colony conditions (30-31°C) where prey was never limiting. Data have been converted to represent the fate of a hypothetical cohort of 1000 newly-hatched L_1's. Egg mortality was not determined.

Life stage	lx	dx	% apparent mortality	% real mortality
L_1*	927	73	7.27	7.27
L_2 (to prepupa)**	775	152	16.43	15.23
Prepupa to cell formation	617	158	20.39	15.80
Cell formation to pupation	554	63	10.25	6.32
Pupation to adult emergence	518 (267♂:251♀)	36	6.39	3.55

Adults (days PE)	male	fem.	tot.	male	fem.	tot.	male	fem.	tot.	male	fem.	tot.
0-10	253	241	494	14	10	24	5.26	4.10	4.72	1.40	1.03	2.43
10-45	203	216	419	50	25	75	19.75	10.13	15.06	4.96	2.54	7.54
45-81	151	140	291	52	76	128	25.36	25.43	30.55	5.15	7.64	12.18
81-113	107	85	192	44	55	99	29.12	39.41	34.05	4.41	5.51	9.92
113-144	40	34	74	67	51	118	62.93	60.00	61.60	6.74	5.08	11.84
144-176	16	21	37	24	13	37	60.48	37.52	50.17	2.43	1.27	3.70
176-210	0	0	0	16	21	37	100.00	100.00	100.00	1.56	2.12	3.76

* first instar larval mortality was estimated by subtracting observed mortality of interval L1-to-adult from interval L2-to-adult.

** second instar larval mortality was estimated by subtracting observed mortality of interval L2-to-adult from interval prepupa-to-adult. All other life stage mortalities were determined by direct observation.

(28.12%), these figures were greater than the sums of real mortalities through these same intervals when all stages from the prepupal phase on (prepupa to cell formation, cell formation to pupation, pupation to adult emergence) were held and observed in individual containers (48.17, 40.09 and 25.6%, respectively).

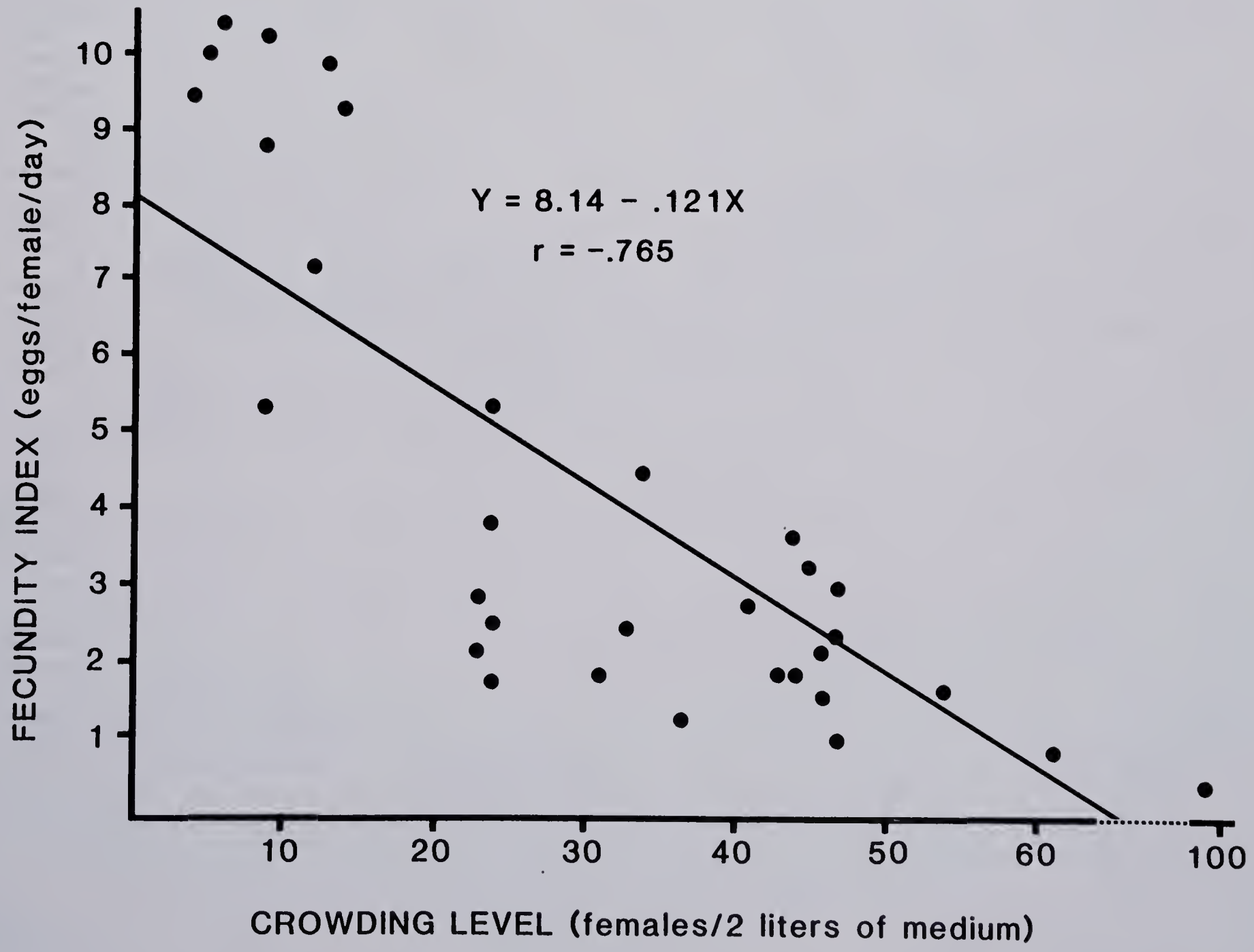
Comparison of Tables 19 and 20 indicate that stage-specific mortality was not directly correlated with stage duration. For example, the pupal stage, which is 6.4 days in duration and comprises 29.7% of immature development time, was also the stage with the lowest apparent mortality rate (6.39%). Overall L2 development time (44.9% of total) approximated apparent mortality for this stage (44.1%), however, inspection of subphases in the second instar show that not all L2 periods present equal risk. Thus, while the period from cell formation to pupation (13.4% of development time) was only slightly less than that from prepupa to cell formation (15.3% of total time), larvae in the latter interval suffered nearly twice the mortality (20.39%) of larvae which successfully constructed cells (10.25%).

The sex ratio of adults at emergence was close to 1:1. In Table 20, an emergence sex ratio of 267 males: 251 females is presented, which was derived from actual observed totals of 187 females and 175 males which emerged from individually-maintained immatures. These latter figures were adjusted to reflect the sexual composition of 518 surviving adults from an initial cohort of 1000 L1's. Sex determinations over 18 months' time of a total of 7,231 beetles which were between 1 and 15 days old at the time of sexing showed an overall

ratio which was even closer to unity (3,647 males and 3,614 females). The former figure was selected for use in Table 20 because the beetles on which it was based were used to track survival for the adult age interval 0-10 days PE. Also, it was feared that the uncertainty of the precise age of recently-emerged beetles from colony jars would obscure the distinction between sex ratios at emergence and sex-specific mortality in the first few days of adult life.

Apparent fecundity of beetles under various levels of crowding. Results of 31 observations of Carcinops apparent fecundity under various levels of crowding are presented in Fig. 30. "Fecundity" was estimated by first dividing the number of L2's present on day 9 post-adult-introduction by the number of females introduced into Coproica rearing jars. (When fewer females were recovered on day 9 than were introduced on day 1, the number of L2's was divided by an accordingly adjusted adult figure ((ni + ni+1) /2). This L2's-per-female figure was then divided by the number of days in which oviposition could have occurred which would give rise to L2's by day 9 post-adult-introduction. This latter figure was determined by subtracting egg (3.0 days) and L1 (2.5 days) development times from the 9 day observation period. The resulting fecundity index thus expressed the minimum number of eggs laid per female per day during the first 3.5 days of introduction to the prey jars. This figure was not adjusted for L1 mortality since this factor may have varied with crowding levels. Thus, the fecundity index used in analysing the

Fig. 30. Fecundity of female C. pumilio under varying levels of adult crowding. Fecundity index represents the minimum number of eggs produced per female per day during the first 3.5 days of introduction to prey jars. Overabundant prey (C. hirtula) were added to reduce influence of competition on results.


Y = 8.14 - .121X
r = -.765
FECUNDITY INDEX (eggs/female/day)
10
9
8
7
6
5
4
3
2
1
10
20
30
40
50
60
100
CROWDING LEVEL (females/2 liters of medium)

crowding data was highly conservative and assumed the following: 1.) adult females began ovipositing immediately following introduction to the prey jars; 2.) no egg mortality; and, 3.) no L1 or early L2 mortality. Attempts were made to obtain a finer estimate based on L1 numbers, however, it was felt that more accurate counts could be made of second than first instars.

These qualifying remarks aside, Fig. 30 illustrates a major and highly significant ($P<.0001$) dampening effect of adult crowding levels on beetle larval production (apparent fecundity). Beetles under very low crowding conditions (4 to 14 females per 2 liters of diet) produced a surprisingly large number of eggs. On three occasions, fecundity index values exceeding a minimum of 10 eggs per female per day were observed, with a peak index value of 10.4 eggs per female per da from a rearing jar with 6 females per 2 liters of Coproica-seeded CSMA. At crowding levels exceeding 14 females per 2 liters, this figure dropped sharply. At levels of 100 females per 2 liters, apparent fecundity was only 0.4 eggs per female per day.

Discussion

Colonization and development of C. hirtula. The Sphaeroceridae, or small dung flies, is a cosmopolitan group of acalyptrate muscoids which are thought to have originated in temperate zones of South America (Hackman 1969, Rohacek and Marshall 1982). Most species feed on a variety of decaying plant and animal material including rotting

seaweed (Marshall 1982), fungi (Papp 1979), rotting fruit (Walker 1957), dead snails (Deeming and Knutson 1966) and grass clippings (Ware 1966). Many are dung feeders, and some have developed specialized phoretic associations with other invertebrates to ensure access to frass or dung, e.g. crabs (Gomez and Diego 1977), ants (Richards 1968), dung beetles (Marshall 1983) and, in Cameroon, millipedes (Disney 1974). Some species are found in association with bat guano in caves (Rohacek and Marshall 1982) as well as in the burrows of small mammals (Hackman 1967), the nests of birds (Hicks 1959), and human sewage (Fredeen and Glen 1964, Mihara et al. 1983b)

Coproica hirtula (frequently referred to in the literature as Leptocera hirtula) has been reported from a number of habitats, including grass clippings (Ware 1966) and bovine (Bai and Sankaran 1977, Poorbaugh et al. 1968, Tenorio 1968) and poultry (Zuska and Lastovka 1969) manure, although it is more commonly found in the latter. Dr. Jindřich Rohacek, a leading authority on the group, made the following remarks about this species: "It seems that Coproica hirtula strikingly predominates (often as the only species) among sphaerocerid fauna on fowl manure. It is interesting especially in relation to the fact that on manure of domestic mammals it is comparatively rare, being replaced by other domestic species of Coproica (C. ferruginata, C. vagans and C. lugubris in pasture lands; C. digitata and C. acutangula on horse dung)." (Rohacek, pers. comm.).

In the present study, C. hirtula was successfully transferred from poultry manure to CSMA medium, indicating the adaptability of

these flies to different habitats and substrates. Similarly, Fredeen and Taylor (1964) were able to establish a colony of Leptocera caenosa (Rondani) on autoclaved horse and sheep manure from flies which were collected from human sewage. In a subsequent study, Fredeen and Glen (1970) reported that flies from this same colony could be successfully reared on alfalfa, birdsfoot trefoil, sweet clover, fescue grass, CSMA and a bacterial culture medium. Hackman (1969) stated that "numerous species...(of sphaerocerids)...have a wide ecological valence and are able to adapt themselves to a variety of climatic conditions".

Under the rearing conditions described in the present study, C. hirtula was found to complete development in 9 days at 30-31°C. While this temprature may at first seem high, it approximates the temperature of the manure zones in which these flies are found in greatest abundance (Chapters II and III). It should also be pointed out that the temperature of the medium itself frequently exceded that of the surrounding air in the rearing room due to metabolic activity of the larvae and microorganisms in the diet. It was not uncommon for the medium to reach temperatures greater than 35°C, although larval mortality showed a sharp increase at temperatures above 40°C. The available information on development time for other sphaerocerid species is summarized in the following table:

Species	dev. time	medium	reference
"many Limosininae"	3-4 weeks	-----	Hackman 1969
Leptocera caenosa (Rondani)	30-40 davs	alfalfa, birdsfoot trefoil, clover, fescue grass, CSMA	Fredeen and Glen 1970
L. caenosa	16-26 days	horse and sheep manure	Fredeen and Taylor 1964
L. pullala (Zetterstedt)	22-26 da-s	boiled grass	Okely 1974
L. parapusio (Dahl)	4 days (egg-pupa)	mushrooms	" "
L. atomus (Rondani)	10-16 days	horse manure	" "
L. vagans (Haliday)	16 days	horse manure	" "
L. brachystomata (Steinhammer)	11 days	seaweed	" "
L. mirabilis (Collin)	8-14 days	horse and cattle manure	" "
L. bifrons (Steinhammer)	8-12 days	cattle manure	" "
L. longicosta	12 days	sheep manure	Wilson and Stoll 1929
L. fuscipennis (Haliday)	12-15 days	sewage sludge	Mihara et al. 1983a
Leptocera sp.	<10 days	cattle manure	Mohr 1943
Coprophila lugubris	16-23 days	cattle manure	Hammer 1941
C. hirtula	18 days	grass cuttings	Ware 1966

Meaningful comparisons of development time among species is difficult due to the lack of information on environmental conditions in

most of the above studies. Fredeen and Taylor (1964) and Fredeen and Glen (1970) conducted extensive studies on the influence of breeding media and temperature on development time, survival, body size and fecundity of Leptocera caenosa. Under initial colony conditions, L. caenosa developed from egg to adult in 16-26 days at 22.2°C on horse and sheep manure (Fredeen and Glen 1964). When reared at approximately the same temperature on CSMA and vermiculite, similar results were observed (Fredeen and Taylor 1970). The latter authors also found that fly survival and fecundity was 2-3 times higher and overall body size was larger at cooler rearing temperatures (17.0° C), although development time was considerably longer (>34 days). Overall, temperature was found to be a more important factor in determining development time than was the type of larval medium, which seemed to have a greater impact on survival and fecundity.

Under rearing conditions described in the present study, newly emerged C. hirtula adults were easily transferred into new culture jars by exploitation of the positively phototactic response of flies in the first day or two of adult life. In assessing the usefulness of L. caenosa as laboratory animal, Fredeen and Taylor (1970) made the following observations: "A major disadvantage of the species is its relatively long life cycle...compared with D. melanogaster and A. aegypti. Another disadvantage is the sluggish behavior of the adults and especially their hesitant and not always positive response to light. Whereas light is used to transfer D. melanogaster adults rapidly, L. caenosa adults can be transferred efficiently only with an

aspirator." Based on results presented here, C. hirtula apears to be an ideal laboratory animal, for biological and genetic studies as well as a source of prey for predators; it has a short generation time (9-10 days), newly emerged adults can be readily separated from the parental population, it is inexpensive to rear, and very large numbers can be raised with relatively little effort.

Colonization of Carcinops - general considerations. In their review of the literature dealing with biological control of medically important arthropods, Legner et al. (1974) indicated that progress in this area was lagging behind similar efforts with phytophagous pest species. A major reason which they cited for this difference was that the reduction in pest numbers achieved by natural enemies of insects of medical importance was "often unacceptable to the general public or local health authority that demanded an even lower population threshold". In many poultry houses in Massachusetts and other areas of the Northeast, Carcinops pumilio (often in concert with the mite Macrocheles muscadomesticae) has been found to maintain house fly populations at essentially zero levels without the additional use of insecticides or costly mass-releases of pupal parasites (Chapter II), indicating the potency and utility of this histerid predator in filth fly IPM programs.

The environmental and biotic factors which act to promote and maintain large predator populations in the virtual absence of house flies on some farms and not others is as yet poorly understood,

although habitat maturity and the presence of abundant alternative prey clearly play major roles in this process (Chapter III, Legner 1971, Legner et al. 1973, Peck 1968, Peck and Anderson 1969, 1970). In the present study, one of the natural prey items of Carcinops in the field, Coproica hirtula, was successfully exploited in the laboratory as a prey base for maintaining large, self sustaining histerid colonies. This development addresses a second problem which was raised by Legner et al. (1974); the difficulty in colonizing and mass-rearing many biocontrol agents of medical/veterinary pest species.

Initial attempts by myself and others to colonize Carcinops using house fly as prey were largely unsuccessful (P. Morgan, pers. comm., E. Schmidtmann, pers. comm., Smith 1975). While this fly seems to be the most logical choice for rearing work, it has several major disadvantages. Because C. pumilio is highly cannibalistic, very high prey densities must be maintained in beetle rearing jars. The predators, however, due to their small size, can only prey on eggs and young larvae of this fly (Peck 1969). Thus, to achieve the prey densities necessary to minimize beetle cannibalism, so many fly eggs and larvae must be introduced that a great surfeit of older larvae which "escape the gauntlet" are produced. In both manure- and CSMA-based cultures, I have found that these overabundant "refugee larvae" adversely affect beetle colonies by disrupting histerid pupation and oviposition cells and by altering the physico-chemical properties of the media. These problems can be avoided by using frozen eggs as the sole prey source for predators. However, to maintain a

sizable Carcinops colony on such prey alone requires the rearing of astronomical numbers of house flies.

Coproica hirtula, on the other hand, was found to be an ideal prey source for colonies of histerids. As indicated in the preceding section, these flies are inexpensive and simple to mass-rear, known numbers of individuals of known age can be readily obtained from stock culture jars, and they can be maintained on a substrate other than manure. This latter attribute is important since poultry manure may harbor pathogens of avian disease, which could be carried by colony beetles into poultry houses during introduction trials. Another advantage of these flies is their small size, in that all life stages from egg to adult are readily preyed on by all feeding stages of C. pumilio.

Sphaerocerids clearly constitute a major portion of the diet of Carcinops under field conditions in modern poultry houses in Massachusetts (Chapters II and III). In addition, there is evidence that this predator-prey association may have preceded the development of intensive poultry production systems and the resulting "monocultures" of avian manure which are produced under these conditions. C. pumilio prefers poultry to bovine manure in agricultural settings (Legner and Olton 1970). Under more natural conditions, this beetle is also more commonly found in birds' nests than in the burrows of small mammals or the droppings of larger ones (Kryanovskij 1977). Hicks (1959) reported C. pumilio (as C. quattourdecimstriata (Stephens)) as having been found in the nests of

storks, owls, starlings, purple martins, Andea cinera, Asio wilsonianus, Ciconia ciconia, Columba sp., Progne subis, Strigidae, Sturnus vulgaris and Tyto alba as well as several other unidentified species. Similarly, at least 24 species of sphaerocerids have been recovered from birds' nests, and some have been found in association with C. pumilio in the same nests (Hicks 1959). From this evidence, as well as the high affinity which Carcinops shows for sphaerocerids under field and lab conditions, it seems likely that the modern association between this predator and its prey is a reflection of an ancestral relationship which had its evolutionary origins in the nests of wild birds prior to man's domestication of fowl. House fly eggs and young larvae may provide supernormal stimuli which release Carcinops feeding behavior and evoke the high rate of discovery (Smith 1975) and predatory potential (Peck 1968, 1969) of this predator on M. domestica immatures.

In light of the above considerations, and in view of the probable Old World origins of the house fly (Legner and McCoy 1966, Sacca 1964), further foreign explorations for natural enemies of this pest should include inspections of the nests of wild birds for as-yet undiscovered and unexploited predators of fly immatures. To date, most of this work has centered on examinations of accumulations of bovine manure (Legner and Olton 1970, Legner et al. 1974, 1981). Similarly, examination of the burrows and droppings of mammals may reveal the presence of histerids and other predators of dipterans which are predisposed to inhabititing the dung of herbivores. Enthusiasm must be tempered with

caution, however, since predators which are quite abundant in isolated or fresh droppings may be repelled by stockpiled, partially composted accumulations of manure (Bornemissza 1968).

Adult longevity. C. pumilio which were provided with overabundant prey continuously throughout life were observed to live an average of ca. 100 days, while those which were intermittently fed lived considerably longer. In general, the Histeridae appears to be a rather long-lived group (Crowson 1981). Lindner (1967), in a study of Hister, Saprinus and Gnathoncus spp., found that adults would live for 2-3 years. Bornemissza (1968) found that field-collected Pachylister chinensis lived for at least 15 months in the lab following collection. Hister coenosis has been found to live for at least 6 months and H. incertus for at least 19.5 months following emergence under laboratory conditions (Summerlin et al. 1981).

Under field conditions in poultry houses, Carcinops populations increase steadily with accumulation time over the season and reach densities exceding 100 beetles/liter of manure (Chapter II). While prey availability and habitat acceptance clearly play roles in this process (Chapters II and III), data presented here indicate that the population dynamics of this species would be expected to result in heavily adult-biased age structures over long periods of time. That is, where prey are abundant, newly emerged beetle adults join the population at a rate considerably higher than can be compensated for by adult mortality. Thus, in the field, the long lifespan of the adults

coupled with short larval development time make major contributions to the frequently-observed greater abundance of Carcinops in older manure. Conversely, sudden drops in the number of adults in a habitat with low to moderate prey availability would reflect either beetle emigration, disease or parasitism. (Flight and dispersal of this species in response to declining habitat quality is discussed in detail in Chapter IV). Over a four-year period of observing and collecting C. pumilio in the field, I have found no evidence for the presence of beetle pathogens or parasites. Since Carcinops appears to be an imported species (Hinton 1945, Legner and Olton 1970), its associated natural enemies may not be present in the U.S. at this time.

Male Carcinops were found to live as long as females under the rearing conditions described here, and were found in roughly equal proportions at emergence. In the field, one generally finds male-biased sex ratios (Chapters II and IV, Smith 1975), suggesting that females in nature are at higher risk than males with respect to cannibalism and predation (see Chapter II for a further discussion of this topic). Since females possess a small, single spermatheca and males have greatly enlarged testes, it seems apparent that females must mate repeatedly throughout life, and that male-male competition for mates must be keen. Further work is needed to determine whether this mating system reflects female need for nutritional or hormonal factors which may be necessary for oogenesis and which are released from the spermatophore following sperm transfer, as has been found in the seed beetle Acanthoscelides obtectus (Huignard 1974, 1975, Huignard et al.

1977).

Ovarian development and mating readiness of beetles. Carcinops females were found to be receptive to mating immediately following eclosion. The term "receptive" may be misleading when applied to newly emerged, teneral beetles, however, since copulation attempts by males may simply be more likely to succeed with such sluggish, soft-bodied individuals than with older, fully hardened females. Males, on the other hand, were observed to require 5-6 days of feeding on prey prior to mating. This feeding may be assumed to be related to development of the testes and production of the first spermatophore. Given the apparent nutritional investment which males invest in spermatophore production, there is probably considerable constraint placed on them with respect to repeated matings. Further studies are needed to determine the number of matings which individual males are capable of per unit time and with known amounts of prey input. Under field conditions, where virtually all females which are collected are found with active sperm in the spermathecae (Chapters II and IV), the opportunities for males to copulate with many females in succession are probably few.

Female beetles were found to develop and deposit the first egg about one week following emergence, and to develop their eggs singly and in succession. This is in agreement with observations of Pachylister chinensis by Bornemissza (1968), who found that reproductive development took one week and that eggs were deposited singly in tunnels beneath manure pats. Single-egg development and

deposition is quite common among beetles in general (Crowson 1981) and appears to be typical of histerids (Hinton 1945). Hammer (1941) noted that Hister unicolor L. females deposited one or two eggs in the soil under cattle droppings, and Summerlin et al. (1981) made similar observations of H. coenosis and H. incertus. These latter authors further noted that the "cells" in which eggs were deposited served as incubation chambers; eggs which were mechanically removed from the cells dessicated and did not hatch. Given the temporary and patchily distributed nature of the resources which are exploited by most histerids (carrion, dung, etc.), single egg deposition may also be a strategy to minimize sibling competition, cannibalism and egg predation and parasitism.

Development of immatures. In the present study, Carcinops was found to complete development in 20-24 days. Smith (1975), on the other hand, found that the development time for this species was 28-37 days. This discrepency may be in part accounted for by differences in rearing methods and prey availability. Under the rearing conditions described here, immatures were allowed to forage freely in culture jars and were left undisturbed until complete cells were formed, while Smith observed the development of individual immatures either on germination paper or in small clumps of manure in petri dishes. In my experience C. pumilio larvae do not behave "normally" in petri dishes, but rather expend considerable energy trying to locate dark refuges in the local environment. Another difference between Smith's method and that used

here was that house fly eggs were used as prey in the former, while sphaerocerid immatures were employed in the latter. I have generally found that Carcinops larvae discover moving prey more readily than stationary prey items such as house fly eggs and Coproica pupae. Thus, one reason for the observed difference in development time may have been related to the amounts of time which the predators spent feeding relative to searching. In nature, where competition and predator avoidance may interfere with foraging, longer development times than those observed either here or by Smith (1975) may be common.

Another factor which presumably influenced development time is rearing temperature, which was 30-31°C in the present study and ca. 27°C in that of Smith (1975). Lindner (1967) found that Hister cadaverensis completed development 41 days at 23°C, however, at lower temperatures this period was considerably longer (55 days at 14-25°C, 69 days at 13-18°C). At rearing temperatures of 20-25°C, Lindner also made the following observations of development times of several other histerid species: Hister unicolor - ca. 40 days, H. striola - ca. 36 days, H. carbonarius - 42-63 days, Saprinus semistriatus - 33-36 days, Gnathoncus sp. - ca. 40 days (Lindner 1967). Bornemissza (1967) found that larval development of Pachylister chinensis required 16 days at 30°C and 20 days at 25°C. He also reported that the pupal period was "long and variable", and ranged from 3-5 weeks at 25-30°C. At 27°C, Summerlin et al. (1981) reported that Hister coenosus and H. incertus completed development in 34.2 and 36.0 days, respectively.

In a landmark study of arthropods associated with cattle

droppings, Mohr (1943) noted that mature larvae of Hister abbreviatus "seemed to be familiar with the possibilities of the dung for they gathered the large fibers about them to form a bristly-coated capsule". Pupal cell formation appears to be fairly common among histerids (Hinton 1945), with many species "cementing" bits of debris or habitat together such as dung or soil (Bornemissza 1968, Mohr 1943, Reichart 1941, Summerlin et al. 1981). Carcinops appears to be quite flexible in its selection of cell-forming materials. In addition to using manure particles for cell construction, Smith (1975) found that C. pumilio larvae would enter empty house fly puparia and close off the opening. In the present study, larvae were also observed to construct cells from moistened filter paper and CSMA medium. The source of the cement used in this process is uncertain, since the larvae of cell-forming beetles lack labial salivary glands (Crowson 1981). In other species, this material is thought to originate from the peritrophic membrane (Rudall and Kenchington 1971) or the malpighian tubules (Mazzi and Bacetti 1956).

Mortality of immatures. Natural selection is thought to favor repeated reproduction and long adult lifespans in species where mortality rates are higher in immature stages than as adults (Murphy 1968). While such arguments tend to be circular, examination of Tables 19 and 20 indicates that this generalization holds true for C. pumilio. Of a hypothetical cohort of 1000 first instar larvae, nearly 50% mortality occurred prior to adult emergence under optimal colony conditions.

Since the average lifespan of the adults is at least twice the development time from egg to adult, immatures clearly suffer proportionately higher mortality rates than the adults of this species. In the lab, where, where prey was not limiting and other predators were excluded, the highest risk period among the immature stages was that during which prepupae constructed pupation cells (20% apparent mortality), while the lowest risk period was the pupal stage (6.39 apparant mortality). In the field, where beetle population densities are considerably higher (Chapters II and III), and predation pressure from Macrocheles may be strong, this differential may be assumed to be even more pronounced, considering the vulnerability of prepupae and the protection provided by the pupal cell.

Further life table work is needed to answer a number of questions which were not addressed in the present study, such as egg mortality and differential mortality of all stages under various levels of crowding and prey densities. For an integrated pest management program for filth flies to be successful in poultry houses, accurate information on predator population dynamics is essential. While laboratory life tables are of limited utility towards this end, they provide a basis for comparison with field mortality rates and can indicate weak points in predator life cycles. It is felt that this information, along with other data on predator-prey dynamics (Chapter II), ecology (Chapter III) and dispersal (Chapter IV), can serve as a foundation for further work leading to the development of predictive, deterministic models of predator and prey population dynamics in the

poultry manure arthropod community.

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