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THE BIOECOLOGY OF POLYDESMUS INCONSTANS LATZEL (DIPLOPODA) IN MICHIGAN

Michigan State University PH.D. 1980

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THE BIOECOLOGY OF *POLYDESMUS INCONSTANS* LATZEL (DIPLOPODA) IN MICHIGAN

by

Renate Machan Snider

A THESIS

Submitted to

Michigan State University

in partial fulfillment of the requirements

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ABSTRACT

THE BIOECOLOGY OF POLYDESMUS INCONSTANS LATZEL (DIPLOPODA) IN MICHIGAN

By

Renate Machan Snider

The present study was designed to comprehensively assess major life history parameters of Polydesmus inconstans Latzel 1884, a polydesmid millipede common throughout Europe and most of North America. Laboratory work focused on effects of temperature on mortality, instar duration and reproduction. Companion studies, conducted in two different sites near Michigan State University, clarified seasonal development and behavior of P. inconstans populations in the field.

Reproducing laboratory cultures provided live material for experiments at four constant temperatures: 10°, 15.5°, 21° and 26.6°C. Instar durations decreased with increasing temperature. Durations did not differ betwen sexes from stage I through VI; but graduation from VII to adult was more rapid in males than in females. Mortality was lowest at 15.5° and 21°C, slightly higher at 10°C, and drastic (up to 100%) at 26.6°C.

Duration of the egg stage was also influenced by temperature, 21°C allowing the most rapid development; eggs could not survive 26.6°C.

As soon as they reached maturity, paired adults reproduced readily. Intervals between ovipositions were shortest at 21°C (about one week) and increased at lower temperatures. Fecundity was highest at 21°C. At both 15.5° and 21°C the highest numbers of eggs were laid during the first eight ovipositions, then steadily declined. A maximum of 22 ovipositions were recorded. During a life time, a mean

of about 500 eggs were produced per female, with a maximum of 1100.

Comparison between field-collected and laboratory-reared adults showed that laboratory-reared females accurately portrayed the reproductive potential of the species. Females of both types, when paired with males, showed curtailed longevity. Females isolated after successful mating lived longer and oviposited more often than paired individuals. Egg viability of isolates, at first as high as that of paired females, decreased steadily with successive ovipositions. Sperm storage capacity of the species was effective during the period of maximum egg production (ovipositions 1 through 9).

Field data were obtained from a home garden in 1976 and 1978, and from a deciduous woodlot in 1979. P. inconstans behaved similarly in all three years: oviposition took place from May through August; young hatched from June through August, and graduated to instars VI, VII and VIII during summer and fall growth. The life cycle in the field encompassed one year. Adults maturing in late fall and in the following spring reproduced from May to August, then died. Semelparity was indicated not only in the field, but was supported by reproductive patterns observed in laboratory culture.

Spatial distribution and density were studied in a woodlot population. Low-lying depressions, with thick litter layers and favorable temperature and moisture conditions, harbored densest populations (100 to 200/m^2 on most dates). In upper slope areas, densities in litter never exceeded 38/m^2. Densities in soil could not be extrapolated to large units because of the large number of nil-captures, but were likely to be lower than those in litter.

Mating behavior, construction of egg and molting chambers, and

aggregations were documented in laboratory and field. Qualitative observations on P. inconstans as prey for beetles, centipedes and millipedes showed that predation and oophagy could be a significant factor in limiting P. inconstans populations.

In memory of my father

ACKNOWLEDGEMENTS

I wish to thank the members of my guidance committee: Dr. Ralph Pax and Dr. Max Hensley, Department of Zoology, and Dr. James Tiedje, Department of Crop and Soil Sciences for their assistance in the course of this study.

To my major professor, Dr. T. Wayne Porter, I express sincere appreciation for his inspiring enthusiasm in all matters of invertebrate biology, and for his help during the preparation of this dissertation.

Very special thanks are due my husband, Richard, for his patience throughout these years of study, and for his encouragement and valuable constructive criticism.

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POLYDESMUS INCONSTANS LATZEL 1884

The Diplopoda have been neglected by American zoologists when measured against impressive taxonomic, morphological and biological compendia amassed by European investigators.

American taxonomic literature, specifically prior to 1940, is of limited value because it considers only one or a few species. Faunistic studies have been published for only three states: Ohio (Williams and Hefner, 1928), New York (Bailey, 1928) and Michigan (Johnson, 1953). Recently, Shelley (1978) added a comprehensive investigation for parts of North Carolina.

The first catalogue of North American millipedes was compiled by Bollman (1893). Chamberlin then published a second in 1947, and Chamberlin and Hoffman, in 1958, cooperated to publish the most recent checklist for North America.

Polydesmus inconstans was described by Latzel in 1884, but was then misplaced. It was redescribed as P. distractus Latzel in 1886, P. coriaceus borealis Porat 1889, and P. rhenanus Verhoeff 1891.

According to Hoffman (pers. comm.) a number of taxonomic difficulties are associated with P. inconstans. For many years it had been designated as P. coriaceus Porat 1870. This description was based on material from the Azores, where it had probably been introduced from southwest Europe. Apparently the description did not accurately fit the European synanthropic species discussed by Schubart (1934b) under the name of coriaceus.

Chamberlin and Hoffman (1958) therefore felt justified to include the species as P. inconstans in their North American checklist,

synonymizing it with P. coriaceus (not Porat) Schubart, 1934. Demange (1970) gave a fully documented account of the situation based on ample Azores material. Known synonyms of P. inconstans are listed below.

Polydesmus inconstans Latzel, 1884. Bull. Soc. Sci. Nat. Rouen, ser. 2, ann. 19:269

Polydesmus distractus Latzel, 1888. Bull. Soc. Hist. Nat. Toulouse, Proc. Verb. :lxxxv

Polydesmus coriaceus var. borealis Porat, 1889. Ent. Tidskr. vol 10:71

Polydesmus rhenanus Verhoeff, 1891. Berliner Ent. Zeitschr. vol. 36:121

Polydesmus coriaceus (not Porat) Schubart, 1934. In: Dahl, Die Tierwelt Deutschlands, Teil 28:165

Polydesmus testi Bollman, 1888. Proc. U. S. Nat. Mus. vol 10:617

Polydesmus socarnius Chamberlin, 1910. Ann. Ent. Soc. Amer. vol. 3:252

Polydesmus pilidens Humbert, 1894. Mem. Soc. Geneve vol 32:14

Polydesmus hortus Williams and Hefner, 1928. Bull. Ohio Biol. Survey no. 18:113

Polydesmus pronomeutes Chamberlin, 1942. Bull. Univ. Utah biol. ser. vol. 6, no. 8:9

Polydesmus wheeleri Causey, 1950. Ent. News vol. 61:197.

The species was found in Michigan for the first time by Johnson (1952). Although under different names, it was already known to occur in New York (Bailey, 1928), Ohio (Williams and Hefner, 1928), Indiana (Bollman, 1888), Utah (Chamberlin, 1910), Colorado (Chamberlin, 1942) and North Dakota (Causey, 1950). Chamberlin (1947) listed Massachusetts and Delaware as distribution records of P. coriaceus (= inconstans), adding that it was widespread in the eastern and midwestern states, and had probably been introduced from Europe. Indeed, Schubart (1934b) and Attems (1940) cite most of the countries

of Europe in their geographic distribution records of the species.

All of Johnson's specimens (Johnson, 1952) were collected in south central Michigan, including Ingham County, within which the present study was conducted. Johnson suggested that water might act as a dispersal agent of the species; he frequently found larvae among debris on stream banks, and showed that young instars could survive submerged for 36 to 48 hours. All other collection sites were hygric or mesic, with a layer of protective leaf litter. Johnson also found the species in gardens and cemeteries, and concluded that man was generally the agent responsible for introduction and dispersal of P. coriaceus (= inconstans).

Johnson (1952, p. 308) describes P. coriaceus in detail. The description is comprehensive, and will not be repeated here. In subsequent chapters characteristics of the species, now correctly named P. inconstans, will be shown in context with results of this investigation.

PART I

THE BIOLOGY OF POLYDESMUS INCONSTANS AT CONSTANT TEMPERATURES

1. INTRODUCTION

Iulus terrestris Koch (now Tachypodoiulus niger (Leach)) was the first millipede for which developmental data were obtained (Newport, 1841). Later in the 19th century, a number of extensive studies investigated embryonic development both of iulids and polydesmids (Metschnikoff, 1971, 1974; Cholodovsky, 1895; Rimsky-Korsakow, 1895;

Heathcote, 1886,1888). All of them stressed details of germ layer, organ and appendage development. Much of this early work was then summarized by Attems (1926), Verhoeff (1928-1932) and Pflugfelder (1932).

Not until Carl Verhoeff successfully began culturing various species did details of anamorphic development become a focal point of investigation. Among diplopod development patterns, that of Iuliformia proved most difficult to follow. In these diplopods, increment of body rings added per instar is variable: as Blower and Gabbutt (1964) illustrate, a female Cylindroiulus latestriatus possessing 38 body segments may belong in any one of four stages. Furthermore, molting does not stop once maturity is attained. Verhoeff (1928) first described alternation of sexually functional males with intercalary males (Schaltmännchen): following Verhoeff, this prolonged anamorphosis is termed *periodomorphosis*, and is now known to occur in several iulids and blaniulids (Rantala, 1970, 1974; Sahli, 1958, 1961, 1966: Halkka, 1958; Blower and Fairhurst, 1968). Drift (1951) observed periodomorphosis in females as well, but characterization of later instars, where segment numbers overlap, is so difficult that even Halkaas (1958) extensive work does not detail the succession of female instars.

The situation is quite different in Nematophora, Polydesmoidea and the first six stages of Pentazonia. Instars are separated by a constant increment of new segments. There is a fixed total number of instars - eight in polydesmids - of which the last (adult) does not undergo further ecdyses. An exception to the rule is provided by Brachydesmus superus (Latzel): the subadult instar may molt into one with the adult number of rings, but without secondary sexual

characters; the gonopods are developed during a supernumerary ecdysis without addition of segments (Stephenson, 1961). Nematophora possess nine instars total (Schubart, 1934a). In Pentazonia, a fixed number of anamorphic instars is followed by four or more epimorphic instars (Verhoeff, 1928; Blower, 1958; Heath et al, 1974).

Segmental and appendage numbers as given by Schubart (1934a) following Seifert (1932) hold true for all polydesmoids. By convention, instars are numbered in roman numerals: I through VIII (adult).

Myriapod eggs are enclosed by a tough membrane, the chorion. As described in detail by Dohle (1964), it splits during embryonic development, but one or more cuticular layers still enclose the embryo, which is now termed the pupoid stage. Verhoeff considered the pupoid to be embryonic and the hexapod larva which hatches from it to be the first post-embryonic stage. Pflugfelder (1932), Halkka (1958) and Dohle (1964) consider the pupoid to be the first post-embryonic stage, and the free-living larva that emerges to be instar II. Most workers,however, consistently adopt the older terminology; since it is only a matter of convenience, the free-living hexapod larva will here be considered to be the first post-embryonic instar.

Once the first instar has emerged, development is achieved by a series of molts. Pflugfelder (1932), Halkka (1958) and Vachon (1947) have shown that anamorphic growth comes about in three steps: a) the proliferation zone forms new segments during a molt, but the segments remain in embryonic condition in the ensuing instar; b) at the next molt, these segments become recognizable body rings, but remain apodous; and c) during the second molt following their formation, these

rings become podous segments.

Field sampling has enabled many workers to reconstruct the life cycle stages of millipedes as they occur seasonally (see Part II). Obviously, age structure at a given time of year is a product of growth rates of individual instars. That growth rates are temperature-dependent is frequently implied; thus Blower (1970) speaks of the different stage distributions of Tachypodoiulus niger in "good" and "poor"years. But little comprehensive work has been done on the influence of temperature on growth rates under controlled conditions.

Early workers (Verhoeff, 1928;Miley, 1927) surely had no way of controlling environmental conditions, and conducted their observations at unspecified room temperatures. Since then, prolonged rearing of millipedes under more or less constant conditions has been reported.

Regarding iuloids, Keirallah (1966) reared Iulus scandinavius Latzel to adulthood. Fairhurst (1974) partially reared Ommatoiulus sabulosus (L.) and recorded stadial durations through instar III. Halkka (1958) commented on growth rate variations due to temperature in Schizophyllum sabulosus (L.); finally, Blower (1974) fully documented the post-embryonic development of Ophyiulus pilosus (Newport) in the laboratory, under somewhat fluctuating temperature conditions.

Developmental data for polydesmoids have been given for a variety of species. Frequently, these accounts cover only a narrow segment of the life cycle of a species, i.e. those segments of particular interest to the investigator at the time. The most extensive observations, mainly under variable conditions, are found in work by Causey (1943) on Orthomorpha gracilis (Koch); by Keirallah (1978) who reared that same species through all stages; by Stephenson (1961) on

Brachydesmus superus (Latzel); and by Banerjee (1970, 1973) on Polydesmus angustus Latzel.

Millipedes generally do not appear to be difficult to maintain in culture, a fact reflected in the frequent use of diplopods as test animals in laboratory studies. Beginning in the 1960's, detailed work on respiratory rates of millipedes as affected by temperature was published by Byzova (1967), Dwarakanath (1978a,b) and Gromysz-Kalkowska (1967, 1970a,b, 1973). Recently, specific observations on leaf palatability (Neuhauser and Hartenstein, 1978) and coprophagy (McBrayer, 1973) have also included polydesmids in their experimental designs.

Probably the most thoroughly studied polydesmid is Polydesmus angustus Latzel, a common inhabitant of some parts of continental Europe (Schubart, 1934b; Meidell, 1967) and British woodlands (Blower, 1955, 1958, 1970; Banerjee, 1967, 1973). As Schubart (1934a) points out, common species are most likely to be investigated; small wonder then that P. angustus has been the subject of respiration studies (Phillipson, 1967), descriptions of developmental morphology (Petit, 1973b, c, 1976), reproductive biology (Sahli, 1969) and regeneration of appendages (Petit, 1973a).

Comparative studies on growth rates under several temperature regimes have, to this author's knowledge, not been reported. Similarly, relationships between temperature and survival are not usually specified. Rather, mortality rates are estimated from seasonal density data in the field, and are suggested to depend on factors such as waterlogging (Miller, 1973, 1974; Heath et al., 1974), dessication (O'Neill, 1969) or food limitation (Miller, 1974; Blower and Miller, 1974), as well as on unspecified biotic influences.

Indeed, all of these probably outweigh the single effect of temperature since millipedes and other terrestrial invertebrates appear to be capable of active search for propitious microclimatic conditions (Perttunen, 1953, 1955; Haacker, 1970). In Haacker's extensive work on millipede ecology in Germany (1968), he related data on temperature preferenda and resistance to extreme temperatures to the geographical distribution records of fourteen species. From the point of view of comparative physiology his results were comprehensive, but by virtue of his experimental design did not include long-term temperature effects.

Data on diplopod reproductive potential are scarce and incidental, owing to the cryptic habits of the animals, and, in some species, to the difficulties encountered in their rearing. Even in otherwise successful cutlures, adults tend to be non-reproductive (Blower, 1974). Polydesmoids, many of which are semelparous (a single egg-laying period after which they die), are probably more conducive to laboratory observation than the often long-lived, iteroparous iuloids.

Table 1 summarizes available information on the reproductive potential of polydesmoids, and includes comments on where and how the information was obtained. As a rule, the potential number of consecutive ovipositions by one female are not known. Recurring accounts of single ovipositions by laboratory-reared females present a singular contrast to the prolonged reproductive periods in field populations (see Part II). In some species, seasonal occurrence of mature eggs in dissected females indicates that more than one brood may be the rule (Lewis, 1971b).

The laboratory investigations reported here were geared toward assessing the following aspects of the biology of P. inconstans:

a) General observations on the biology of the species in captivity, including nesting and molting habits and qualitative observations on the species' predators;

b) Temperature-dependency of growth rates, i.e. duration of the stages when reared at constant temperatures;

c) Temperature-dependency of survivorship of each instar;

d) Fecundity, with a comparison between laboratory-reared and field-collected females.

Table 1. Summary of available information on the reproductive potential of polydesmoids.

SPECIES	AUTHOR	NO. EGGS OBSERVED	COMMENTS
Oxydesmus sp.	Toye 1967	731 range 456-1034	In culture, at least 5 females per species
Habrodesmus falx	-"-	1436 range 576-2353	-"-
Sphenodesmus sheribongensis	Lewis 1971a	81 (167, 56, 49)	Counts of large ova, 3 females, field-collected
Tymbodes falcatus	-"-	172	-"-
Habrodesmus dubosqui	Lewis 1971b	1213 (702,887,1213,2050)	Counts of large ova, 4 field-collected females; "at least 2 broods/year"
Xanthodesmus sp.	-"-	291 (337,232,323,271)	Counts of large ova, 4 field-collected females; "presumably 2 broods"
Xanthodesmus physkon	-"-	1434 (871, 1997)	Counts of large ova, 2 field-collected females
Ampylodesmus iyonis Murak.	Murakami 1965a	usually 4-6 range 1-7	59 nests observed in culture
Platyrrhacus amauros Attems	Pflugfelder 1932	60-80	In culture
Strongylosoma pallipes (Oliv)	Seifert 1932	40-60	In culture??

Table 1 (cont'd)

Orthomorpha gracilis (Koch)	Causey 1943	300 (17,42,52,63,151)	One clutch found in greenhouse In culture;1 batch laid per female; still contained mature eggs upon dissection.
Apheloria coriacea (Koch)	Eaton 1943	1076	In culture; single observation
Luminodesmus sequial Loomis & Dav.	Davenport et al 1952	(70,160,165)	3 egg masses counted
Euryurus erythropygus (Brandt)	Miley 1927	526	1 nest in culture
Brachydesmus superus (Latzel)	Stephenson 1961	49 range 42-56	22 nests observed; usually only one brood
Polydesmus complanatus (L.)	Verhoeff 1928	200	possibly more than 1 brood, with decreasing no. of eggs.
Polydesmus complanatus (L.)	Voges 1916	25-40	n = ? In culture
Polydesmus angustus Latz.	Effenberger 1909	100	In culture
Polydesmus angustus Latz.	Banerjee 1973	184 range 125-246 157 range 135-251	In field In culture

2. MATERIALS AND METHODS

A continuous supply of P. inconstans was assured by maintaining a number of stock cultures at 15° and 21°C. Originally field-collected in Baker woodlot, (mixed deciduous woods on Michigan State University campus), these stocks usually contained mixed stages. Once the animals were adult they readily reproduced in culture, and their progeny were raised in numbers large enough to provide most of the experimental live material needed. Occasionally, stocks were replenished by field-collection; these animals were allowed a period of adjustment lasting no less than two weeks. Where pertinent, the exact provenance of experimental animals will be mentioned in the discussion of results.

After some trial and error, culture conditions were kept constant in the following ways:

a) The basic substrate consisted of plaster of Paris and charcoal, mixed with water, poured and set. Layered above it, a mixture of moist duff, decaying wood and leaves, and dark woodland soil; these materials provided cover, food and nesting materials for the animals. Distilled water was added to the duff when needed to keep it moist but not wet. Whenever the amount of faecal material exceeded that of unconsumed duff, the organic matter was replaced.

b) Powdered yeast was provided as an additional food source. It was replaced when it had either been eaten or when it had led to fungal growth. Yeast was readily accepted as food by all instars.

c) Cultures were kept in controlled-temperature cabinets (temperatures available: 10°, 15.5°, 21° and 26.6°C), in

constant dark except during observation periods.

All rearing containers were cylindrical jars of clear plastic with tight snap-on lids. Container size varied depending on the density of the populations and their estimated needs for space. Two sizes were used most often: 5 cm diameter x 4 cm high; and 3 cm diameter x 2.5 cm high.

Specific details of rearing methods are difficult to incorporate here since they were the outcome of various observations and experiments. Each rearing container harbored a population or an individual distinct from those of other containers; each container also provided a set of environmental conditions differing, to an unknown degree, from those of other containers. Throughout any rearing program minor adjustments were made constantly, based on subjective judgment - in fact, to be most efficient and hopefully optimal, manipulations had to vary between jars. But in all cases, the general procedures outlined above were followed, to assure uniformity of overall culture conditions.

Millipede cultures are subject to infestation by parasitic mites and nematodes introduced with the organic matter used as substrate. These infestations can become very heavy within short periods of time. Transferring parasitized individuals to new containers may postpone the buildup of parasite populations, but cannot solve the problem. Infested stock cultures were therefore simply discarded. Parasitized experimental cultures were also discontinued, and the records pertaining to them were not used in the calculation of results.

3. RESULTS

3.1 General Observations on the Biology of P. inconstans

A) Mating:

P. inconstans pairs assume the same general copulatory attitude described for other polydesmids (Seifert, 1932; Harz, 1962) (Figure 1). The male first approaches the female along her dorsal midline, then curves his anterior body downward and draws the female around so that the ventral surfaces of the pair are opposed. The female is held tightly by the male's legs, especially in the region where gonopods and vulvae touch, and the gonopods are inserted into the vulvae. The last four or five segments of the partners are often only loosely joined, frequently even separate.

Mating has been reported to last from approximately 10 minutes to 30 hours in other polydesmid species (Schubart, 1934a). One pair of P. inconstans, the exact location and position of which had been recorded, apparently did not move for 24 hours. Frequently, durations of several hours were recorded. In general, the animals did not readily interrupt mating activity, even when picked up with forceps, transferred from jar to jar, and subjected to mild illumination and heat.

The "outstanding sexual drive of polydesmids" was reflected in the behavior of recently molted adults in laboratory culture. Copulation frequently took place within a few hours of emergence from the molting chamber. Twice, a male was observed grasping a female which had eaten her exuvium, but was still curled in her chamber and had been artificially exposed by destroying the chamber wall. Two or

Figure 1. Mating pair of P. inconstans; male on the right, female covered and held by male's legs.

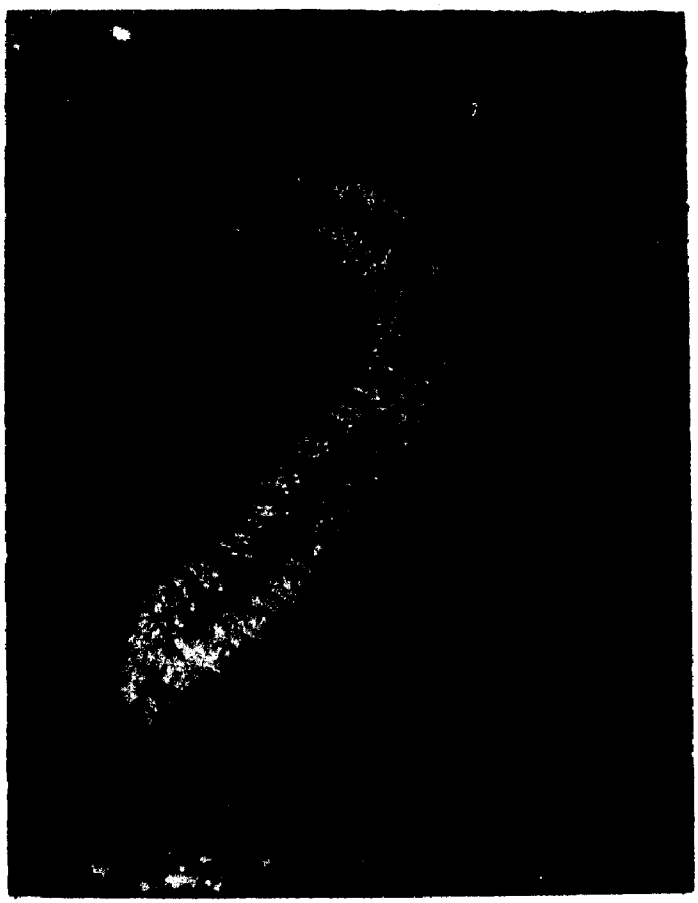

Figure 1.

more males were sometimes found clustered around the molting chambers of females which had just begun to chew their way out of the chamber. Pheromones could possibly have been involved. Schömann (1956) first discovered chemical recognition signals in Polyxenus lagurus L. and they have been implicated in conspecific behavior of iulids (Haacker and Fuchs, 1970; Haacker, 1969b), spirobolids (Haacker, 1970), chordeumids (Haacker, 1971) and glomerids (Juberthie and Tabacaru, 1968; Haacker, 1969a).

In culture, at constant temperature, mating was frequent and not at all a seasonal occurence - as might be expected.

B) Nesting:

Figure 2 illustrates the sequence of events in egg nest construction by a P. inconstans female. As a rule, the preliminary preparation of a nesting site entails the removal of debris (sand and organic matter) from a roughly circular area of the substrate. A low wall is built, and the female bends her anterior segments over the opening and deposits her eggs (Figure 2A,B,C). Then nest construction proceeds to completion. The dome that finally encloses the eggs varies in cross-section, from a half-circle to a pointed cone with virtually straight walls. While Polydesmus complanatus L. is reputed to set a "ventilation chimney" on top of the dome (vom Rath, 1891; Voges, 1916), no such structures were ever observed in P. inconstans. If undisturbed, the females covered the chamber with organic debris, an action reminiscent of camouflage (Figure 2 E,F).

Voges (1916) recounted the protective behavior of P. complanatus females, which remained with their nests for several days, and quickly

Figure 2. Construction of an egg chamber by a P. inconstans female; from a low circular wall (A) to egg deposition (B, C), closure of the nest dome (D) and camouflage of the nest with debris (E, F).

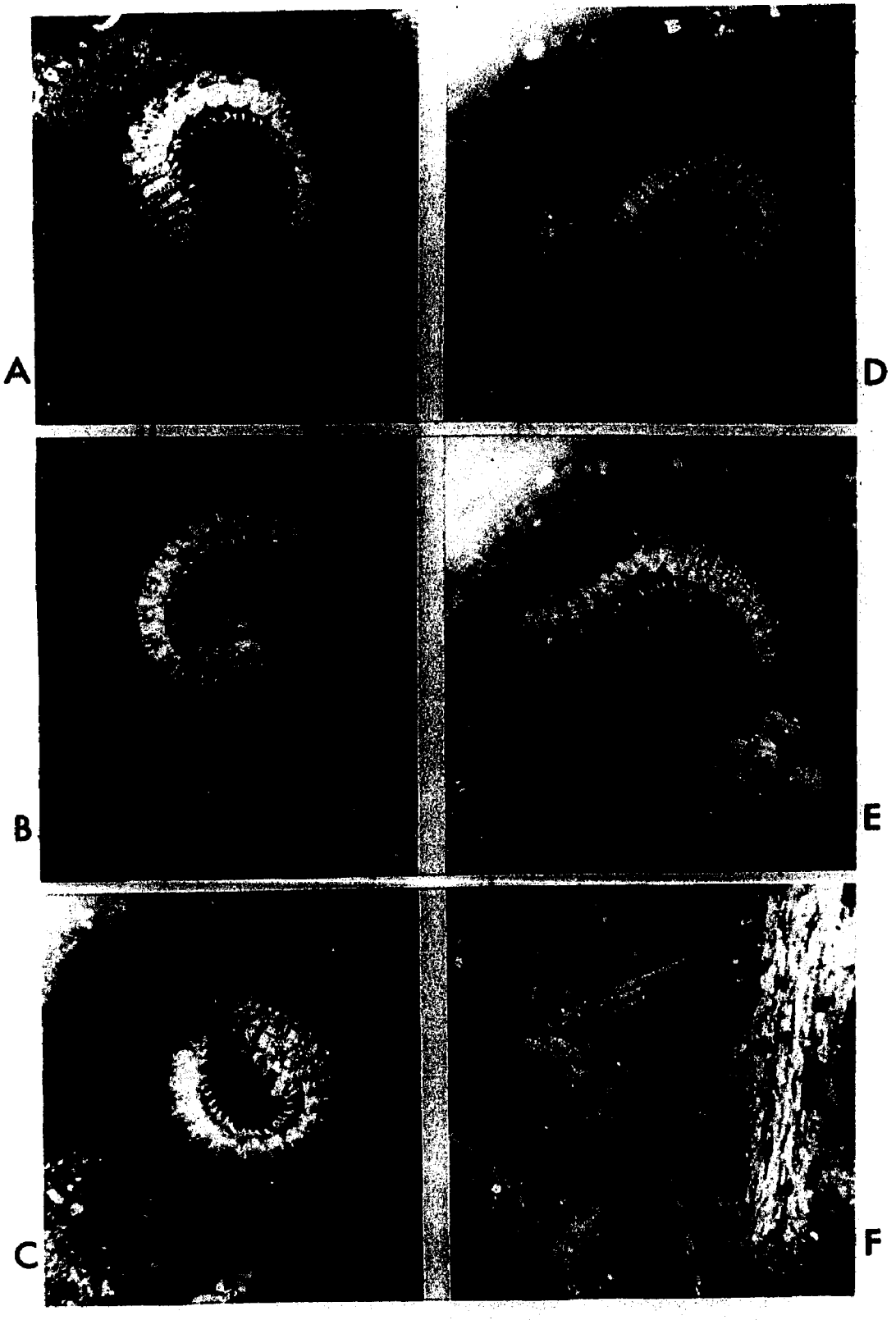

Figure 2.

returned to it if forcibly removed. P. inconstans did not show this kind of behavior.

The material used for building an egg chamber varied according to availability; most commonly, organic matter. It was mixed with soil, if there was some in the vicinity, or even with charcoal if the plaster-charcoal substrate happened to be soft enough to be ingested. Given nothing but moist sand, females still constructed chambers (by ingesting sand?) - clumsy, irregularly shaped structures which dried out and crumbled easily. Under normal conditions, the nest wall was thin but strong and elastic.

Much disputed in earlier work (Verhoeff, 1915; vom Rath, 1891; Voges, 1916), the mechanics of polydesmid nest-building are no longer in question. The female ingests material from the surroundings and the resultant faecal matter, extruded in moist droplets and patted into place by the rectal pad, constitutes the actual wall material. Females of P. inconstans could often be observed "foraging" in the vicinity of a chamber, all the while keeping uninterrupted contact with the edge of the nest by means of their posterior leg pairs.

Nesting substrates chosen by P. inconstans in culture appeared to have one common characteristic; they tended to be relatively smooth, and solid. The plaster-charcoal substrate, smooth pieces of wood and undecomposed pieces of leaves (Figure 3), or the container wall were utilized (in order of preference, as calculated from a total of 500 observations). Seifert (1932) stated that polydesmids in general tend to nest on smooth substrates. The only egg chambers found in field localities during the present study were built on smooth-surfaced branches and bits of wood.

Figure 3. Egg chambers built on wood and leaf debris.

Figure 3

C) Molting:

All larval stages of P. inconstans constructed molting chambers much in the way that egg chambers are made, except that the former were built from the inside. In later stages of construction, the rectal pad and last pair of legs could often be seen at work around the small opening still left to be closed.

More often than not, already existing structures were used or incorporated in the chamber design. One isolated individual molted three times (from I to IV) inside the same seed capsule, until it finally outgrew the space available. All instars took advantage of large pieces of organic matter; they crawled underneath and enclosed themselves by a cylindrical wall which connected debris and solid substrate beneath.

Equal-aged, grouped individuals of P. inconstans, e.g. clones from one egg nest, tended to undergo molts at the same time and in the same area of the culture. Rather than active aggregation, this may simply represent a choice of the one most suitable spot in a somewhat heterogeneous environment. Cast skins were always consumed before the new instars emerged from their chambers. To emerge, they usually ate an amount of chamber wall just sufficient to allow passage of the body. Blower (1974) observed an extended period of fasting (maximum of 30 days) prior to the onset of ecdysis in Ophyiulus pilosus (Newport). Cessation of feeding prior to a molt was not timed in P. inconstans, but is probably a general occurrence in invertebrates; centipedes and isopods (pers. obs.), and Collembola (Palévody, 1974; Joosse, 1975), to name a few.

Duration of the molting act as such - specifically, from

completion of the chamber to emergence of the next instar - was timed in isolated P. inconstans at 15.5° and 21°C. Table 2 gives the results. Ecdysis from instar I to instar II was of shorter duration than later ecdyses. Increases in molt duration were slight but constant from stage to stage. The last ecdysis, from VII to adult, was of the longest duration at both temperatures. In general, the higher temperature decreased the time needed to complete a given ecdysis.

Table 2. Mean duration of molts of P. inconstans at two temperatures. Time refers to days elapsed between comple tion of a molting chamber and emergence of the next instar.

		INSTAR						
T°C	Days	I	II	III	IV	V	VI	VII
15.5	mean	5.8	6.4	6.9	7.2	7.5	8.7	12.0
	± SD	0.9	1.1	0.9	1.1	1.1	2.0	2.0
	n=	30	30	30	27	22	27	28
	range	4-8	4-9	5-8	5-9	5-9	5-13	9-16
21	mean	3.4	4.3	5.0	4.6	5.7	7.1	9.7
	± SD	0.6	0.9	1.2	1.1	1.2	1.1	1.9
	n=	14	14	14	14	14	14	10
	range	3-5	3-6	4-8	4-8	4-7	5-9	8-13

D) Predation and oophagy:

Predation on P. inconstans was discovered purely by accident: a pair of adults in culture disappeared overnight, after new and not very thoroughly examined duff had been added to their culture jar. What remained were some single segmental rings of P. inconstans and a large and active carabid larva (Pterostichus melanarius).

Time constraints prohibited large-scale quantitative observations, but as a point of interest several qualitative studies were then undertaken. During field collections in late summer and fall, any potential predators encountered were brought back to the laboratory. They were offered whatever stages of P. inconstans were available and, where appropriate, a choice of other prey species.

All predators were obtained from habitats known to harbor P. inconstans: Baker woodlot, litter and logs; the wooded area of the Water Quality Management site near Michigan State University and an orchard near Grand Rapids, Michigan. Experimental conditions included the use of plaster-charcoal substrate in the usual clear plastic containers, 5 cm diameter; and a few small pieces of decomposed wood - to give some food to P. inconstans, but not enough to cover the floor of the container. Observation intervals varied from 24 hours to 3 days. Feeding rates could not be calculated; frequently, all prey had been consumed at the time of observation, without accurate checks on the time span involved. Total observation periods also varied between individual predators (range from one to three weeks, after which time most of them were still alive and feeding). The results are summarized in Table 3.

Table 3. Summary of acceptance of various prey by larval and adult predators.

	Polydesmus inconstans								Ophyiulus pilosus			Collembola			
	I	II	III	IV	V	VI	VII	VIII	small	med.	large	F.	cand.	H.	arm.
Amara sp., ad.	-	0	-	-	-	-	0	0	0	-	-		-		-
Pterostichus melanarius, ad.	+	+	++	++	+++	+++	+++	+++	++	0	0		+		+
Staphylinidae, ad.	+++	-	+++	-	-	0	-	-	-	-	-		-		-
Pterostichus melanarius, larv.	+	++	++	++	+++	+++	+++	+++	-	-	-		+		+
Tidabius tivius, ad.	++	-	-	-	-	-	-	-	-	-	-		+++		-

-: not offered
0: not accepted
+: occasionally accepted
++: usually accepted
+++: always accepted

CARABIDAE, ADULTS:

Pterostichus melanarius Illiger:

Collected in Baker woodlot and Grand Rapids (n=9). Offered: *Folsomia candida* (Willem) and *Hypogastrura armatus* (Nicolet) (Collembola); *P. inconstans* I through VIII; *Ophyiulus pilosus* (Newport) of "small, medium and large" sizes.

All individuals of this species shared a common preference: the larger stages of *P. inconstans*, particularly adults and subadults. Depending on prior feeding history, a maximum of ten adults and/or subadults were consumed by one beetle in 24 hours. Also accepted were smaller stages of *P. inconstans*, small *O. pilosus*, and the collembolan *H. armatus* (a sluggish species).

Figure 4 illustrates the segmental debris left by a carabid feeding on millipedes.

Surprisingly, two of the carabids laid eggs (one and three eggs respectively). Two of the eggs hatched. The larvae were offered a mixture of *F. candida*, *H. armatus*, and instars I, II and III of *P. inconstans.* Of these prey, *Folsomia* was not eaten. *Hypogastrura* was accepted, as were all three stages of the millipede. The greatest number of prey consumed by one larva within 24 hours were: four *Hypogastrura* and all millipedes offered (five each of stages I, II and III).

Amara sp.:

Collected in the water quality management area (n=11). Did not accept any species or stage of diplopods as food. Discontinued after one week.

Figure 4. Debris of partly chewed millipede segments left by a predatory carabid.

Figure 4.

STAPHYLINIDAE, ADULT (unidentified):

These observations of woodlot-collected beetles lasted for six days (number of beetles = 3). Offered P. inconstans stages I, III and VI. Instars I and III were always accepted, but never instar VI (about twice as large as the predators).

CARABID LARVAE

Pterostichus melanarius Illiger:

Collected in Baker woodlot in August (n = 9). Offered: all stages of P. inconstans, and the Collembola F. candida and H. armata. All were accepted, especially the larger sized millipedes. These larvae were as voracious as the adults of the species, and extremely active. Five or six large millipedes, plus a few small stages, were commonly eaten within 24 hours.

CHILOPODA

Tidabius tivius (Chamberlin):

T. tivius is a diminutive lithobiid (7-9 mm), collected in Grand Rapids, which has been routinely reared in the laboratory on a diet of F. candida. Adults of this centipede were observed for three consecutive 24-hour periods, in the following experimental setup:

a) Ten males and ten females, starved for five days, versus ten individuals of each sex which had been well fed. Every 24 hours, each of them was offered 20 P. inconstans, stage I.

b) The same replication as in a), also fed and starved. Each was offered 20 P. inconstans, stage I, and 20 F. candida as alternative prey.

The weights of individual predators were not recorded. Possible effects of having fed on F. candida, the alternative prey in b), were not known. Rather than performing questionable analyses, only the mean number of prey consumed were calculated.

a) In Table 4, starved and fed T. tivius of each sex are opposed. Starved animals consumed more prey in 24 hours, as might be expected, but standard deviations of the means were generally large. Little if any difference became apparent between the sexes.

Table 4. Mean number (± S.D.) of first instar P. inconstans consumed by adult Tidabius tivius (Chilopoda) in each of three consecutive 24-hour periods.

	Females		Males	
	starved	fed	starved	fed
0 - 24 hours	7.4 ± 6.3	5.8 ± 4.0	8.4 ± 6.0	3.3 ± 2.6
24 - 48 hours	7.6 ± 4.8	6.2 ± 4.9	7.9 ± 3.3	4.7 ± 1.7
48 - 72 hours	9.2 ± 7.8	3.2 ± 2.2	6.4 ± 4.2	5.7 ± 4.1

b) Table 5 shows that, given a choice of prey, the centipedes preferred the Collembola to the millipedes, with starved individuals consuming more than fed individuals. Since neither weights nor physiological condition of the animals were known, the relatively high consumption rate of fed females (vs. fed males) cannot with certainty be attributed to sex.

Table 5. *Tidabius tivius* given a choice of prey species: number of prey eaten in each of three consecutive 24-hour periods (means ± S. D.).

	Starved females			Fed females		
DAY	1	2	3	1	2	3
P. inconstans I	2.6	1.6	0.5	1.0	0. 8	1.1
	±2.2	±1.9	±1.2	±1.1	±0.8	±0.9
F. candida	15.2	13.4	8.0	11.4	11.2	6.9
	±3.7	±3.7	±2.9	±5.1	±3.6	±1.8
	Starved males			Fed males		
P. inconstans I	1.9	1.6	1.0	0.8	0.3	0.8
	±2.5	±1.6	±0.9	±0.9	±0.5	±0.9
F. candida	13.6	10.4	8.1	5.5	5.7	4.8
	±4.2	±4.5	±2.0	±3.7	±2.5	±1.6

Given a choice of prey, *T. tivius* still occasionally fed on *P. inconstans* I. First instars of the millipede are white and resemble *F. candida* in size. The millipedes were certainly not preferred over the Collembola: their continued, but decreased, acceptance by the predator may represent accidental attack rather than purposeful feeding.

Feeding habits of centipedes have most often been investigated in laboratory studies, with a limited number of prey species offered as food to the predators. Roberts (1956) and Lewis (1965), however,

analyzed the gut contents of field-collected chilopods: none were found to contain remains of diplopods. All eight centipede species investigated had apparently been feeding on mites, opilionids, spiders, and other centipedes.

DIPLOPODA

Diploiulus coeruleocinctus (Wood) and Ophyiulus pilosus (Newport):

Ten adult individuals of each species were introduced to culture jars containing eggs of P. inconstans. In order to avoid starvation effects, yeast was also added. Yeast was already known to be an acceptable food for both species.

Both iuloids consumed eggs of P. inconstans, whether they were freshly laid or had developed to the stage where the chorion had ruptured. Generally, the large Diploiulus consumed more than the slender Ophyiulus in 24 hours (a maximum of 80 eggs versus a maximum of 28 eggs). Both species continued feeding on the eggs until none were left, or, in the case of developed eggs, until these began hatching.

Given intact egg chambers, both iuloids also attacked those. O. pilosus slowly consumed the chamber wall, and some of the eggs still remained untouched after nine days. Of eight nests offered to eight D. coeruleocinctus, no traces of either nests or eggs remained after four days.

These results are tentative. It is probable that exposed eggs will be eaten, since P. inconstans occasionally cannibalizes its own eggs. Feeding on intact nests, on the other hand, could indicate a need for organic matter rather than an attempt to get at the eggs.

Variation of experimental conditions and accurate quantification

are clearly needed for all observations on predation and oophagy. Specifically, proof of predation on P. inconstans in the field is of utmost importance. Once that proof has been obtained for a number of potential predators (e.g. through gut content analyses), laboratory-derived feeding rates and preferenca will gain greater validity.

3.2 Growth and Development

A) Methods:

As a rule, live animals for the study of stage duration were obtained from laboratory stocks reared at the same temperature as that used for a given experimental series. But this constancy of temperature could not always be maintained. For observations at 26.6°C animals from 21°C stocks had to be used, because attempts to rear stocks at 26.6°C were unsuccessful. For experiments at 10°C, individuals grown at 15.5°C supplemented, when needed, the slow-growing stocks kept at 10°C. For experiments at 15.5° and 21°C, stocks reared at those respective temperatures were available.

Freshly molted individuals of each stage were obtained by checking the stocks once a day; thus the day of entry into a stage was known, and was recorded as day no. 1 in the development of newly emerged instars.

At each temperature, for instars I through VII, replicate culture jars were made up in the usual way (see Section I.2) and ten newly-molted individuals were introduced to each. With only four exceptions (due to the depletion of stocks of the right age) a total

of about 100 animals of each stage were observed at each temperature.

At intervals of 1 to 3 days the cultures were then checked for molting activity, and all animals that had emerged from their chambers (and now belonged to the subsequent instar) were counted, sexed and removed. From instar IV on, each of the replicate containers was stocked with five males and five females. In a few instances equal numbers of each sex were not available, but the overall sex ratio per series was kept as close to unity as possible.

For the study of embryonic development, some of the many egg batches laid by paired females were set aside and observed. These eggs were kept at each of the three temperatures at which they had been laid: 10°, 15.5° and 21°C. By removing only the top of the nest dome, embryonic development could be observed without completely depriving the eggs of their protective enclosure.

B) Embryonic development and hatching

At the time they are laid, eggs of P. inconstans are white, opaque, and measure 0.4 mm in diameter. They soon become ovoidal, and the chorion splits after a temperature-dependent interval of embryonic growth (Table 6). The embryo is well visible through its translucent membranes (Figure 5). Hatching occurs soon thereafter at 21°C, but is retarded by lower temperatures (Table 7). At 10°C in particular, embryonic life may last approximately 3 months.

Hatching begins with slow movements of the embryo. It stretches from its curled position - with legs held straight back along the body - until the head and most of the rump are freed from the chorion caps. This first phase may last from 7 min to half an hour (n = 6

Figure 5. Egg development and hatching. A: freshly laid eggs; B: chorion ruptured, translucent embryos visible; C, D: larva freeing itself from chorion; E: first instars after feeding has begun.

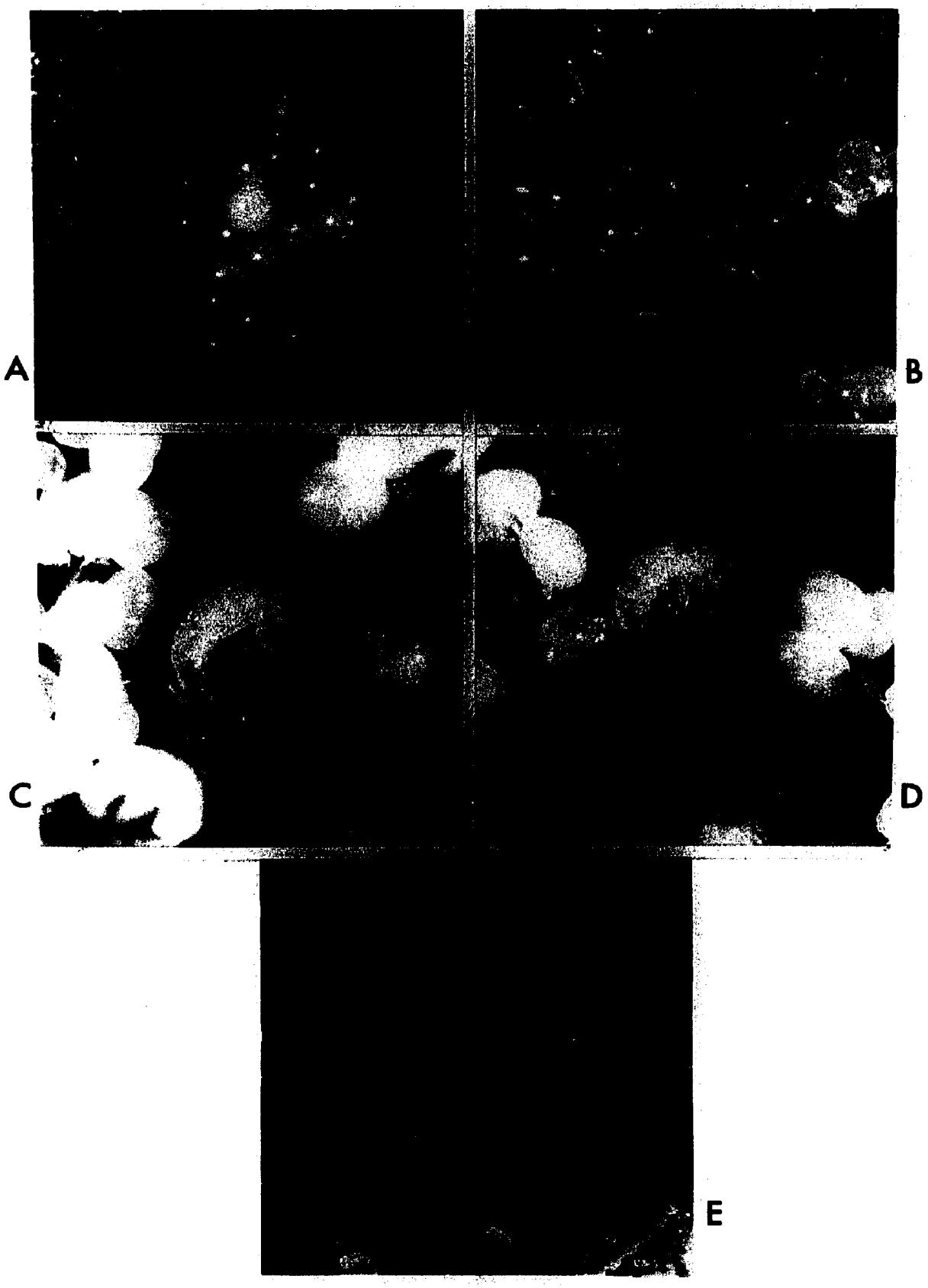

Figure 5.

observations), and is followed by alternating periods of immobility and further stretching. During the next 30 to 100 minutes (n = 8), the legs are brought forward to their normal position, and the tip of the abdomen is freed from the gaping chorion shells. After a total of 1 to 2 hours (n = 5) the larva is capable of walking about. Figure 5 illustrates some of the stages discussed above.

Table 6. Number of days between deposition of eggs and rupturing of the chorion.

	10°C	15.5°C	21°C
mean days ± S. D.	29.5 ± 2.1	12.3 ± 0.7	8.2 ± 0.7
range	26 - 33	11 - 13	7 - 9
n (batches observed)	15	12	20

Table 7. Mean total duration of embryonic development, from egg deposition to the time when the majority of each batch have hatched.

	10°C	15.5°C	21°C
mean days ± S.D.	82.6 ± 3.4	18.6 ± 0.9	12.8 ± 0.8
range	76 - 87	18 - 21	11 - 14
n (batches observed)	18	19	17

In nests which had been opened for observation of embryonic

development, hatched larvae began leaving the nest enclosure soon after free movement had been attained. This may not be the normal sequence of events. In chambers built against the transparent container wall, hatching could be observed while the nests were intact: a maximum of 6 days (at 10°C) of slow milling-about of the larvae inside the chamber could follow the onset of hatching.

Larvae emerged from intact nests by chewing their way out. Figure 6 illustrates that several such escape holes may be made, in various locations - although most frequently all larvae escaped through a single hole made near the bottom of the chamber dome. The larvae began feeding within a day of hatching; the dark gut contents were then visible through their white dorsum (Figure 5).

C) Post-embryonic development

Since intervals between observations often encompassed more than 24 hours, the data on stage duration were summarized at five - day intervals. The median days of these time spans were then used to calculate mean durations: e.g., if five animals molted to the next instar between days 41 and 45, day 43 was used as the emergence day for all of them.

Table 8 details the results. It should be noted that mean duration of each stadium represents the amount of time spent in a stage plus the amount of time needed to undergo ecdysis (from day 1 of a stadium to day 1 of the next stadium).

Animals reared at 10°C developed extremely slowly. With the exception of stadium I, durations varied greatly between individuals. At 15.5° and 21°C deviations from the means were quite small, in all

Figure 6. Escape holes made in chamber walls by first instars of P. inconstans.

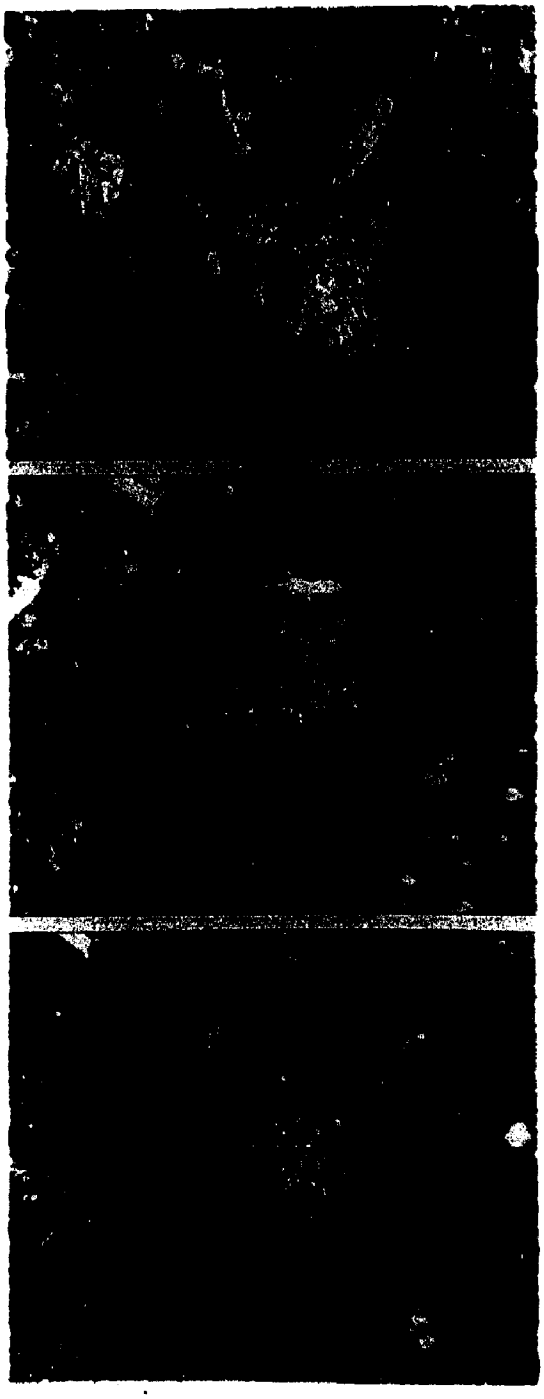

Figure 6.

stadia except VII. Illustrated graphically, (Figure 7), the data clearly show that there was little difference between the developmental rates at these two temperatures. At 26.6°C mortality was so high that only a few records of stadium duration could be obtained (Table 8). The ten animals that survived stage IV into stage V showed an interesting lengthening of stadium duration by comparison to lower temperatures. But for valid conclusions, the observations would have to be repeated under different conditions: alteration of types and layering of substrates, or prior acclimation of test animals, should be considered in this regard.

Since there are indications that male polydesmids mature faster than females, part of the results were tested for sex-specific differences in stadium duration. Given the variability encountered (Table 8), major differences seemed to occur only in the penultimate stadium and only at 15.5° and 21°C.

Variances and coefficients of variation were both unequal, and Welch's (1938) approximate degrees of freedom and Behrens (1929) t-like test statistic were applied to the data. At both temperatures, the duration of stadium VII proved to be significantly greater in females that in males ($p < 0.0005$).

Two other observations provided support for these test results:

a) A number of P. inconstans were reared in isolation from the day of hatching to the day of adulthood. Replication was low, and no statistical tests were performed. But again, mean duration of the entire life cycle was shorter in males than in females, at both 15.5° and 21°C (Table 9).

b) Some of the clones which were routinely reared to adulthood as

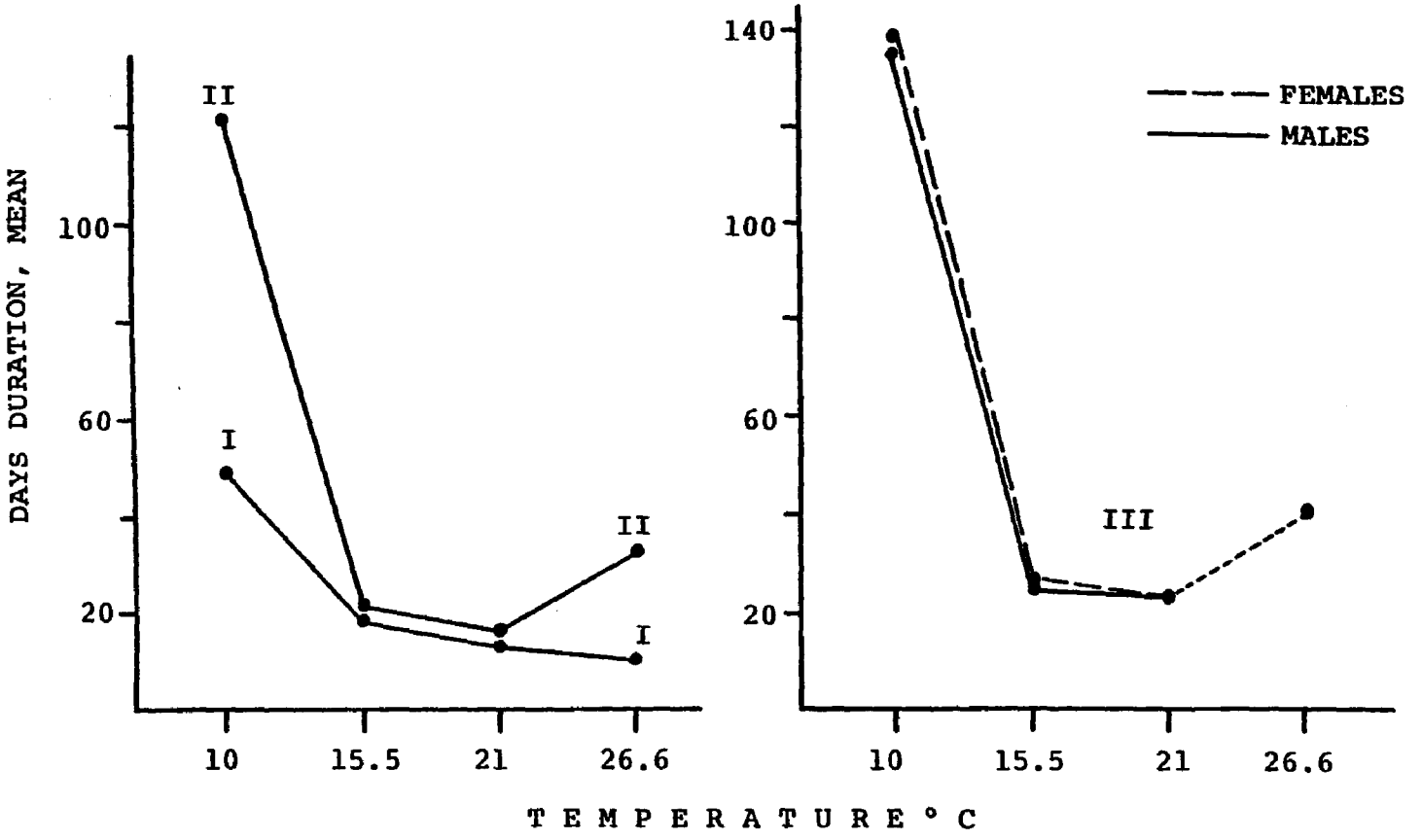

Figure 7. Stadium durations at four temperatures (26.6°C included if any animals survived; for S.D. of means see Table 8).

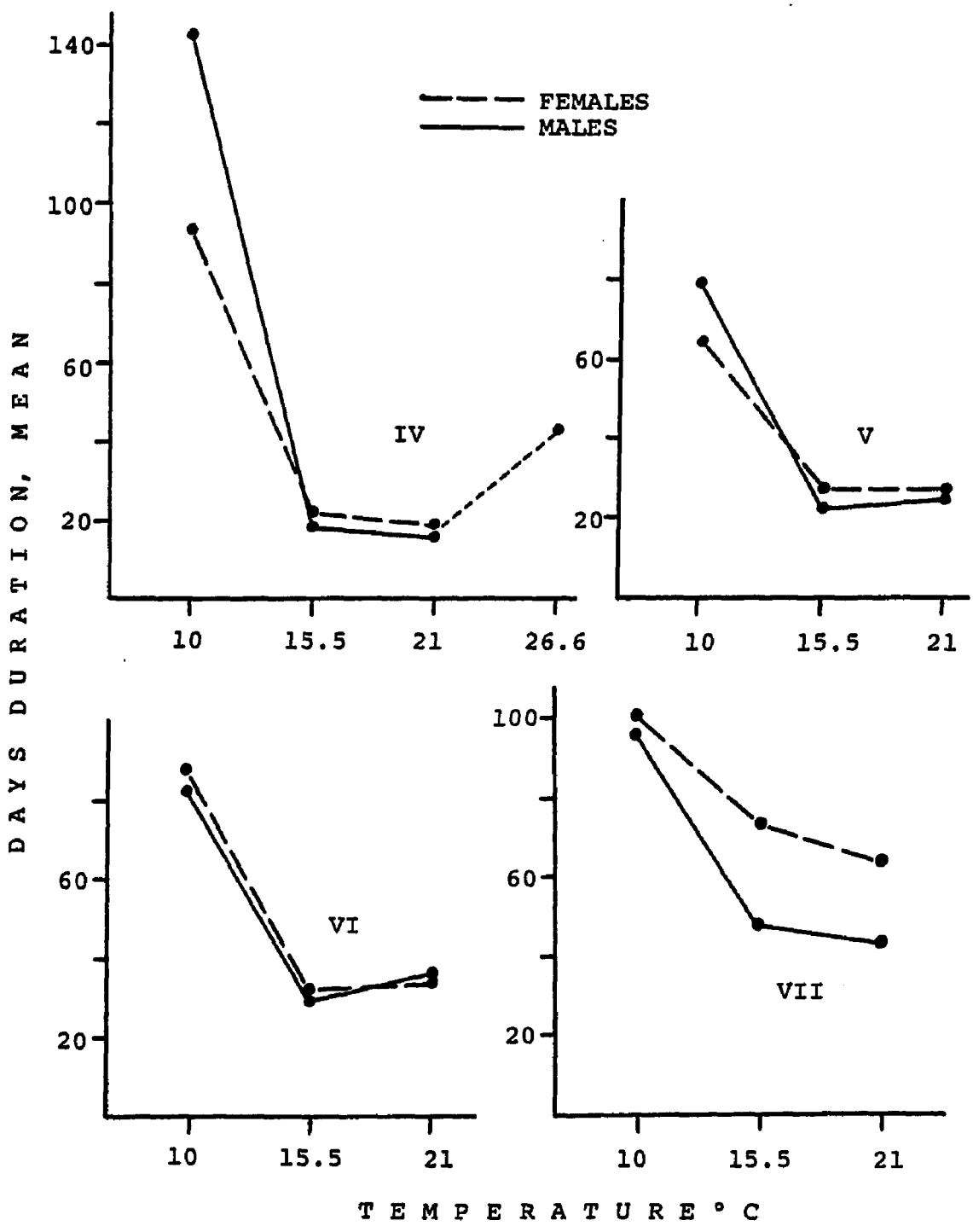

Figure 7 (cont'd).

Table 8. Mean duration, in days, of the stadia at four temperatures.

		DAYS											
STADIUM		I	II	♀ III	♂	♀ IV	♂	♀ V	♂	♀ VI	♂	♀ VII	♂
	n	44	81	50	49	42	52	50	49	49	47	23	24
10°C	mean	48.6	121.3	138.5	135.1	93.4	142.4	64.6	79.1	88.4	82.9	101.5	96.1
	± SD	5.6	62.5	27.2	21.0	63.8	57.0	26.3	42.5	37.5	28.4	29.9	26.9
	n	95	95	46	53	50	48	50	49	48	50	20	23
15.5°C	mean	18.9	21.5	25.6	26.3	22.5	19.7	28.1	23.4	32.8	30.2	73.7	48.2
	± SD	3.0	3.2	5.7	4.3	2.9	2.4	7.7	8.0	6.9	5.4	23.7	20.4
	n	99	97	52	46	49	50	49	40	49	47	38	48
21°C	mean	13.3	16.5	23.7	23.0	19.0	16.6	28.0	26.3	35.8	36.1	64.5	43.3
	± SD	1.4	3.8	4.2	6.3	2.9	2.3	7.1	10.4	7.8	7.1	18.3	15.6
	n	3	1	2		10							
26.6°C	mean	10.7	(33)	40.5		43.1							
	± SD	0.9				6.1							

part of stock culturing were also checked for the first appearance of adults. At 21°C (n=5 clones) males appeared first in all of them, maturing earlier than females by a mean of 44 days (range 15-80 days). At 15.5°C (n = 17 clones) males matured earlier in 15 of the cultures, preceding females by a mean of 27 days (range 5-58 days).

Males thus tend to mature earlier than females, mainly due to a relatively short duration of stadium VII. In the field (Section II. 2.4.) a similar trend was apparent in fall samples: among individuals maturing in September-October, there was a preponderance of males which lasted, however, no longer than 5 to 6 weeks.

Table 9. Mean total duration, in days, of the post-embryonic development of P. inconstans reared in isolation from hatching to adulthood.

		mean ± S. D.	n=
15.5°C	female	241.9 ± 41.7	12
	male	213.6 ± 31.6	16
21°C	female	190.0 ± 38.2	10
	male	168.2 + 26.2	15

D) Sex ratios in culture:

Seven egg batches, produced by paired, laboratory-reared females, were reared until all progeny had reached instar IV. Mortality during that time was not assessed. Thus, only the final number of individuals in each clone was known (Table 10). They were killed and sexed

(including those extracted from molting chambers).

Percent females per clone ranged from 39.0 to 59.5, with a mean of 48.5%. Sex ratio of progeny produced in culture was thus close to unity.

During the time when stock animals were used for observations on instar duration and mortality, this observation was indirectly confirmed. More than 2500 laboratory-reared individuals were needed for these observations; there was never a dearth of animals of either sex, from instar IV to VII (although there was, eventually, a lack of animals of specific instars). All stocks appeared to contain roughly equal numbers of each sex.

Table 10. Percent females in laboratory-reared clones.

Clone no.	1	2	3	4	5	6	7
no./clone	37	71	47	56	39	25	39
% females	59.5	59.2	44.7	48.2	48.7	40.0	39.0

3.3. Survival

A) Methods:

The records obtained for the durations of immature stadia of *P. inconstans* were also used to estimate temperature-specific survivorship. Mortality in these cultures was not assessed on a daily basis. Dead *P. inconstans* were difficult to locate without severe disturbance of the cultures and their inhabitants, especially if death had occurred inside a molting chamber. Therefore, 2 to 4 weeks after the ecdyses of the presumed last live individuals of a given stage, the

cultures were thoroughly examined for dead animals. Virtually all of them could be located.

B) Survival of immatures

The data for immatures were expressed as total percent survival per stage and temperature. Rather than time-related mortality rates, they thus reflect the survivorship potential of individuals from the time they entered a stage to their emergence as the next higher instar. Approximately 100 individuals of each stage were observed, the exception being stage VII of which not enough were available.

Survival at 26.6°C was so poor that instar VII was not subjected to that temperature. Stage IV had the highest survival percentage (10%), while no V and VI, and only very few I, II and III, survived (Table 11).

At 15.5° and 21°C survival frequently reached 100%, with little evidence of differences between the two temperatures or between instars. Overall, both males and females appeared to survive equally well (Table 11).

Only 44% of the instar I reared at 10°C successfully molted to instar II. Percent survival then rose to 79% for II, and finally reached levels of 90 to 98% similar to those recorded at 15.5° and 21°C.

High mortality of small stages at 10°C may be at least partially an artifact. Toward the very end of these observations the substrate used for instars I and II cultures was found to differ slightly from that used for other instars: the duff was coarser, contained less leaf mold and organic debris and seemed to have a lesser capacity for water

retention. If first and second instars were indeed forced to molt under inadequate conditions, then mortality of small stages would have been overestimated.

Survival data are graphically summarized in Figure 8, without differentiation between sexes. If one disregarded the data for I and II at 10°C, survivorship was high - virtually equally so - at temperatures ranging from 10° to 21°C. High mortality at 26.6°C may be interpreted as a result of the long periods of exposure of animals to that temperature: there is evidence from board captures in the field (see Section II.3.3.) that brief periods of high temperature can be endured by P. inconstans.

C) Survival of adults

P. inconstans used in studies of temperature-dependent reproduction (Section I.3.4.) stemmed from laboratory stocks. They were collected and paired upon completion of their final molt (day 1 of adult life). Since their day of death was known, the records were used to assess the effects of temperature on adult longevity.

At 21°C, observations were carried through to the death of all individuals. At 10° and 15.5°C, the study was discontinued on day 330. At that time, 4 females and 6 males were still alive at 10°C; 2 females and 1 male were alive at 15.5°C. Longevity was calculated without regard to these survivors, and longevity means are therefore approximate rather than exact values.

Figure 9 shows that between 10° and 21°C the relation between longevity and temperature appears to be linear, for both males and females; and that 26.6°C probably comes close to the upper lethal

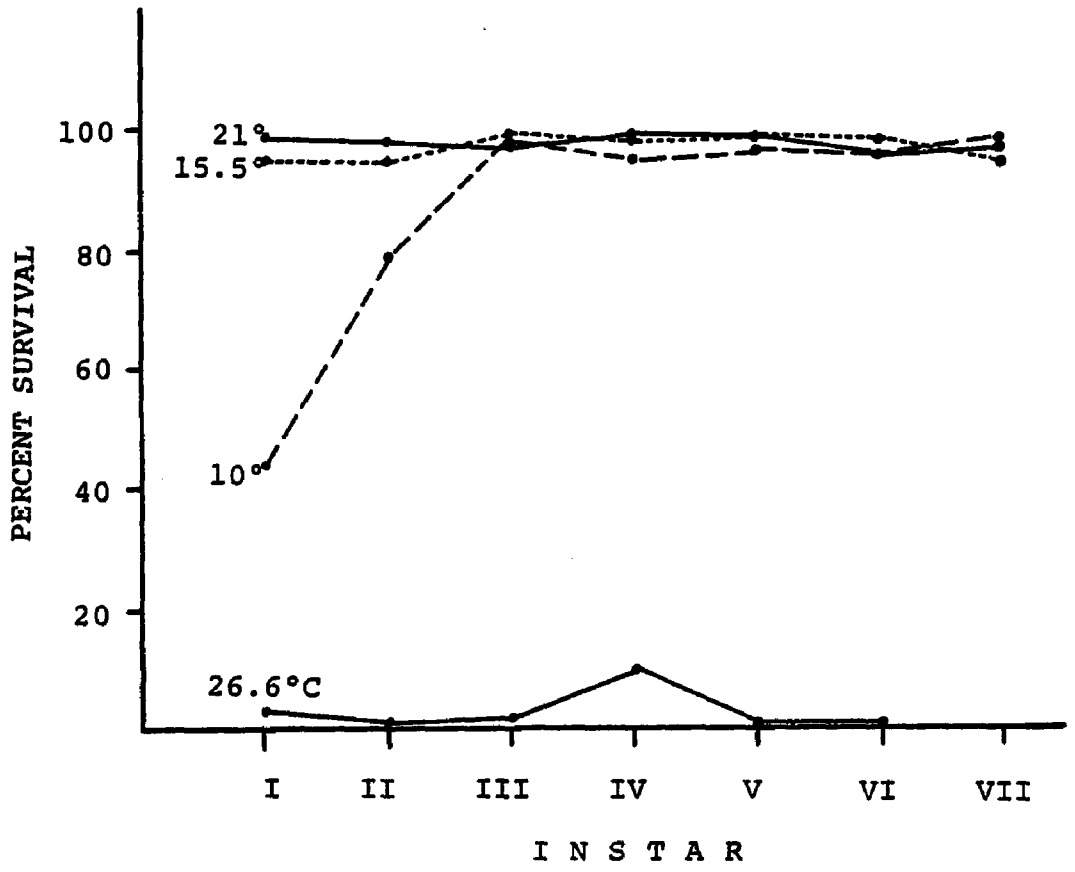

Figure 8. Percent survival of immatures at four temperatures.

Table 11. Survival of immatures at four temperatures, calculated from the number of animals of a given stage that successfully molted to the subsequent stage.

		INSTAR										
		I	II	III	IV		V		VI		VII	
					♀	♂	♀	♂	♀	♂	♀	♂
	n	100	100	100	46	54	51	51	50	50	24	25
10°C	% surviv.	44.0	79.0	99.0	91.3	96.3	98.0	96.1	98.0	94.0	95.8	96.0
	n	100	100	100	51	49	50	50	49	51	29	26
15.5°C	% surviv.	95.0	95.0	99.0	98.0	98.0	100	98.0	98.0	98.0	100	92.0
	n	100	99	100	50	50	50	40	50	50	40	50
21°C	% surviv.	99.0	98.0	98.0	98.0	100	98.0	100	98.0	94.0	95.0	95.0
	n	100	100	100	100		100		100			
26.6°C	% surviv.	3.0	1.0	2.0	10.0		0.0		0.0			

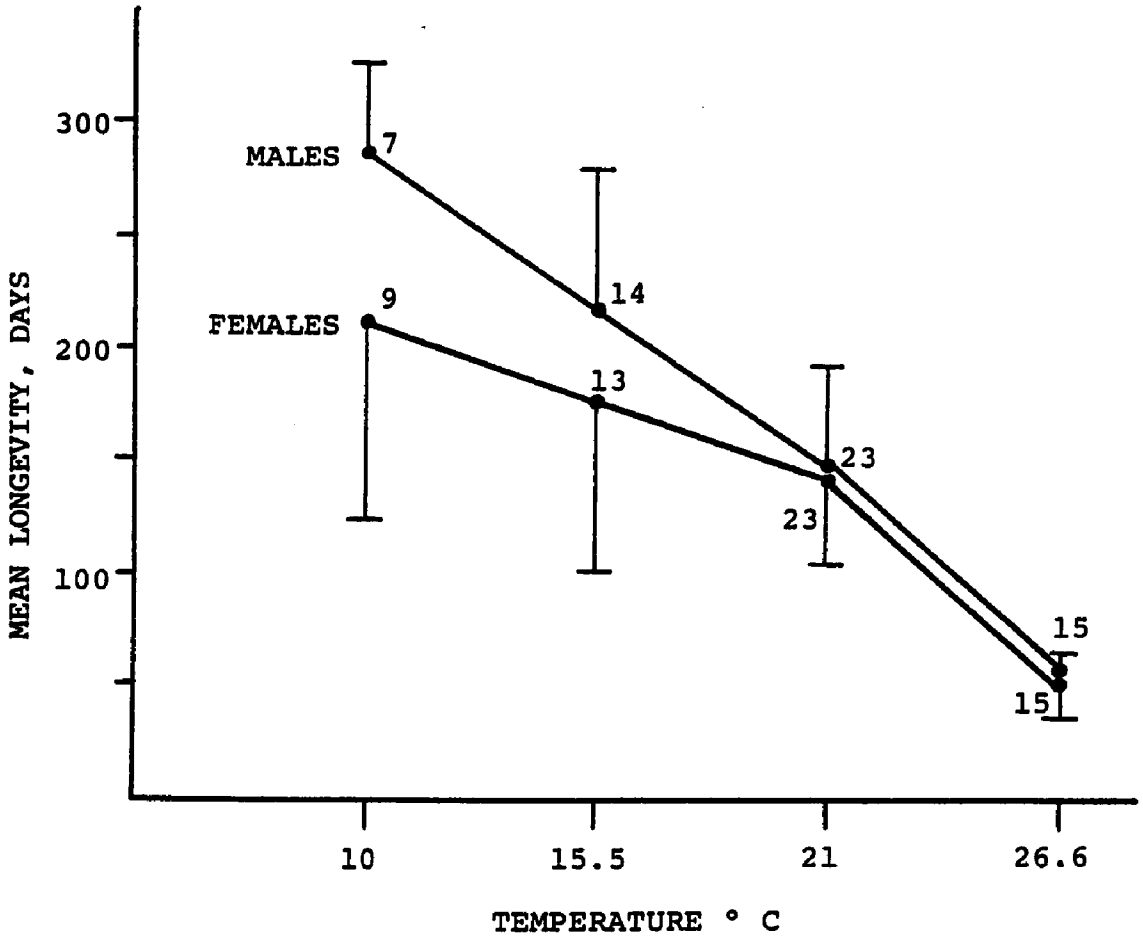

Figure 9. Longevity of adults at four temperatures (means ± S.D.). Numbers in the figure indicate the number of replicates per temperature and sex.

temperature for P. inconstans. A possible dichotomy in longevity between males and females at 10° and 15.5°C was tested with Behrens' (1929) t-statistic. At 10°C males lived significantly longer than females ($p < 0.05$), but not so at 15.5°C ($p < 0.1$).

The progressive mortality of females over time is illustrated in Figure 10. At the two lower temperatures the lines are open-ended because observations had to be discontinued after 330 days, but survival percentages were calculated from the total original number of replicates. The life span of adult females in culture apparently can exceed 330 days at 10° and 15.5°C.

Further aspects of adult longevity will be discussed in later sections, particularly those pertaining to the reproductive potential of P. inconstans.

3.4. Oviposition and fecundity

A) Methods

Freshly-molted adults were collected from 15.5°C stock cultures and distributed, in pairs, over three temperature regimes. At 10°C, 13 pairs were established; 15 pairs were incubated at 15.5°C, and 45 pairs at 21°C. From those 45 pairs, 22 were randomly selected for assessment of sperm storage capability: after the females had oviposited twice, the males were removed from their cultures. A simple chart (Figure 11) summarizes the experimental design. At 21°C all animals were observed until death, but at 10° and 15.5°C the last survivors were discontinued after 330 days.

A second experimental series was established with animals collected in Baker woodlot between mid-March and mid-April 1979. Most of the collected females were paired either with field-collected or

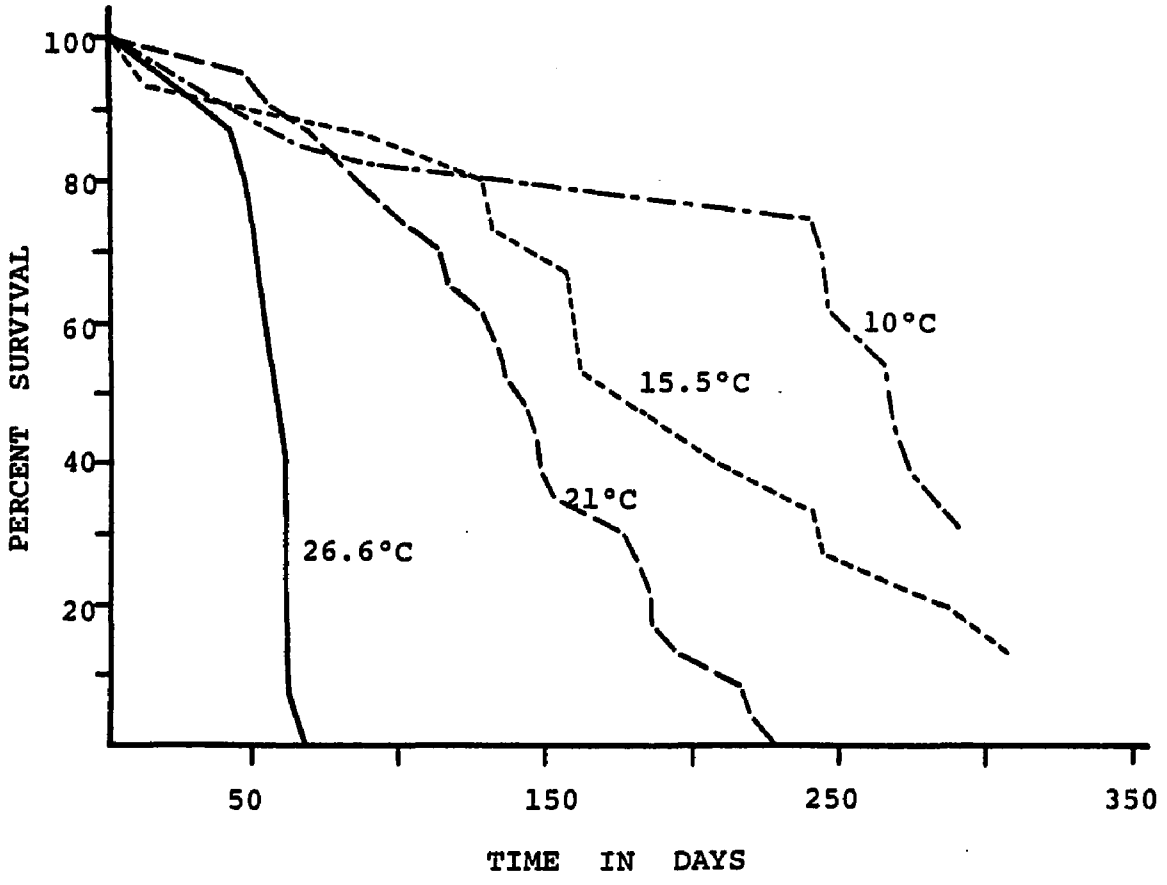

Figure 10. Survival of paired, laboratory-reared adult females at four temperatures.

with laboratory-reared males, while some were isolated immediately after collection. Replication and experimental history of all collected animals are summarized in Figure 12.

Rearing methods followed the general rules outlined previously. The cultures were observed at intervals of 2 to 4 days. Those that became infested with mites were discarded and the data pertaining to them were not used. The replications given in Figures 11 and 12 include only those females and pairs that did not become parasitized.

In both series (laboratory-reared and field-collected) records were kept of the dates of oviposition, the choice of nesting sites, the number of eggs laid, and of egg viability.

In general, the parents were transferred to a new container every time an egg chamber was discovered. Simple inversion of the old jar over a new one proved to be the fastest means of transfer, and did not appear to cause even slight disturbance to the parents. Whenever an egg nest had been built on loose debris, the intact chamber (on its substrate) was transferred to a different jar.

Egg chambers left in a jar after removal of the parents were kept moist by occasionally adding a drop of water to the substrate on which they had been built. The eggs were allowed to hatch; the larvae were then counted and the chamber was opened and checked for any undeveloped eggs. Egg chambers invaded by fungus were teased apart, so that the eggs could be enumerated. If there were indications that manipulation or unusual culture conditions had played a role in egg development, the eggs were counted but the data on viability were not included in the summary of results.

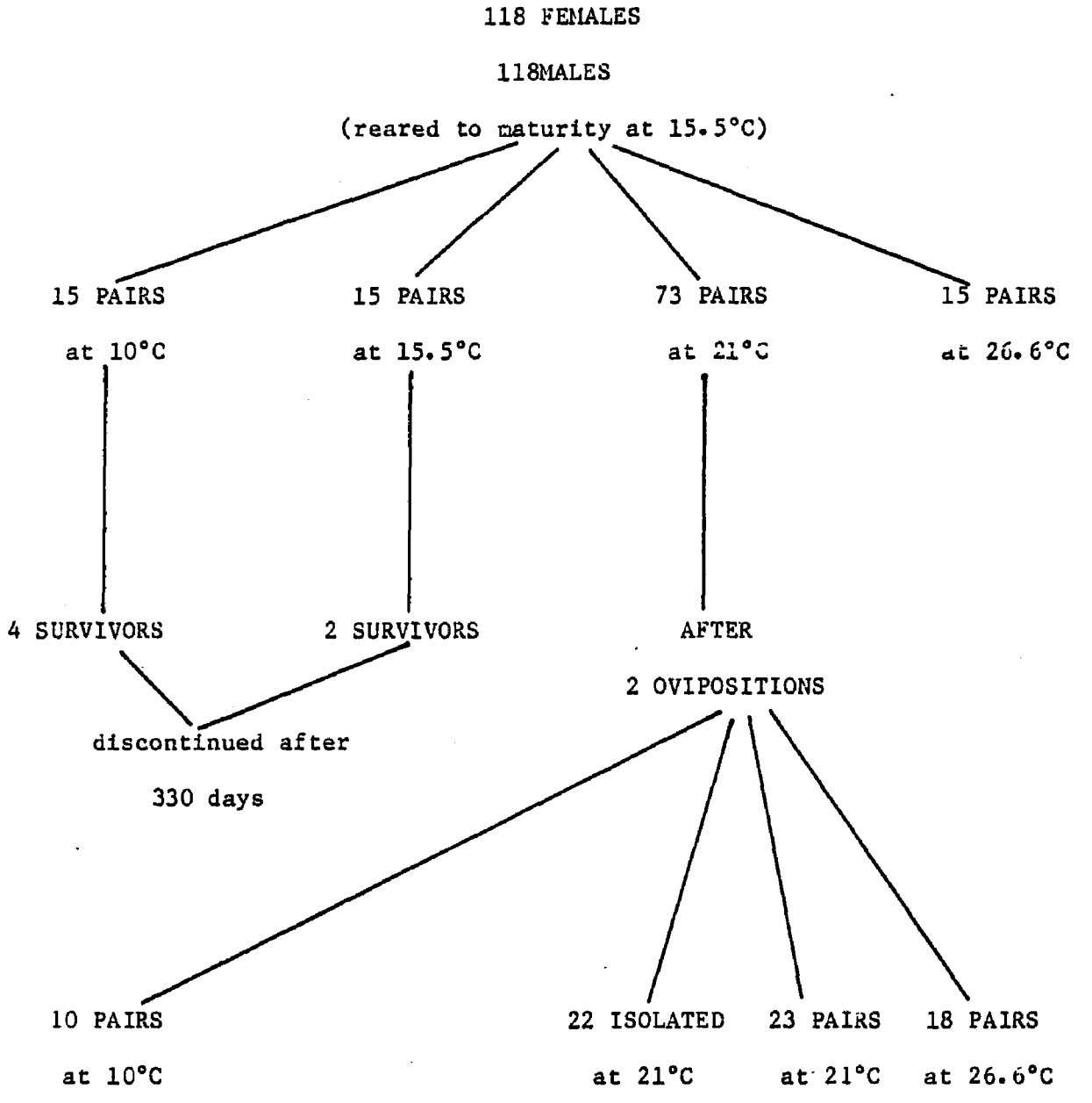

Figure 11. Flow chart of the experimental use of males and females reared to maturity in laboratory stocks at 15.5°C.

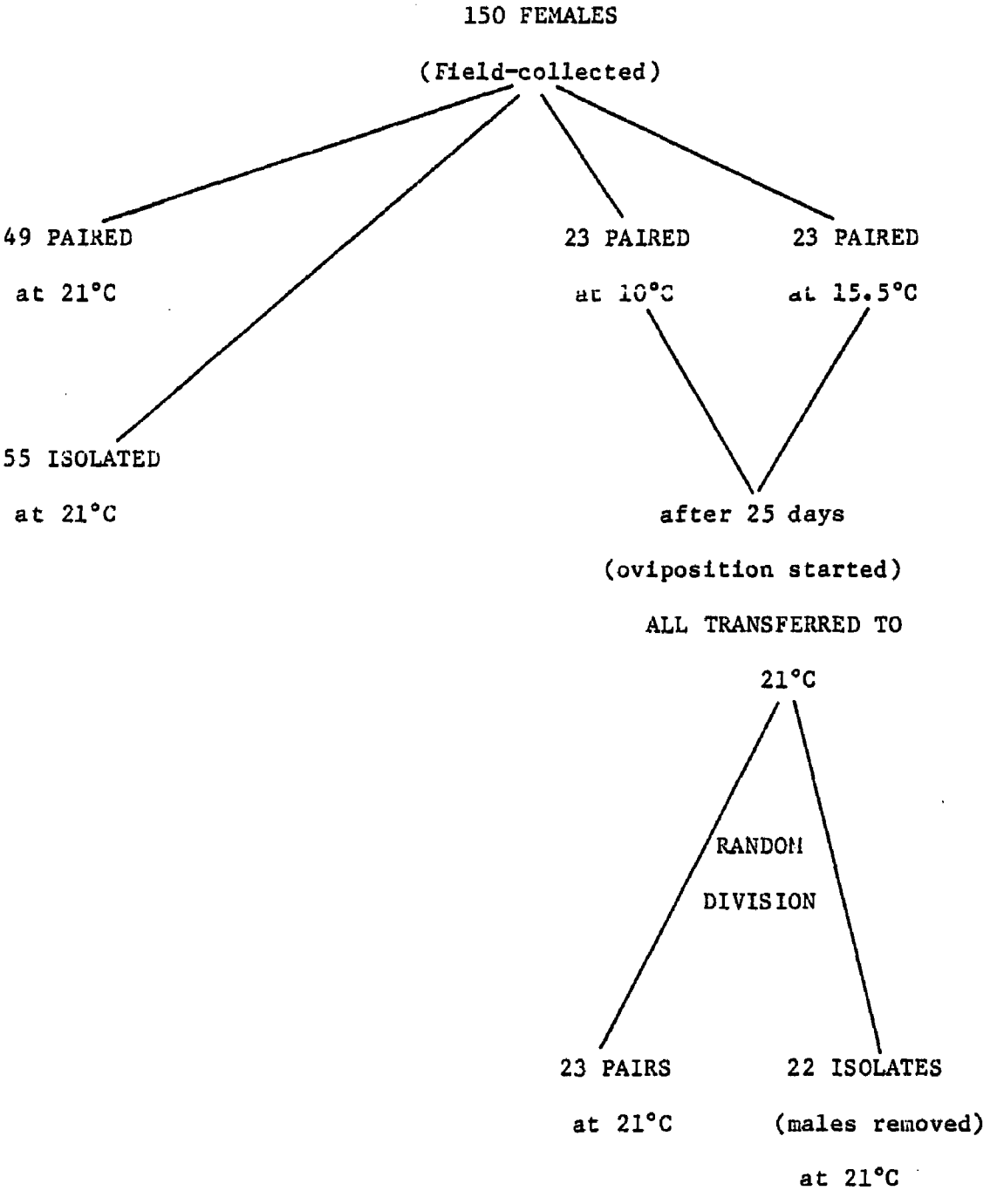

Figure 12. Flow chart of the use made of field-collected females (Baker Woodlot, March-April 1979).

B) Fecundity and egg viability

Table 12 shows the mean number of ovipositions observed in paired females at three temperatures, as well as the mean total number of eggs laid. At the time that observations on surviving individuals at 10° and 15.5°C were discontinued (see Figure 11), egg-laying had become sporadic and few eggs were laid at any one oviposition.

Table 12. Total number of ovipositions and total number of eggs laid per female (paired, laboratory-reared).

	10°C	15.5°C	21°C
n females observed	12	15	22
oviposit./female			
mean ± S.D.	4.4 ± 2.4	9.8 ± 3.5	11.0 ± 3.7
(range)	(1-9)	(4-16)	(3-18)
eggs/female			
mean ± S.D.	223.9 ± 123.2	468.7 ± 148.4	521.9 ± 221.0
(range)	(51-442)	(187 - 687)	(54-839)

The highest fecundity was recorded at 21°C, being slightly higher than the mean totals observed for females at 15.5°C. At 10°C mating and ovipositon did occur in the cultures, but the females were sluggish; some did not begin egg-laying until they had been in culture for over two months.

Low temperatures not only depressed fecundity rates, but also

decreased the frequency of ovipositions. Intervals between them encompassed roughly one week at 21°C, 11 days to two weeks at 15.5°C, and a month or more at 10°C (Table 13), and increased with successive ovipositions.

The reproductive pattern of paired females is illustrated in Figure 13. The mean number of eggs laid per oviposition increased soon after reproduction began, then decreased steadily over a relatively long period of time. Fecundity peaked early at 15.5°C, at the third oviposition. At 21°C the highest mean number of eggs was recorded in the 6th oviposition, and means remained relatively high throughout the gradual decline.

The few egg-layings recorded for females initially incubated at 10°C may mislead: had there been more replicates, a pattern of increase and decline may have emerged more clearly. However, egg laying did appear to be curtailed by low temperatures: the ten females transferred to 10°C after they had begun reproducing at 21°C (see Figure 11) showed an equally low frequency of oviposition, and most of them stopped egg-laying after a total of 8 or 9 ovipositions (2 ovipositions at 21°C, 6 or 7 at 10°C).

A few copulas were observed in pairs originally incubated at 26.6°C, but no eggs were ever laid. Five of the 18 females that were tranferred to 26.6°C from 21°C (see Figure 11), produced one egg batch each, but none of these developed. The females died soon thereafter.

How temperature affects the realization of reproductive potential in P. inconstans is further illustrated in Figure 14, by cumulating mean numbers of eggs laid per batch. Within any given period of time (e.g. 100 days) 21°C allowed for the production of a higher number of

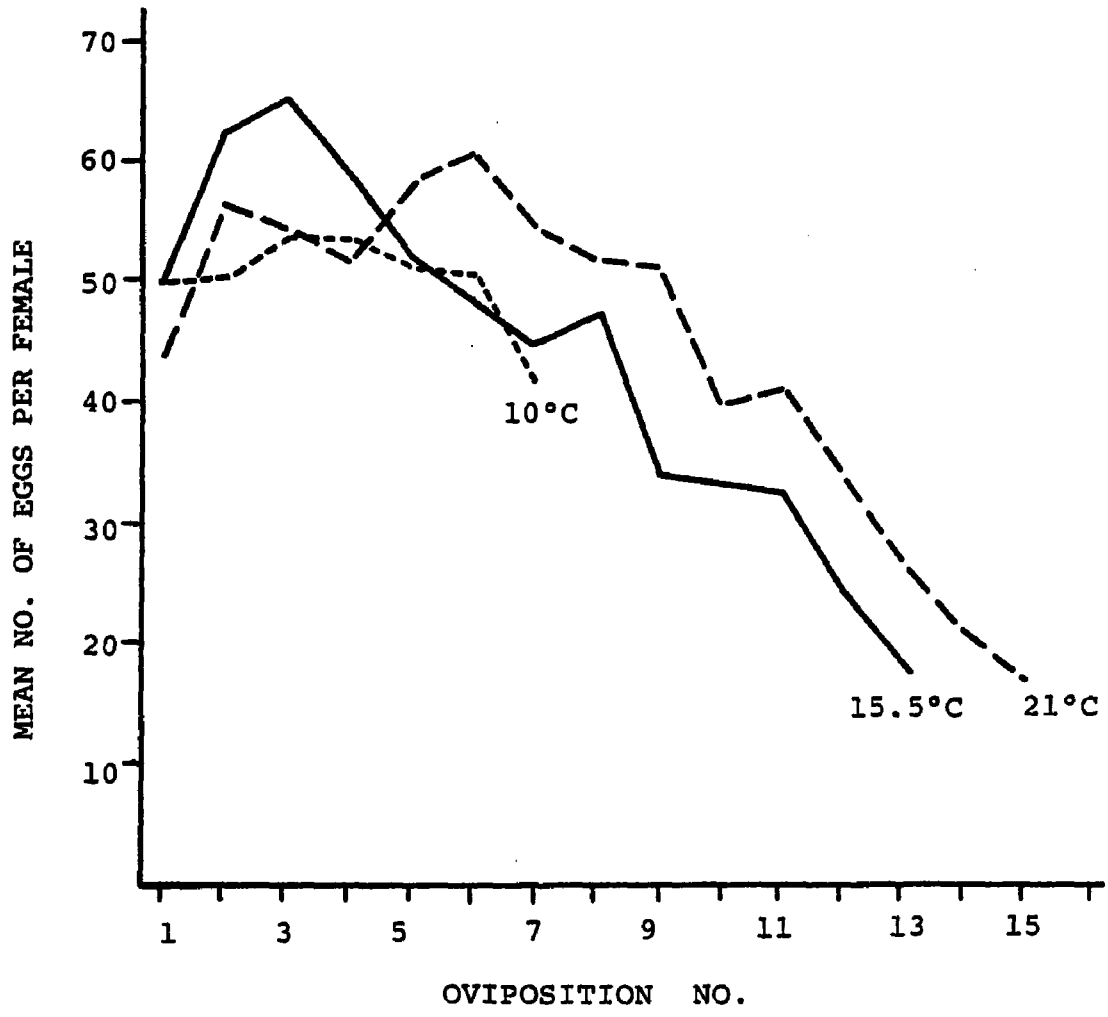

Figure 13. Mean number of eggs per female and oviposition at three temperatures.

Figure 14. Mean number of eggs per female, cumulated through successive ovipositions, and plotted against time elapsed since the beginning of egg-laying.

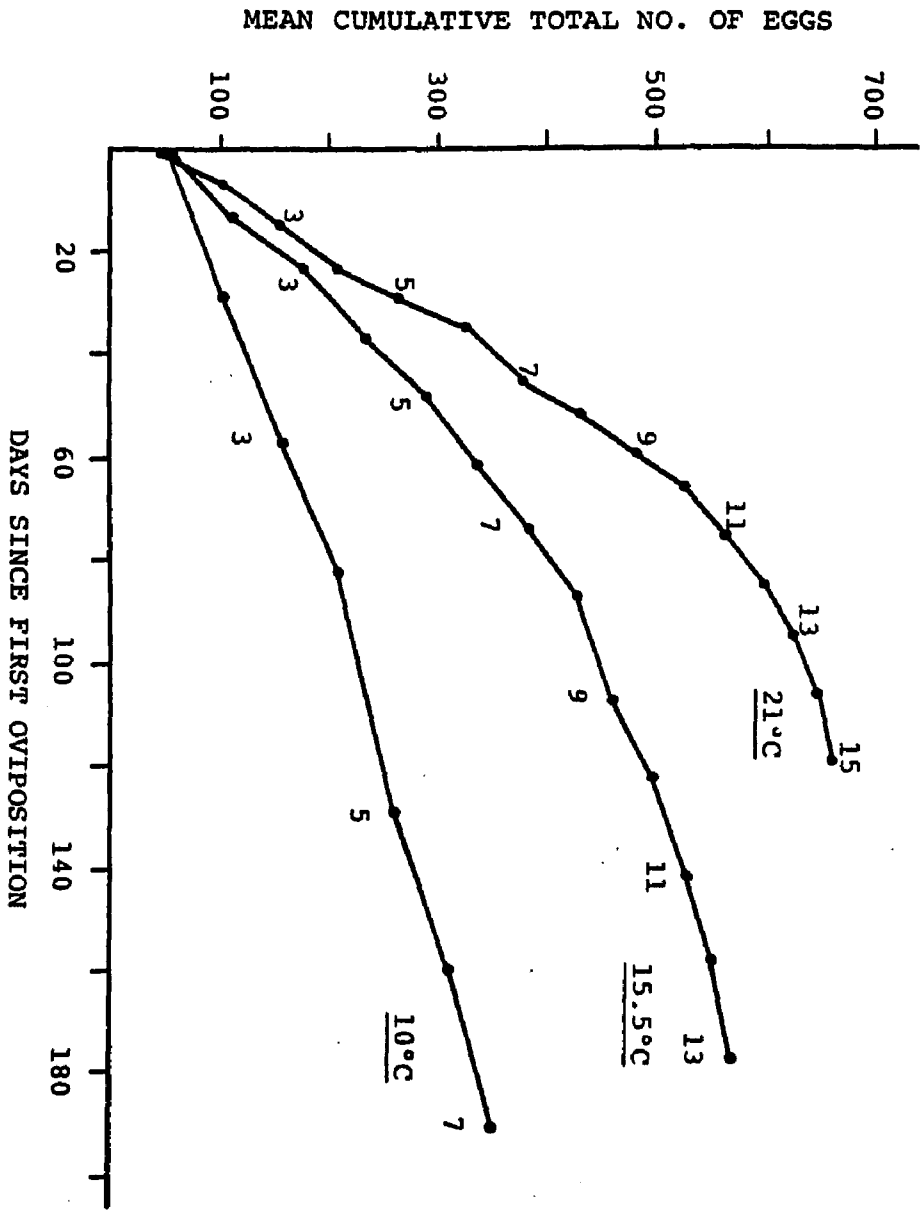
MEAN CUMULATIVE TOTAL NO. OF EGGS
100
300
500
700
20
60
100
140
180
DAYS SINCE FIRST OVIPOSITION
21°C
15.5°C
10°C

Table 13. Intervals, in days, between successive ovipositions (paired, laboratory-reared females).

	10°C			15.5°C			21°C		
Ovipos.	n	mean	(±S.D.)	n	mean	(±S.D.)	n	mean	(±S.D.)
1-2	10	28.2	(13.3)	15	12.4	(3.9)	22	7.1	(2.1)
2-3	9	28.4	(16.9)	15	11.3	(2.4)	22	7.3	(2.3)
3-4	7	25.6	(9.1)	15	12.5	(4.0)	21	7.1	(2.0)
4-5	7	46.6	(21.3)	15	11.8	(3.4)	20	7.1	(1.2)
5-6	4	31.0	(7.0)	13	12.6	(3.2)	19	6.7	(1.8)
6-7	2	29.5		13	13.2	(4.0)	19	7.7	(2.9)
7-8				10	13.3	(5.6)	19	7.8	(1.9)
8-9				8	19.5	(12.5)	16	7.9	(2.1)
9-10				7	15.6	(3.7)	16	8.0	(1.5)
10-11				7	19.0	(8.0)	13	8.2	(2.2)
11-12				6	16.3	(3.4)	13	8.9	(4.3)
12-13				4	18.8	(2.5)	8	10.6	(5.3)
13-14							5	10.8	(4.5)
14-15							3	12.3	(2.9)

progeny both through more frequent egg-laying and through a slightly higher fecundity (Figure 13). Of the temperatures used in this investigation, 21°C appeared to be optimal for the species, at least with regard to reproductive rate.

C) Egg viability:

Data on egg viability proved to be difficult to summarize. Recognition of non-viable eggs, after the remainder of a batch had hatched, presented no problems. But when fungi invaded a chamber and smothered its contents, one could not tell whether non-viability allowed fungal growth or whether culture conditions enhanced fungal invasion of otherwise viable eggs.

Finally, in view of the fact that fungal attack was observed in the field and may indeed be a common occurrence (Seifert, 1932), any eggs that failed to hatch were included in viability calculations. The only exceptions were eggs that had been manipulated, and those in debris-based chambers: these nests were difficult to keep moist once they had been removed from the parent cultures.

Table 14 shows the viability counts for eggs laid by paired females. The highest viability percentage was recorded at 15.5°C, but the value did not differ significantly from that obtained at 21°C ($p > 0.25$). Viability amounted to 85% at 10°C; according to the sparse evidence available for 26.6°C, eggs were totally unable to develop at that temperature. Fungal contamination, under the conditions of these experiments, accounted for 67% (at 10°C), 73% (at 15.5°C) and 53% (at 21°C) of all non-viable eggs.

Table 14. Average percent viability of eggs laid by paired, laboratory-reared females.

	Incubation Temperatures		
	10°C	15.5°C	21°C
mean % viab.	85.2	93.7	91.7
S.D.	±20.4	±6.6	±7.4
n of females	11	15	21
n of eggs	2687	7030	11484

D) Reproductive period and longevity

The duration of the reproductive period was measured as the number of days elapsing between the first and last oviposition of each female. As mentioned earlier, observations at 10° and 15.5°C were discontinued after 330 days. But by that time, few egg batches were being laid, and the long intervals between them, as well as the low number of eggs in them, indicated that little bias was introduced by discontinuation: reproduction was indeed naturally coming to a close.

In Table 15, longevity of paired females is opposed to the duration of reproductive activity at three temperatures. Longevity values include a pre- and post-reproductive period. At 15.5° and 21°C pre-reproductive time (from the day of incubation) was of the order of a few days only; but at 10°C it lasted as long as 40-90 days.

Assuming that culture conditions were adequate for P. inconstans, a gradual decline in fecundity (Figure 13) was naturally followed by a variable period of senility (post-reproductive period), and eventual death. At none of the temperatures were there any indications that egg-laying could be resumed after a period of rest (which would have suggested iteroparity).

Table 15. Mean number of days from first to last oviposition, and average longevity of females (paired, laboratory-reared).

	10°C	15.5°C	21°C
reprod. period			
mean ± S.D.	110.1 ± 77.3	127.1 ± 60.6	80.5 ± 35.5
(range)	(1-250)	(58-251)	(14-180)
	n=12	n=15	n=22
Longevity			
mean ± S.D.	212.2 ± 89.7	176.4 ± 77.7	140.3 ± 51.1
(range)	(29-290)*	(13-308)*	(48-227)
	n=9	n=13	n=23

* on day 330, 4 females were still alive at 10°C, and 2 at 15.5°C; they were not included in longevity calculations.

E) Comparison between field-collected and laboratory-reared females:

The results narrated below concern a comparison between lab-reared and field-collected females (March-April collected in Baker woodlot). By comparing the reproductive biologies of the two groups, answers to the following questions were sought:

a) Under the rearing conditions specified in this study, do individuals reared in the laboratory from eggs yield valid data which reflect the true potential of the species?

b) Does the spring-population of females in the field consist of two generations of adults (one-year olds and two-year olds)? If so,

would they be recognizable by their differential reproductive biology?

c) Is there evidence of iteroparity in females which have not been subjected to constant laboratory temperatures throughout their development?

d) What is the sperm storage capability of females, and how does it affect egg viability?

e) Does the continued presence of males affect the life span or reproductive capacity of females?

The data used in this comparison stem from pairs and isolates collected from the field in early spring and incubated at 21°C (F females)and from pairs and isolates obtained from laboratory stocks and reared at 21°C (L females)(see Figures 11 and 12).

Three of the main parameters of reproductive activity are summarized in Table 16. Both groups of isolated females produced a larger mean number of nests, laid more eggs, and had a longer egg-laying period than either of the groups of paired females.

Variances of each set of data were tested with Bartlett's (1937) X^2 statistic and were found to be equal. The means of each set of results were then tested by the Bonferroni t-test (non-orthogonal contrasts); the results are summarized in Table 17.

Concerning the number of ovipositions (nests), the most significant differences lay between paired and isolated females, within the L as well as within the F group, but F-pairs laid slightly fewer egg batches than L-pairs ($P < 0.01$). The two groups of isolates did not differ significantly.

Isolated females, both L and F, also laid significantly more eggs

than their paired counterparts. Within paired (L and F) and within isolated (L and F) females, differences in egg production were not significant.

Similar relationships between the four groups became apparent in the duration of their mean reproductive periods. L pairs behaved much like F pairs, but both differed significantly from their respective isolated counterparts.

Longevity in culture followed much the same trend as reproductive activity: isolated females lived longer that paired females, whether laboratory-reared or field-collected (Table 18). Calculation of 95% confidence intervals showed, however, that the means differed significantly both within and between groups (Scheffé's interval, variances being unequal). Confidence intervals for each contrast are given in Table 19. Knowing the past history of each group, a simple explanation for these differential life spans presents itself: pairs differed from isolates (within L and within F) apparently due to the presence of males. L pairs lived longer than F pairs, and L isolates longer than F isolates, because animals from the field had already spent part of their life span at the time they were collected.

The parameter that remained to be tested was egg viability. In order to avoid bias, the few females which never laid viable eggs over their entire reproductive period were included; as a result, viability often ranged from 0 to 100 percent. On the average, viability was slightly higher in paired females than in isolates (Table 20); but when they were statistically contrasted (Scheffé's 95% C.I.), none of the differences proved to be significant (all confidence intervals included zero).

Table 16. Reproductive activity of females at 21°C (ranges in parentheses; L = laboratory stock, F = field-collected).

Groups	n=	total nests mean ± S.D.	total eggs mean ± S.D.	duration egg-laying mean ± S.D.
L paired	22	11.0 ± 3.7 (3-18)	521.9 ± 221.0 (54-839)	80.5 ± 35.5
L isolated	22	14.1 ± 3.8 (4-22)	694.7 ± 193.0 (217-1036)	116.1 ± 40.6
F paired	48	8.6 ± 3.6 (1-21)	490.5 ± 193.6 (48-1106)	66.0 ± 31.9
F isolated	55	12.4 ± 3.6 (3-22)	617.4 ± 159.0 (155-920)	107.3 ± 32.5

Table 17. Bonferroni t-test of the mean total number of ovipositions, number of eggs, and duration of reproductive period at 21°C (L = lab-reared, F = field-collected).

	Significance Level		
Contrasts	no. of ovip.	no. eggs	repro. per.
L paired vs. L isolated	$P < 0.02$	$P < 0.02$	$P < 0.01$
F paired vs. F isolated	$P < 0.1$	$P < 0.01$	$P \ll 0.01$
L paired vs. F paired	$P < 0.01$	$P > 0.1$	$P > 0.1$
L isolated vs. F isolated	$P > 0.1$	$P > 0.1$	$P > 0.1$

Table 18. Average longevity of females at 21°C: (L = lab-reared; F = field-collected).

	Longevity, days	
Groups	mean ± S.D.	range
L paired	140.3 ± 51.1	48 - 227
L isolated	206.8 ± 51.4	107 - 270
F paired	97.3 ± 37.2	51 - 190
F isolated	142.9 ± 36.0	70 - 209

Table 19. Longevity of females at 21°C: Scheffe's confidence intervals on the differences between selected mean. (L = lab-reared; F = field-collected).

Contrasts	95% C.I.
L paired vs. L isolated	-66.5 ± 39.0
F paired vs. F isolated	-45.6 ± 18.7
L paired vs. F paired	43.0 ± 30.5
L isolated vs F isolated	63.9 + 30.7

Effects of isolation on egg viability could, however, be shown by summarizing egg development data for successive ovipositions (Figure 15). In F females especially, isolation did not significantly decrease viability during the first 9 to 11 ovipositions. At that point, paired females experienced rapid mortality, but isolates continued to lay eggs, of which fewer and fewer hatched (Figure 15A).

In L females, the discrepancy between pairs and isolates was

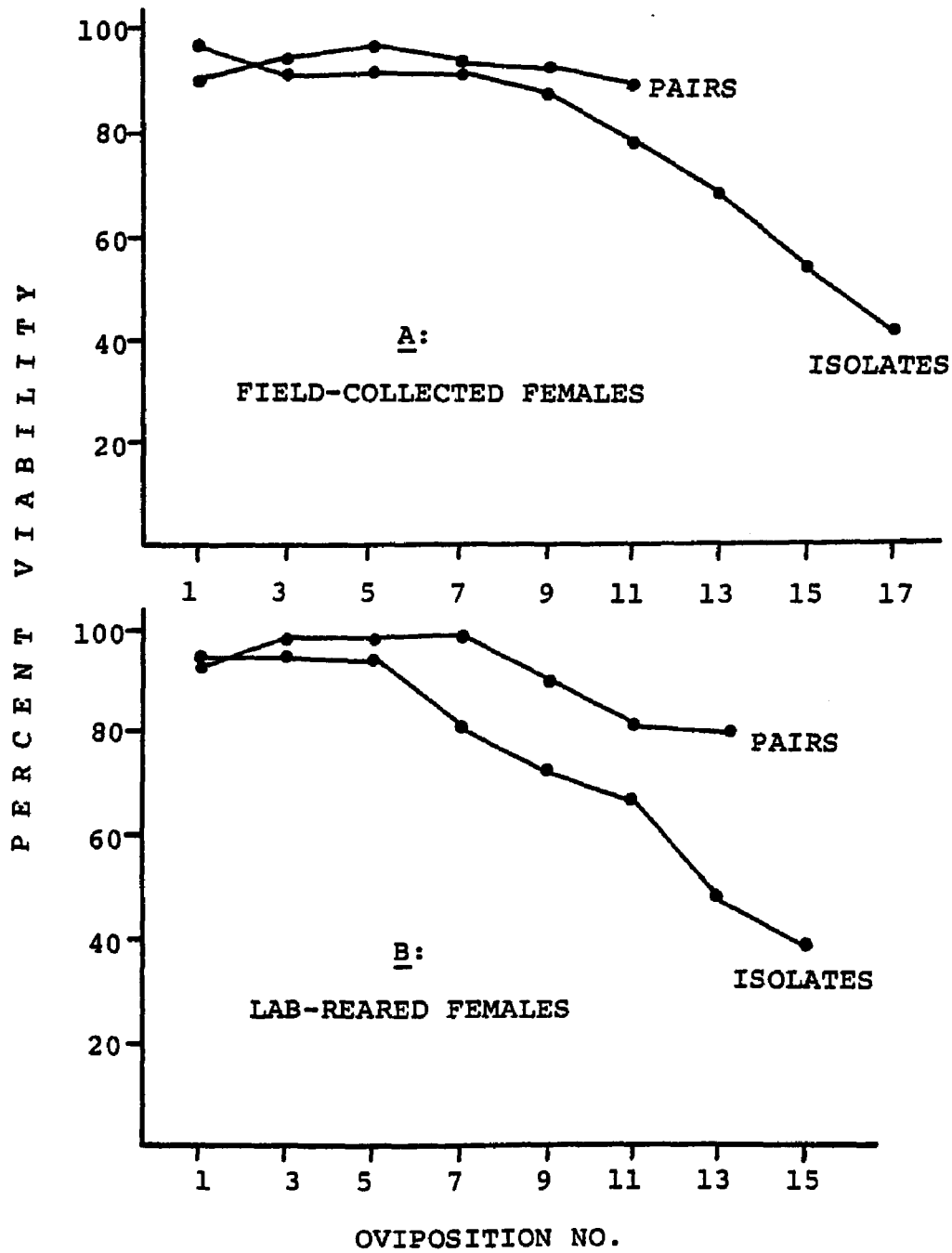

Figure 15. Percent viability of eggs laid at selected ovipositions.

somewhat greater during early ovipositions (Figure 15B), but the decline in viability of eggs laid by isolates was equally pronounced.

In general, repeated mating appeared to be unnecessary for the production of viable eggs - at least during the period of highest fecundity (greatest number of eggs per oviposition). Increased longevity of isolates allowed them to oviposit for a longer period of time; they produced more nests, but with fewer eggs in each, and progressively fewer of these eggs hatched.

Table 20. Viability of eggs laid by lab and field females at 21°C. Percent viability is the mean viability per female. (L = lab-reared; F = field-collected).

Female group	n (females)	n (eggs)	% viability mean ± S.D.	range %
L - paired	22	11,481	87.5 ± 20.4	0 - 100
L - isolated	22	15,284	83.4 ± 12.6	54 - 100
F - paired	48	23,545	90.7 ± 17.0	0 - 100
F - isolated	55	33,957	83.9 + 21.9	0 - 100

4. DISCUSSION

Comprehensive diplopod rearing programs have rarely been conducted in the past. Blower's (1974) work is an outstanding exception: he reared Ophyiulus pilosus from egg to adult. The data were later used to clarify details of the species' life cycle in the field (Blower and Miller, 1974). Rantala (1970, 1974) followed the development of

individuals of Proteroiulus fuscus for a period of several years, providing an unusual demonstration of rearing success. A number of other species have been reared through parts of their life cycle. Although even partial rearing indicates adequate culture conditions, indiscriminate use of the term "successful rearing" does not always appear justified.

Three major criteria may be used for "success": a) production of viable offspring in long-term culture, through more than one generation; b) low mortality of all stages at the most favorable temperatures; and c) compatibility of laboratory data with corresponding field observations. Not all of these criteria are met all the time. Blower (1974) considers the rearing of O. pilosus to adulthood, on sycamore leaves alone, a result of note. But the species would not reproduce in culture, and the author suggests that rearing conditions were not adequate. In general, the criterion of successful reproduction appears to be the most difficult to meet in the laboratory.

At least in polydesmids, single ovipositions followed by death of the females probably do not reflect their true potential. In the present study, records of up to 22 ovipositions per female give the impression of a fully realized reproductive potential. Culture methods were adequate, since P. inconstans could be reared through two generations without signs of deterioration. In fact, all criteria for success were well met: Mortality of all stages was low. Continuous production of viable eggs was maintained through more than one generation. And reproductive behavior and longevity were similar in laboratory stock and field-collected individuals.

Life cycle data obtained in the laboratory carry the stigma of partial invalidity due to the constancy and artificiality of conditions. Usually this cannot be prevented. But it was shown here that past development history of P. inconstans did not affect the validity of results concerning reproduction. Females reared from eggs under constant conditions behaved in a manner very similar to those that reached maturity under fluctuating field conditions.

Studies on the effect of food type on millipede development suggest that choice of food materials can play an important role in rearing success (Gere, 1955; McBrayer, 1973; Keirallah, 1973; Keirallah, 1978). In the laboratory, deciduous litter is probably the most commonly used food source. Others include soil and potato slices (Baker, 1978a), soil, moss and potato (Perttunen, 1955) and filamentous algae (Keirallah, 1973). Blower (1974) suggest that pre-dried food lacks microflora, a necessary food item for millipedes. McBrayer (1973) shows that re-ingestion of feces allows the animals access to microbes and their cellulases, and enhances weight gain over time.

In the present study, decayed litter and wood were always used fresh, and the added yeast may have provided a semi-natural, readily available source of energy for P. inconstans. In cultures that had been neglected for some time, additions of yeast produced an immediate response: the animals lined up around the yeast and fed much like cattle around a trough.

Under the conditions of this study, P. inconstans developed fastest at 21°C, which induced the shortest durations of egg and immature stages as well as the highest fecundity and oviposition frequency. Mortality was low at both 15.5° and 21°C, and also at

10°C - with the possible exception of very young instars, as discussed earlier. The highest temperature used, 26.6°C, approximated the upper lethal limit for the species. Neither eggs nor immatures could survive prolonged exposure to it.

Survival of adult females was influenced not only by temperature, but also by the presence of males. Paired females died sooner than those kept in isolation. Pairing in small containers is a forced situation, in which the "sexual drive" (Sahli, 1969) of males results in frequent copulation, even interrupting egg-laying activity. Sahli (1969) also observed, in P. angustus, that many matings diminished the life span of females.

It is probable that repeated matings take place in the field as well, contributing to the natural mortality rates of females. This is not necessarily a negative effect. Paired females in culture generally showed rapid die-off only after their major contribution to recruitment had been made, e.g. at a time when the number of eggs per oviposition clearly began to decrease. In the field, food availability can be a limiting factor during the summer months (Miller, 1974; Stachurski, 1968, 1972). Removal of adult females from the population would reduce intraspecific competition for food at a time when the new recruits of the season are present in large numbers.

Of all stadia, the penultimate was of the longest duration in both males and females; this seems to be generally true for polydesmids (Miley, 1927; Causey, 1943; Keirallah, 1978). Males were able to mature earlier than females by shortening the duration of their penultimate stadium. In O. pilosus, although most males mature slightly earlier than females, males tend to defer maturity. Blower

(1974) recorded inactivity periods of more than two months for subadult males, and interprets them as adaptive inactivity designed to synchronize maturation of males and females. B. superus adopts a different strategy of deferral. Stephenson (1961) found that the majority of B. superus females mature in the spring, and that males overwinter in an intercalary stage: gonopods are developed during a supernumerary spring molt in these otherwise mature males.

Early maturation of males is adaptive insofar as it assures insemination of females as soon as the latter are mature. In P. inconstans, sperm storage allows mated but isolated females to produce approximately ten batches of eggs with near-normal viability, which decreases rapidly in subsequent egg batches. Blower (1969b) suggests that the frequent deposition of eggs by semelparous Polydesmus spp. is a means of "seeding" not yet colonized areas with new individuals. Even single females, once mated, can successfully invade new habitat areas because of their sperm storage capability. P. inconstans appears to be well suited for the type of population expansion described by Blower (1969b). It has the potential of depositing large numbers of small broods in many different places.

A different strategy is hypothesized by Lewis (1971a) for polydesmoids in which adults are distinctly surface-active. Increased predation on these species is apparently offset by the production of large numbers of eggs (about 1000) per brood, which would tend to reduce the effect of predation as a limiting factor.

Even in species which are not clearly surface-active, predation conceivably represents a major limiting factor. Seifert (1932) mentions that eggs and juveniles of Strongylosoma pallipes frequently

fall prey to the centipede Lithobius sp. and to carabid beetles, and that egg chambers may be plundered by other millipedes. Cole (1946) suggests, based on circumstantial evidence, that some spiders may feed on Scytonotus granulatus. Baker (1974) comments on the possibility that soil mites may prey on first instars of B. superus, a millipede implicated as pest of sugar beets (Baker, 1974; Pierrard and Biernaux, 1974). And Miley (1927) observed a beetle larva eating three molting individuals of Euryurus erythropygus. Apparently the defensive secretions of millipedes (Bano and Krishnamoorthy, 1978; Duffey and Towers, 1978; Roper, 1978) are ineffective against certain predators.

Small polydesmids such as P. inconstans may be prime candidates for population control by predation. The smooth, round, strongly sclerotized iulids are more difficult to grasp. Medium and large-sized O. pilosus for instance cannot be held and crushed by carabid mandibles. Using the typical winding motion so aptly described by Haacker (1974), O. pilosus simply winds its way out of the mouthparts of the beetle.

However, there is no good field evidence regarding the extent to which millipede populations are limited by predators. Judging by the data presented here, there are indications that carabids may be able to consume large numbers of millipedes, and also that the array of invertebrate predators immune to defensive secretions may be large. If that were true in the field, the high reproductive capacity of P. inconstans could effectively be counteracted by predator activity.

PART II

THE LIFE HISTORY OF *POLYDESMUS INCONSTANS* IN THE FIELD

1. INTRODUCTION

The humificative function of Diplopoda, which are among the major saprophages in forests and grassland, has been recognized for many years. Qualitatively, their importance is envisioned as lying in the mechanical breakdown of organic matter and in the mixing of detritus with the soil itself; by the process of comminution, microbial activity is enhanced and, with it, the chemical process of humus formation.

Even though litter breakdown is axiomatic, the specific importance of diplopod feeding can be shown conclusively only where they are the dominant large detritivore, e.g. in the absence of earthworms (Ghilarov, 1947). Quantification of their effects in terms of litter disappearance has been attempted as early as the 1920's and 30's (Soudek, 1928; Bornebusch, 1930; Ulrich, 1933; Fourman, 1938). Since then, major studies have shown that the magnitude of the diplopod contribution to decomposition varies with the climatic and vegetational characteristics of specific localities (Drift, 1951; Dunger, 1956, 1958, 1960; Gere, 1956, 1962; Kurceva, 1960; Volz, 1954).

Much laboratory work has attempted to elucidate the precise nature and effect of diplopod feeding activity. Sakwa (1974) found that the attractive properties of rotting substances seem to involve a combination of sugar-presence and polyphenol-absence; on the other hand, Neuhauser and Hartenstein (1978) were unable to relate food preferences to the phenolic content of leaves. Despite such

discrepancies, many authors (Schmidt, 1952; Nielsen, 1962; Keirallah, 1966; Sakwa, 1974; and others) have suggested that millipedes can generally assess the nutritive value of their food and that environmental conditions, through their effects on microbial activity, should correlate with palatability.

Many of the field studies concerned with turnover rates of organic matter include analyses of the ecosystem's faunal components. These publications are too numerous to mention here; one may refer to soil zoological compendia such as those of Doeksen and Drift (1963), Burges and Raw (1967) or Wallwork (1976). With few exceptions, the organic matter cycle has not been correlated with population densities and age structures of specific millipede populations. Purely phenological data, on the other hand, are quite numerous.

The majority of these phenological investigations concerns iuloid species in England and other parts of Europe (Halkka, 1958; Blower and Gabbutt, 1964; Blower and Fairhurst, 1968; Blower 1969 a,b, 1970; Brookes, 1974; Fairhurst, 1974; Cotton and Miller, 1974); in Australia (Baker, 1978 a,b), and the Western Indian Ocean (Spaull, 1976). Glomerids, especially Glomeris marginata (Villers) have been of interest to zoologists for over 100 years; Bocock and Heath (1967), Bocock et al (1967) and Heath et al (1974) have dealt most extensively with the life history and ecology of the species in England.

The polydesmoids whose life history has been studied in the field share some common characteristics. Their life cycle is relatively short when compared to most iuloids: it is frequently completed in about one year (Seifert, 1932;Stephenson, 1961; Murakami, 1962, 1966a; Lewis, 1971 a,b). Polydesmus complanatus (Linné) probably takes two

years in England (Blower, 1970), and Murakami (1965 b) reports that Ampelodesmus iyonis Murakami in Japan may have a three-year life cycle.

In temperate climates, peak seasonal activity coincides with reproductive activity, and is usually measured by the relative number of individuals caught in pitfall traps. A spring-summer peak is usually the only one occurring, or is the more pronounced one in populations where a second peak is apparent in the fall (Stephenson, 1961; Blower, 1970; Haacker, 1968; Barlow, 1957).

Egg-laying takes place over a period of two to several months, and most species construct protective chambers around their eggs (Evans, 1910; Seifert, 1932; Voges, 1916; Murakami, 1965 a,b; Stephenson, 1961). Molting also takes place in chambers. In Nigerian paradoxosomatids and gomphodesmids, these chambers enable diapausing larvae to survive the dry season (Lewis, 1971 a,b). In temperate zones, polydesmids usually overwinter as adults and larvae (Stephenson, 1961; Verhoeff, 1929; Blower, 1955; Banerjee, 1967). Of several polydesmids investigated by Verhoeff (1929), one overwintered as larvae only - as does Oxidus gracilus (Koch) in Japan (Murakami, 1962, 1966).

The earliest biological and ecological studies on North American polydesmoids were those by Miley (1927) on Euryurus erythropygus (Brandt). Causey (1943) studied the biology of the hothouse millipede, which cannot survive winters outdoors in our climates. Eaton (1943) investigated Apheloria coriacea (Koch), but his field data were based on only two collections. As part of a large-scale study on cryptozoa, Cole (1946) noted some aspects of the biology of Scytonotus granulatus (Say), specifically those dealing with

aggregation in the field. Johnson (1952), in his survey of Michigan polydesmoids, included brief autecological notes on most of them, P. coriaceus (now P. inconstans) among them.

In many studies, density estimates are precluded by the methods used to sample a population. Pitfall trapping gives a measure of activity only, since catches depend on active movement of animals. Hand-sorting of area units of substrate and hand-collecting along transect lines are also commonly used, but yield density estimates only if all colonizeable substrate layers are included.

Funnel-type extraction is one of the less time-consuming methods of sampling, and yields both qualitative and quantitative data. Extraction efficiencies may vary with the type of funnel, the species in question, and possibly the developmental stage (Blower, 1970). In most cases extraction efficiencies are not assessed; it is debatable whether they would indeed by useful. Molting individuals are immobile for long periods of time, and the proportion of the population in that state varies with the season. Short of laboriously checking extraction efficiences at every sampling date, it might be preferrable to disregard them - knowing, however, that the density estimates obtained are likely to be slightly underestimated.

Determination of age structure requires repeated sampling. Again, all habitat subdivisions must be included, since some species show stage-specific substrate preferenda (Causey and Tiemann, 1969; Blower, 1970; Lewis, 1971 a). Furthermore, it requires the ability to recognize a given stage. In iuloids, segment numbers vary within one instar: rather than segmental counts, Vachon (1947) and Saudray (1952) have used ocellar patterns for stage assignment, Halkka (1958) noted

the size and color of defense glands, and Blower and Gabbutt (1964) used arithmetic probability paper analysis. In polydesmids as well as nematophorans a fixed number of segments characterizes each instar, so that simple segmental counts suffice. In polydesmids, however, the immatures of different species closely resemble each other; if these species cohabit, stage distribution data sometimes have to be tentative (Blower, 1970).

In the present investigation, field work was conducted in 1976, 1978 and 1979. Two sites were studied: a backyard garden and a deciduous woodlot, both in the vicinity of Michigan State University campus. Polydesmus inconstans was the only polydesmid ever encountered in either site.

The goals of the field study included assessment of:

a) the biology of the species in the field, including sexual activity, molting, and parasitism;

b) the life cycle of the species, i.e. seasonal stage distribution;

c) the spatial distribution of the population: in vertical subdivisions of the habitat (litter, soil) and in two horizontally opposed areas (uphill, low depressions);

d) the sex ratios in field populations.

2. MATERIALS AND METHODS

2.1 The garden site

A) Site description:

In 1976 and 1978, an effort was made to monitor a population of

P. inconstans in the immediate surroundings of a home located near Michigan State University campus. The site included a variety of small, more or less well defined habitats: grassy areas along the northern foundation wall of the home; bare soil, densely shaded by shrubbery, on its east and west sides; and a number of locations dispersed throughout a backyard garden planted with various perennials and annual vegetables.

The garden was rarely irrigated, and no pesticides were applied. The soils, generally sandy, varied in organic matter content from 3.5% in the garden to 6.6% under shrubbery on the west side. Garden soil had a pH of 7.7 to 7.9 (mean 7.8), and soil under shrubbery was only slightly more acid (7.2 to 7.6, mean 7.3).

B) Sampling methods:

In 1976, square soil samples (10 x 10 cm) were taken to a depth of 8 cm with a narrow spade. These samples included the variable, but small, amount of organic debris on top of the soil. The animals were recovered by heat extraction (modified Tullgren funnels). Eight samples were taken on each date.

In 1978, two different techniques were employed to assess the P. inconstans population. One was the "cryptozoan board" technique, similar to that used by Cole (1946): boards of weathered wood, 25 x 12 cm and 2 cm thick, were set down on the soil in permanent locations. A total of 20 boards were thus positioned, 7 in shady areas around the foundation of the home, and 13 in sunny areas in the garden. Distances between any two boards measured not less than 1 m. Periodically, the boards were lifted and P. inconstans were collected from their

underside as well as from the soil and crumb-layer beneath them. The animals were staged and sexed in the laboratory, and returned to the boards they came from.

Simultaneously, a mark-recapture program was conducted with the board-collected animals. Subadults and adults were marked with acrylic paint, in a pattern that allowed distinction between sexes, stages, and provenance from specific boards. Every 20 to 30 days the color scheme was changed to allow distinction between collection dates, at least on a monthly basis.

Beginning on April 16, 1978 and ending on April 18, 1979, a total of 30 collections were made. Conditions under the boards (amount of leafy debris, moisture, soil texture) varied greatly between boards and were not monitored. But soil temperature was monitored from May to November 1978, at the time of collection. These temperature measurements, made with a YSI portable telethermometer, were meant to oppose the shady and sunny areas, and to assess the mediating effect of the boards when compared to nearby, non-covered locations. Thus temperature measurements were made:

a) on the soil surface and at depths of 1, 3 and 5 cm;

b) under boards as well as in close vicinity to them, on and in unprotected soil;

c) in shaded areas (three boards along the northern foundation) and in sunny locations (three boards in the garden).

2.2. The woodlot site

A) Site description:

In the fall of 1978, a dense population of *P. inconstans* was

discovered in the NW corner of Baker woodlot (Michigan State University campus). The woodlot is a 73 - acre beech-maple woods dominated by maples (Table 21). It is criss-crossed by paths and frequented by students to the extent that the herbaceous vegetation is partially decimated in certain areas.

The herb layer is varied and consists of ferns, may apple, common barberry, and other species characteristic of mixed woodlots in this area. Well-travelled locations, where soil compaction and destruction of litter and vegetation were obvious, were avoided during this study.

In the part of the woodlot chosen for sampling, soil types vary considerably. Hillsdale sandy loam (coarse, well-drained) and Colwood loams (fine, somewhat poorly drained) predominate. In the two types of sampling locations described below (uphill, depressions) a number of soil samples were taken in March of 1980 and analyzed for pH and organic matter content. The soil types were assessed manually (Dr. Mokma, Crop and Soil Science, Michigan State University). Table 22 gives the results.

Following several hand-collections in late 1978, a sampling program was conducted through 1979, in two types of location:

a) depressions at the bottom of slopes (termed LOW): their size varied from about 1 m^2 to over 3 m^2. The smaller depressions were sampled quantitatively only once, but were sometimes revisited later to be hand-collected. The larger ones were sampled up to three times quantitatively, on different dates.

b) Upper slope areas (HIGH), slightly below the crest of elevations. These areas lay above the LOW depressions, the slopes being inclined toward the latter. Distances between HIGH and LOW

Table 21. The species composition (importance values) of the trees in Baker woodlot.*)

	Import. value	% Rel. freq.	% Rel. domin.	% Rel. dens.
Acer saccharum	104.9	30.4	32.0	42.5
Acer rubrum	41.1	16.5	9.2	15.3
Fagus grandifolia	28.4	11.2	7.1	10.0
Quercus ruber	25.2	6.0	14.9	4.3
Fraxinus americana	24.9	7.7	11.5	5.8
Tilia americana	22.2	10.0	10.0	6.0
Prunus serotina	16.6	14.9	7.5	4.3

*) From an unpublished manuscript by Y. H. Beach and W. D. Stevens, Dept. of Botany, Michigan State Unviersity: " A study of Baker woodlot. II. Vegetation and ecology".

Table 22. Soil characteristics of the Baker woodlot sampling sites.

	LOW AREAS	HIGH AREAS
SOIL TYPE *)	Colwood-Brookston loams	Riddles Loam and Hillsdale sandy loam
MEAN pH ± SD	6.1 ± 0.4	6.4 ± 0.2
MEAN % O.M. ± SD	8.6 ± 1.2	5.9 ± 1.1

*) According to: Soil Survey of Ingham County, Michigan; U.S. Department of Agriculture, Soil Conservation Service (1979).

localities were on the order of at least 10 m, and usually much more.

In both localities, one criterion for choosing actual sampling spots was stricly adhered to; no samples were taken close to logs or large branches. That is, structures that might serve as refugia for P. inconstans were avoided. The differentiation of niches on the forest floor is so complex that, had such potential retreats been included, the sampling program would have surpassed available time and space resources.

B) Sampling methods:

Litter samples: a square metal frame, 25 x 25 cm, was set down on the litter. A sharp knife was then run along its inside periphery, cutting through the litter and the smaller twigs. While leaving the frame in place, litter and debris from the inside of the square were transferred to plastic bags. Larger twigs, if short and lying within the frame, were included;if long, they were examined on the spot for P. inconstans and moved aside.

In LOW areas especially, the leaf litter was characteristically mingled with soil. The distinction between litter and soil (the soil-litter interface) was therefore made arbitrarily: those organic aggregates that were easily gathered by a gentle brushing motion of the fingers were included with the litter samples. The soil surface was then examined for P. inconstans and any animals moving over it were also included.

Soil samples: on selected dates, after the litter samples had been removed, two soil cores were taken from each 25 x 25 cm square. The cores reached a total depth of 15 cm, and each was subdivided into

a 0-8 cm and a 8-15 cm subsample. The inside width of the core sampler was 5.5 cm.

Extraction of animals from the soil and litter samples: until late June 1979, both types of samples were handsorted in the laboratory, in hopes of finding egg nests and molting individuals. Since neither was ever detected, the laborious handsorting was then replaced by Tullgren funnel extraction from 5 to 7 days (depending on the moisture content of the samples).

Hand-collecting: interspersed between area-specific litter and soil sampling, P. inconstans were collected by hand from the same general area of Baker woodlot. While hand-collecting can be used as a quantitative tool, in the present study the technique was simply meant to provide supplementary material for evaluating the stage distribution within the P. inconstans population. Neither specific area units nor collection-time limits were adhered to; rather, an attempt was made to thoroughly inspect all habitats available to the species: litter, duff, soil aggregates; all branch sizes; loose bark around the entire periphery of a given log; the outside surface of logs as well as any accessible channels within them.

C) Physical parameters of the site:

Litter thickness: usually, litter is characterized as dry weight of litter per unit area (Miller, 1974). Lebrun (1971) followed the temporal progression of leaf fall and determined the total number of leaves per m^2 of forest floor, as well as the gram percent of each species of tree in fresh weights. Dunger (1958) summarily described the litter cover in a flood plain as consisting of two to four layered

leaves in late fall, which disappeared rapidly during spring so that virtually no litter was left by late summer.

In this study, neither questions of organic matter breakdown nor of food availability were addressed. Thus, occasional measurements of litter thickness were made only as a gross check on general conditions on the woodland floor. First, a sharp knife was used to make a vertical cut through the litter for a distance of about 15 cm. Any dry top leaves were compacted until they touched the moist layer underneath by slight downward pressure with the palm of a hand. Total litter thickness was then measured with a ruler held against the cut surface. In addition, the number of dry and moist leaves were counted along a randomly chosen vertical line on the transect. "Crumbs and debris" thickness (decomposed skeletal leaves mixed with soil) was measured separately.

In both HIGH and LOW locations, from five to seven replicate measurements of this kind were made per date, on five dates from late April to late August.

Soil temperature and moisture:

On most sampling dates, temperature was measured with a YSI telethermometer on the litter surface, the soil-litter interface, and at depths of 1, 3, 5 and 10 cm in the soil.

Water content of the soil was assessed by weighing, drying and re-weighing a number of soil samples. At the time of weighing they were briefly checked for stones and roots, which were removed. They were then dried in a 60°C oven until no further weight loss occurred, and weighed again. In both LOW and HIGH areas four cores were taken per date, each of them subdivided into a 0-8 cm and a 8-15 cm

increment.

3. RESULTS

3.1. Habitat characteristics

A) Temperature:

The garden site: Temperature records from under boards when compared to those of open areas near boards showed clearly the mediating effect of board cover.

Figure 16 illustrates the differences between mean temperatures in the two contrasted locations. In sunny locations, the exposed soil surface was almost invariably warmer than that under boards, even in October and November. Discrepancies between surface and depth measurements (5 cm) were often large. Not so in shady locations, where surface and depth data were closely related, and where open area temperatures frequently exceeded board temperatures by only 1°C or less.

As an example of temperature profiles under the boards, Figure 17 shows the data obtained on six selected dates, and contrasts sunny and shady boards. On cloudless days (May 7, May 19, July 6) the differences in temperature persisted to a depth of 5 cm at least. At times with no sunshine, but after several days with high maximum air temperature (June 17, July 18) temperatures were high in both locations and at all depth levels. Mild days, with temperatures propitious for millipede activity, still occurred late in the fall (November 11).

In general, soil surface temperatures under the boards stayed within a range of 16° to 24°C, but occasionally rose to 26°C and

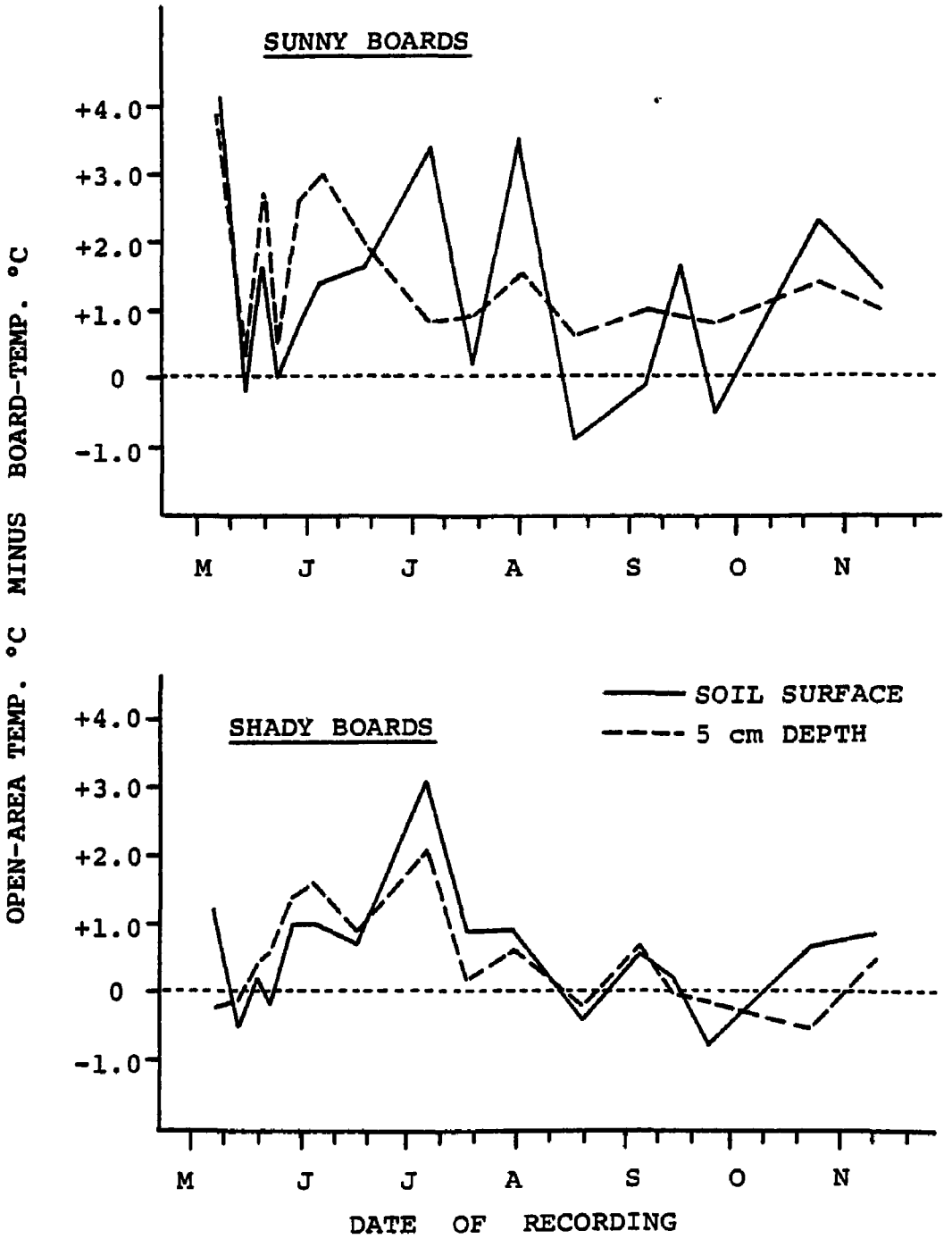

Figure 16. Differences between temperatures under boards and temperatures in non-covered areas, garden, 1978.

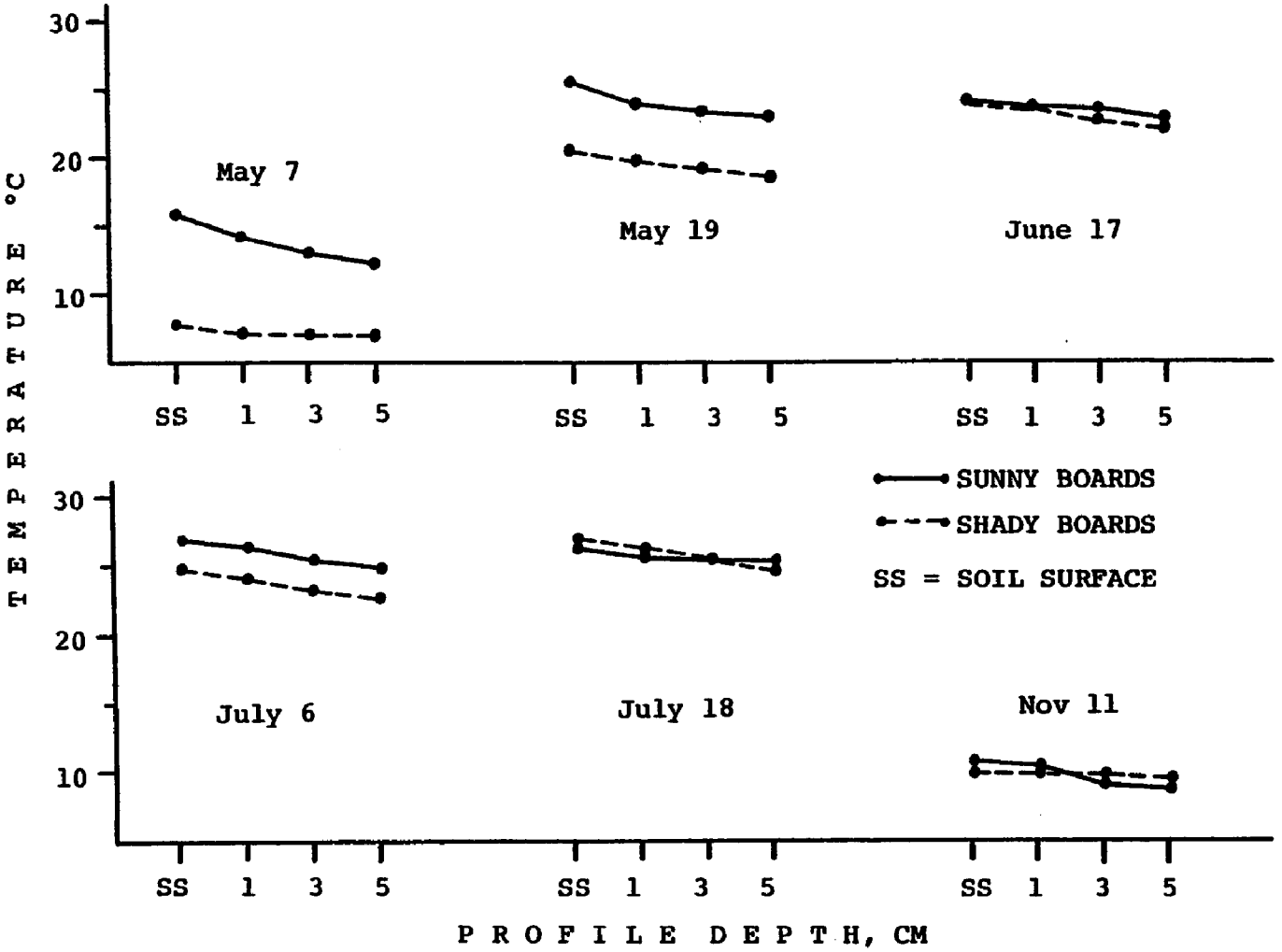

Figure 17. Temperature profiles under sunny and shady boards on selected dates.

beyond.

Official soil and air temperature records for East Lansing (recorded by Michigan State University Meteorological Station) in 1978 showed that the data obtained in the garden probably represent maximum daily soil temperatures. As illustrated in Figure 18, records taken in East Lansing at 8:am were consistently much lower than the garden records taken between 1:pm and 4:pm on the same days and at the same depth. Figure 18 shows again that the boards had a mediating effect on soil temperature, and ilustrates the relationsip between maximum air temperature and soil temperature.

The woodlot site: Since no continuous record could be made, the point measurements made on eight dates had to suffice for a characterization of the temperature profile in HIGH and LOW areas of the woodlot.

Figure 19 gives mean temperatures in each of the habitat subdivisions and at each of the depth levels monitored. Large differences between HIGH and LOW were apparent only on July 14, but depressions generally allowed temperatures to remain cooler during spring and summer.

The data for October 9 provide an example of the inversion of this relationship: in spite of leaf fall being well under way, HIGH areas apparently cooled down more rapidly, or responded more rapidly to falling air temperatures, than the well-protected LOW areas. At the same time, the usual temperature gradient (lower temperature with increasing depth) was also reversed.

From May to September, temperatures at the soil-litter interface and at 1 cm depth never rose above a favorable level for

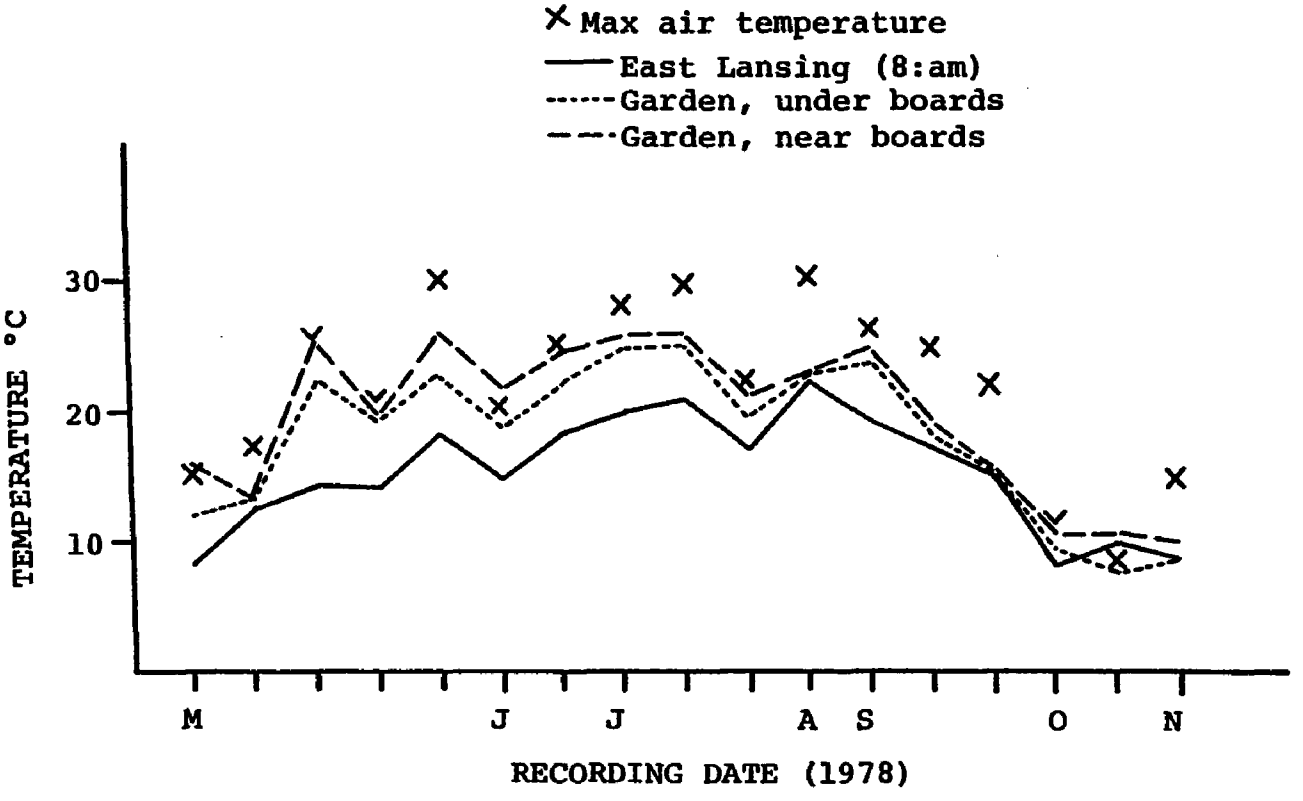

Figure 18. Soil temperatures at 5 cm depth: afternoon records (garden) and 8:am records (Michigan State University Meteorological Station, East Lansing).

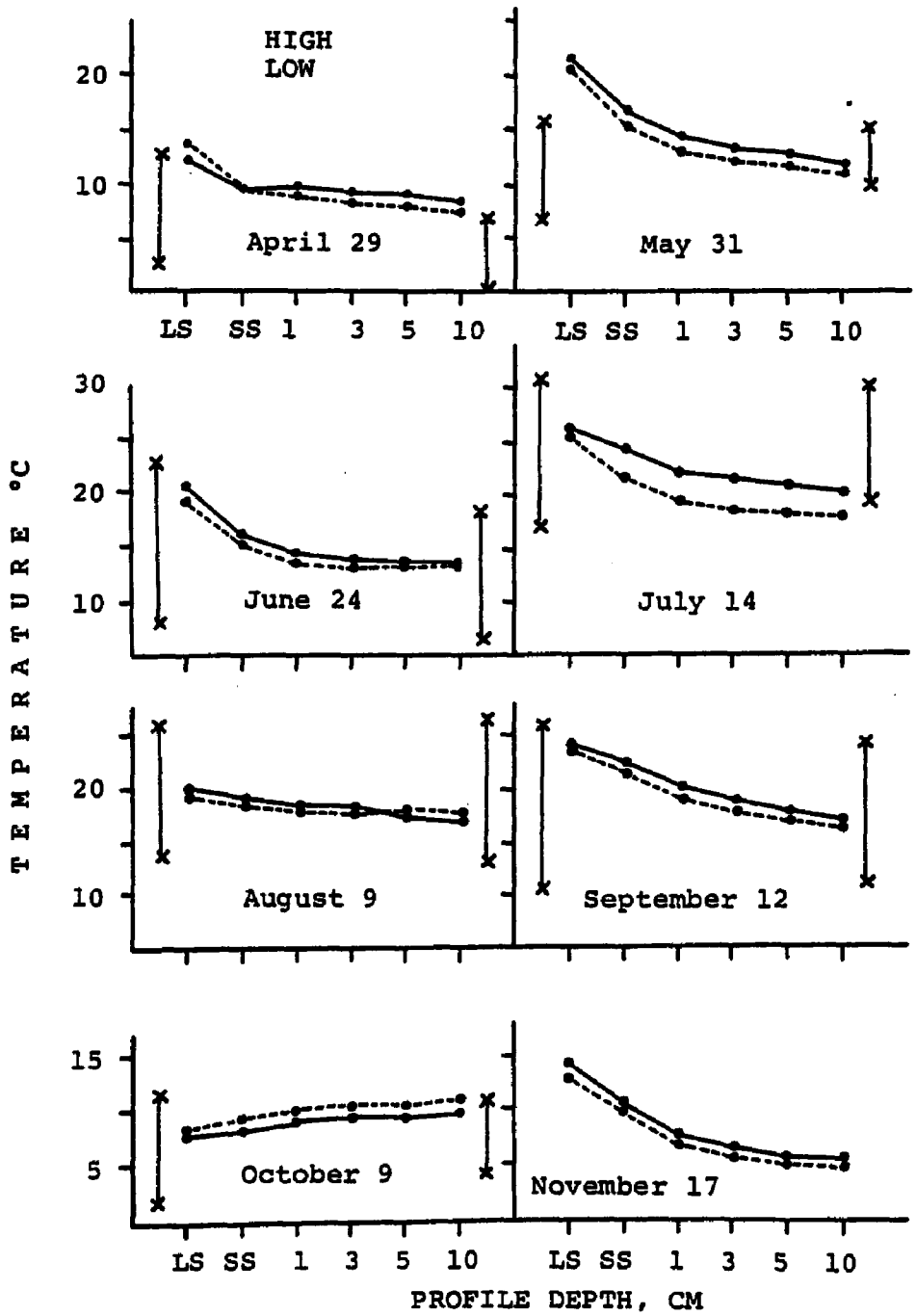

Figure 19. Depth profile of mean temperature in HIGH andLOW locations. LS=litter surface; SS=soil surface; vertical lines: max-min temperatures day before and day of sampling.

P. inconstans. As shown in the laboratory (Section I.3.3), 15° to 21°C seem to be optimal temperature regimes for the species. At least in LOW areas (Figure 19) this range was probably maintained throughout the summer, under the protective litter cover, allowing uninterrupted feeding and reproductive activity of P. inconstans.

During April, October and November, P. inconstans was conspicuous on the sides of logs, on moist branches, and in the uppermost litter layers (Figure 20). Judging by the temperature data for April 29 and November 17, temperatures above the soil were higher at those times then within the soil and, more pertinent, the litter and litter-surface temperature levels approached those levels at which P. inconstans was definitively active in the laboratory (15°C).

B) Litter cover:

Table 23 summarizes the data on litter thickness, and gives exact sampling dates. On upper slopes, the crumb layer was virtually non-existent at all times. In fact, a scoring system of "thin- patchy- none" would have been equally accurate. The layers of moist and dry leaves varied with prior weather condition. In LOW areas, there was always some habitat propitious for millipedes because the complex crumb layer was relatively thick and, as the season progressed, was kept replenished and even increased by input of skeletonized leaves from above.

In addition to the measurements of litter thickness, qualitative observations were made at times of hand-collecting and quadrat sampling. Except for small, isolated patches ($\leq 0.25\ m^2$) HIGH areas were actually never totally denuded of leaves. But in mid- and late

Figure 20. Loose aggregations of P. inconstans on the sides of logs in October.

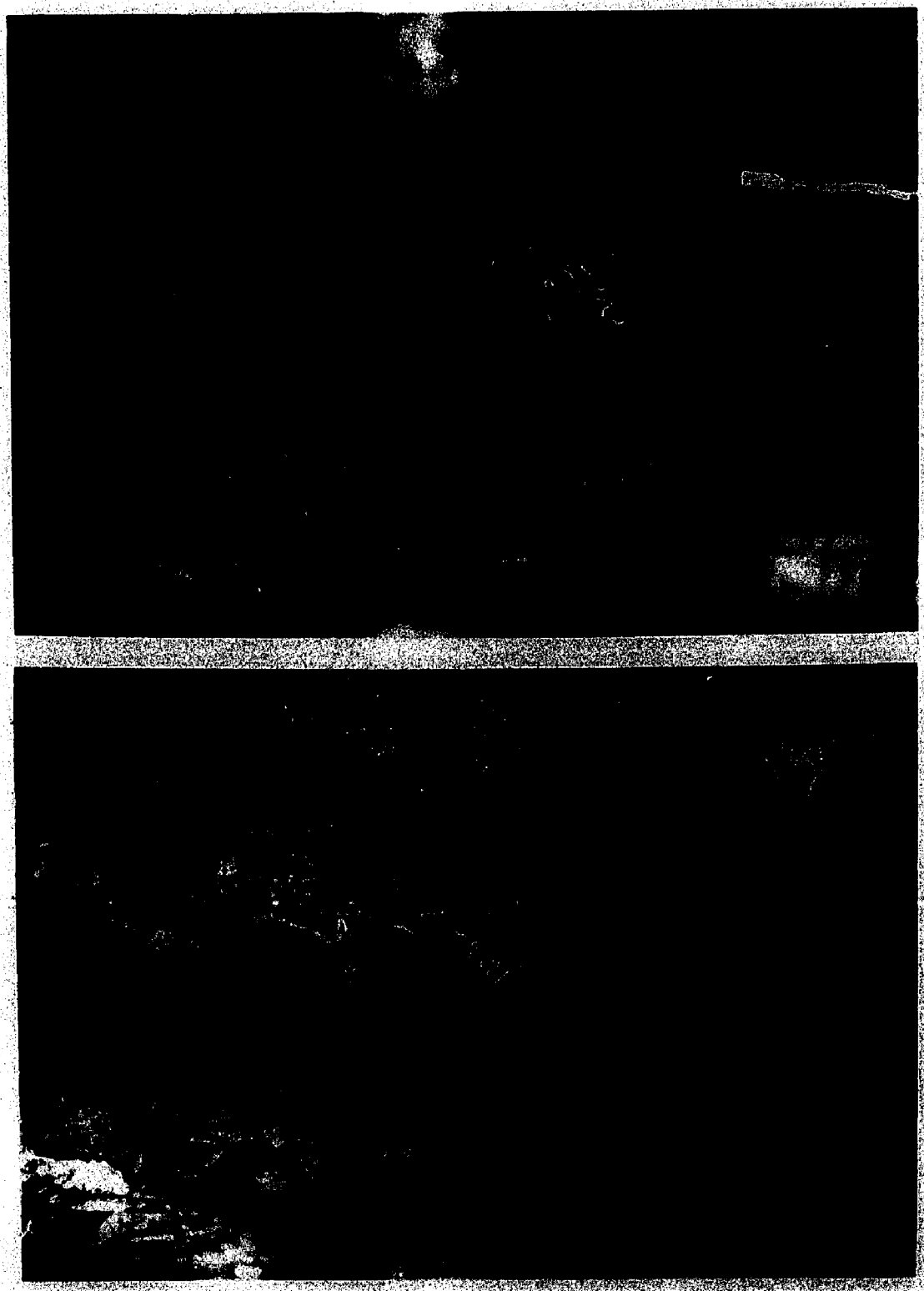

Figure 20.

Table 23. Thickness, in cm, of litter and crumb layers, and number of superimposed leaves in Baker woodlot. Means of at least five measurements per date and locations, ± S. D.

		Litter	Crumbs	no. of leaves dry	no. of leaves moist
Apr. 29	HIGH	0.6 ±0.3	0.3 ±0.1	3.0 ±0.7	2.3 ±0.8
	LOW	4.0 ±1.3	1.1 ±0.5	7.9 ±2.5	10.7 ±1.8
May 31	HIGH	0.7 ±0.2	0.3 ±0.1	4.6 ±1.2	0.8 ±0.7
	LOW	3.4 ±0.6	0.8 ±0.3	9.4 ±1.0	5.0 ±1.7
June 24	HIGH	0.7 ±0.2	0.2 ±0.2	5.8 ±1.3	0.5 ±0.8
	LOW	2.3 ±0.5	0.5 ±0.2	15.3 ±3.6	2.3 ±1.5
Aug. 9	HIGH	0.3 ±0.1	0.2 ±0.1	3.6 ±1.4	1.0 ±0.6
	LOW	1.0 ±0.3	1.8 ±0.7	6.8 ±1.7	3.0 ±1.3
Aug. 25	HIGH	0.2 ±0.1	0.1 ±0.1	2.9 ±1.0	0.6 ±1.0
	LOW	1.3 ±0.3	1.3 ±0.4	12.0 ±3.1	1.6 ±1.0

summer, litter cover consisted of only one to three dry leaves. In contrast to that, the continued richness of litter in LOW areas was very much evident. In both locations the only intact leaves left by the end of summer were those of beech and oak.

C) Moisture:

Soil moisture levels in HIGH areas were generally lower than those in depressions (Figure 21). Frequently the upper 8 cm of the profile contained more water than the 8-15 cm level. Rainfall in 1979, compared to 1978 (Figure 22) was unevenly distributed. With the exception of the September drought, the distribution was not reflected in soil moisture levels. The drought was evident in both HIGH and LOW areas, moisture levels remaining low well into October.

The amount of precipitation actually received by the soil depends on litter thickness as well as on the state of canopy develoment. Noirfalise (1962) calculated a seasonal "interception coefficient" concerning canopy development. Bare canopies (winter) allowed 85% of the rain water to reach the soil; during leaf development and leaf fall, 75% of the precipitation reached the soil; and during summer, 65% actually penetrated to the ground.

These data are intriguing, but their application to the present study is complicated by other parameters. In LOW areas the continued presence of a thick litter cover must reduce evaporation from the soil. That same litter cover must have an interception potential of its own, especially when rains are of short duration and/or low intensity. In HIGH areas, litter cover is generally thin and often consists of dry leaves not adhering tightly to the soil - therefore allowing air movement and evaporation.

These relationships appear to be quite intricate, and are probably also dependent on air temperature, as Lebrun (1971) has shown. In this study, they were not further quantified. But, as Figure 21 shows, the differential moisture content of the soil in HIGH and LOW areas was

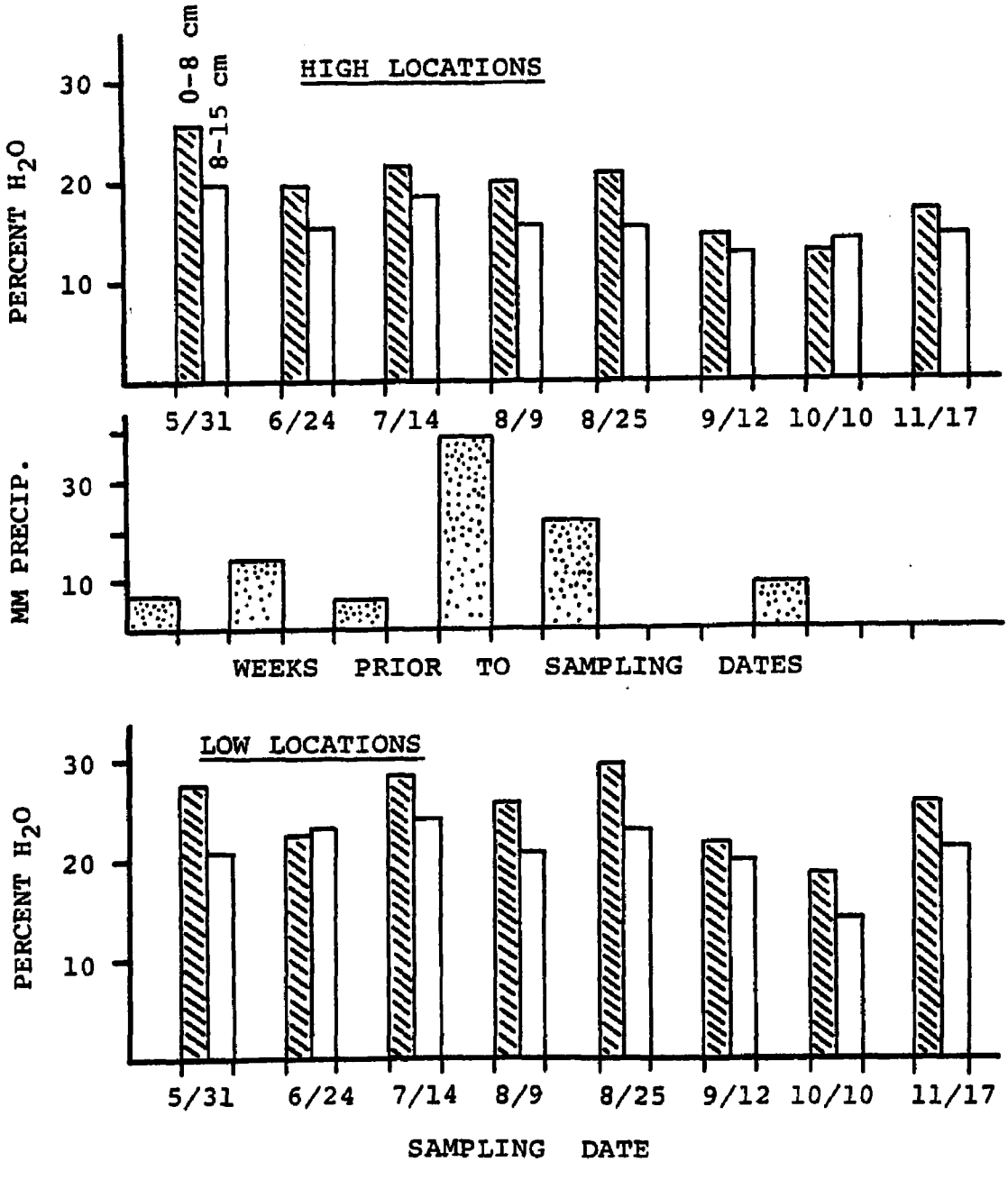

Figure 21. Soil moisture in HIGH and LOW areas, 1979, and total precipitation during the seven days prior to each sampling date.

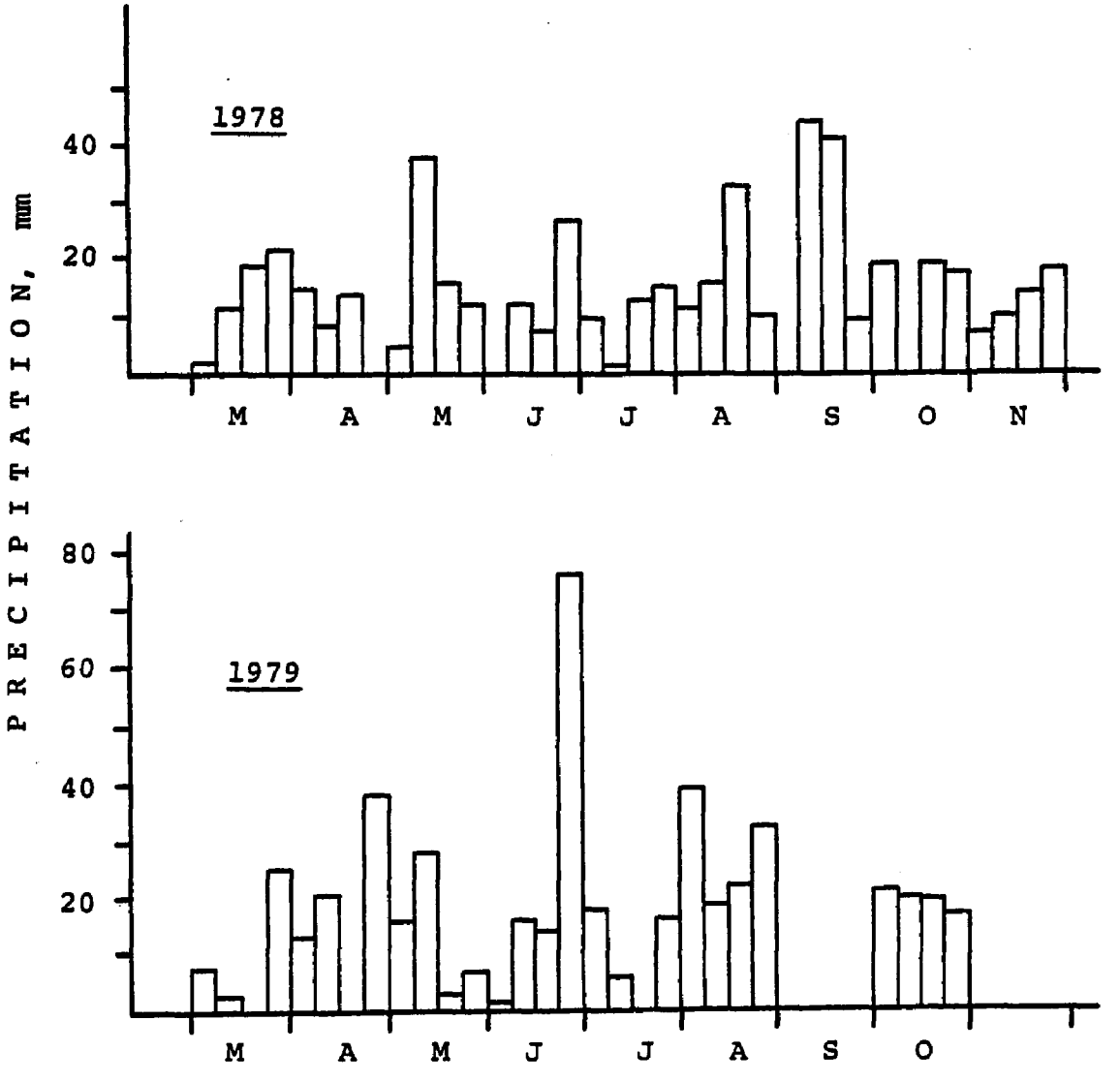

Figure 22. Weekly precipitation totals for 1978 and 1979 (Michigan State University Meteorological Station, East Lansing).

clear on all sampling dates, and served to enhance interpretation of the spatial distribution of P. inconstans.

3.2 General observations on the biology of P. inconstans

A) Reproduction:

Mating polydesmids were easily found in the field because the partners did not readily separate. They often remained in copula throughout collection, transport to the laboratory, and transfer to culture jars.

In four successive years, the first matings were always observed in early to mid-April. During May, copulas occurred with increasing frequency. None were seen in late July and August. Again in October, and as late as November 17, mating occurred both in the woodlot and the garden population.

Egg chambers were located only in Baker woodlot, in 1979 - the first one on June 7. Two others were discovered on June 28, seven more on July 12, and the last one on August 9. All of them had been built on pieces of wood with smooth surfaces. The preference for smooth substrates as nest-building sites, recorded in laboratory cultures, appeared to be true in the field as well.

Of these nests, four contained eggs:

June 28: 89 eggs, on which the chorion had just recently ruptured;

July 12: 62 eggs, freshly laid; and 68 eggs, chorion ruptured;

August 9: 70 eggs which had been invaded by fungus and were not

viable.

Three nests (July 12) were empty, but the split and discarded chorions were still in them: the eggs had hatched. Four nests were empty, but contained no chorions: possibly they had been plundered, since two of the chambers had irregular holes in the top and sides, larger than those usually made by escaping young. The remaining three each contained a beetle larva, which may or may not have been responsible for the absence of eggs.

Overall, the evidence on egg-laying in the field is meagre. But there are indications that destruction of eggs is a factor that limits the potential of the species. Fungal mycelium, tightly packed inside the chamber, has also been observed by Seifert (1932) in the field. That author furthermore implicates millipedes, centipedes and carabids as nest plunderers and predators on first instars of Strongylosoma pallipes Oliv.

B) Molting and aggregation:

Seifert (1932) noted that the first three instars of Strongylosoma pallipes remained closely aggregated. Having separated them and distributed them over a larger area, he observed the re-formation of the original aggregations. Harding (1969) used "feeding flocks" as a descriptive term for first instar larvae of P. coriaceus, and Blower (1967) mentioned that aggregations of Polydesmus spp. may be family groups.

The "feeding flocks" of Harding were observed only twice in the woodlot site. The two groups contained 24 and 17 instar I respectively. They were obviously tight groups, though the individuals

rarely touched each other. In culture, the offspring from one nest also travel together, in loose formations, but with all individuals moving in the same direction. Later stadia often aggregate in one small area of a culture jar; that could, however, simply indicate localized optimal conditions. Aggregations observed in the field, particularly in the fall of the year, consisted of a mixture of stages from the fourth up to adults.

Molting individuals were extremely difficult to locate in field situations. A total of 18 molting chambers were found during hand-collection in August, September and October of 1979. Two general types of location had been chosen by the animals:

1) The underside of logs, i.e. that part of logs that is tightly apposed to the soil underneath; the chambers were built on the log itself, but protruded into the soil beneath it. (n = 5 chambers)

2) The frass channels inside logs, near the log's surface. Eight animals, all located close together, had chosen small round holes (such as xylophagous beetle larvae would make) in the light-colored wood of a relatively undecayed log; the chamber walls were of the same light color and consistency as the frass around the holes. Five other individuals were located in a channel of a dark-colored, well decayed log. Again, the chamber walls appeared to be made of decayed wood.

Seifert (1932) mentions that S. pallipes is one of the last litter-inhabitants to disappear for hibernation, and one of the first to reappear in the spring. Peaks of activity in most temperate-zone species seem to occur mostly in spring and to a lesser degree in the fall (Banerjee, 1967; 1973; Barlow, 1957). P. inconstans, in our regions, shows a similar behavior pattern. In early March, while snow covers the

ground in patches (and logs cannot be moved because they are frozen to the ground), even short periods of warming weather trigger millipede activity. Wherever the sun penetrates to the litter, and around thawed dead branches, P. inconstans can be found between wet leaves and on the sides of exposed woody debris. No aggregations are obvious at that time; in small-scale favorable areas, the individuals appear quite well dispersed.

Throughout spring and summer, P. inconstans shows no distinct aggregations, with the possible exception of instar I, as mentioned earlier. But in the fall, especially in early to mid-October, large aggregations can be found on the sides of logs (Figure 20). Most of these are quite loose, and contain up to about 20 individuals of all stages present in the population at that time (IV to adult). The animals frequently congregate right at the wet-dry line which can be found on the sides of logs at various heights. In November, on mild days, the same behavior can be observed. Not until late November does the species finally retire for the winter.

C) Parasitism in the field:

Gregarines have been found to be endoparasites of various millipede species (Seifert, 1932; Johnson, 1952). Nematodes, also mentioned by Baker (1978 a), occur as ectoparasites of P. inconstans. They penetrate the soft pleural tissue between segments, and are most easily seen on live specimens: they appear as tiny transparent curls. But of the many hundred individuals collected in Baker woodlot, only a few were parasitized by nematodes. At least in 1978-79, the degree of nematode infestation appeared to be negligible.

The ectoparasitic deutonymphs of a mite, however, were found with greater regularity. The species was not determined with certainty, but behaved much like Histiostoma sp., which has been implicated by Baker (1978 a) as a major cause for the deterioration of iulid cultures.

These parasites are again most easily counted on live animals. Once immersed in alcohol, they tend to release their hold on the hosts. From November 1978 to October 1979, twelve catches of live animals (range of total P. inconstans per catch: 67-334) were examined for mite parasitism. The percentage of animals parasitized (Table 24) ran from a low of 0.36% (April 29, 1979) to a high of 7.76% (October 10, 1979). Over the entire season, 2.67% of all examined animals carried mites. Twenty-three of these millipedes (or 37.1%) were adults; 19 (or 30.6%) were subadults; 13 (21.0%) were instar VI; 5 were stadium V and one, the smallest stage found to be parasitized, was a IV. Small stages appear to be parasitized only rarely by mites - although in cultures containing stadia I and II, mite infestation can be a severe detriment.

Overall, mite infestation of the woodlot population could not be called extensive. Most millipedes carried a total of only 1 to 4 mites (mean number of mites per animal: 2.77). Ninety-seven percent of the time, the mites were attached to appendages; only two stadia VI had parasites on their ventral pleurae. None carried mites on their heads - as often happens in heavily infested laboratory cultures.

Table 24. Parasitism of P. inconstans by ectoparasitic mite deutonymphs in the woodlot.

	1978 // 1979												
Date	11/3	11/8	11/10	3/18	3/23	4/14	4/16	4/29	5/31	6/6	9/15	10/10	Totals
No. examined	148	101	334	67	318	186	189	276	247	134	202	116	2318
No. parasit.	1	4	4	3	5	3	11	1	14	5	2	9	62
% parasitiz.	0.7	4.0	1.2	4.5	1.6	1.6	5.8	0.4	5.7	3.7	1.0	7.8	2.67

3.3 Seasonal stage distribution

A) Garden population

The yield in total numbers of *P. inconstans* from the 1976 funnel extractions was generally poor. In March and April for instance (Table 25) virtually no specimens were obtained, although hand collecting at that time recovered a number of adults for laboratory rearing. Later in the season, total numbers increased suddenly. As illustrated in Figure 23, adults and subadults remained elusive, while the bulk of the population consisted of the new recruits of the season. First and second instars occurred in large numbers in June. By July, most had graduated to II, III and IV. Progressively, the population advanced to instars VI and VII in September. The last extraction, on October 1, again brought very poor results.

During 1978, frequent sampling from cryptozoan boards gave somewhat better results (Table 26). For reasons of clarity, up to three collection dates were combined in one given data point. Any combined collections span no more than 10 days total, and the dates given in Table 26 are median dates between the first and last day of combined collection dates.

In April and May the majority of the population consisted of adults, with some VII and an occasional VI (Figure 24). From mid-June to mid-August, the adult stage was no longer represented: immatures now dominated the population. Not until September and October did adults and penultimate stages reappear. At that time, stadia IV to adult were all present with a slight preponderance of VI and VII (Figure 24).

While population recruitment was obvious in June of 1976, no

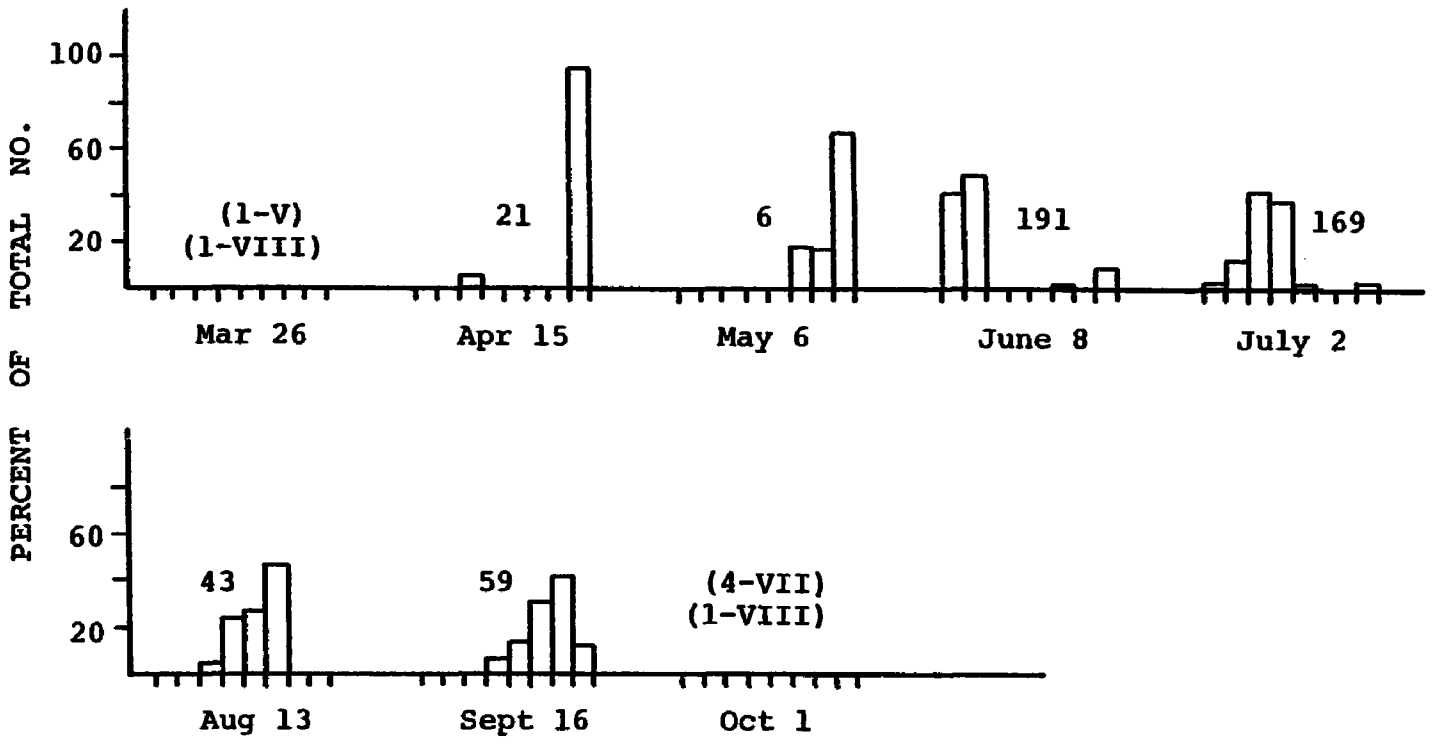

Figure 23. Stage distribution, in percent of total number per date, in the 1976 garden population. Numbers above each date = total number extracted; eight subdivisions per date = stages I through VIII.

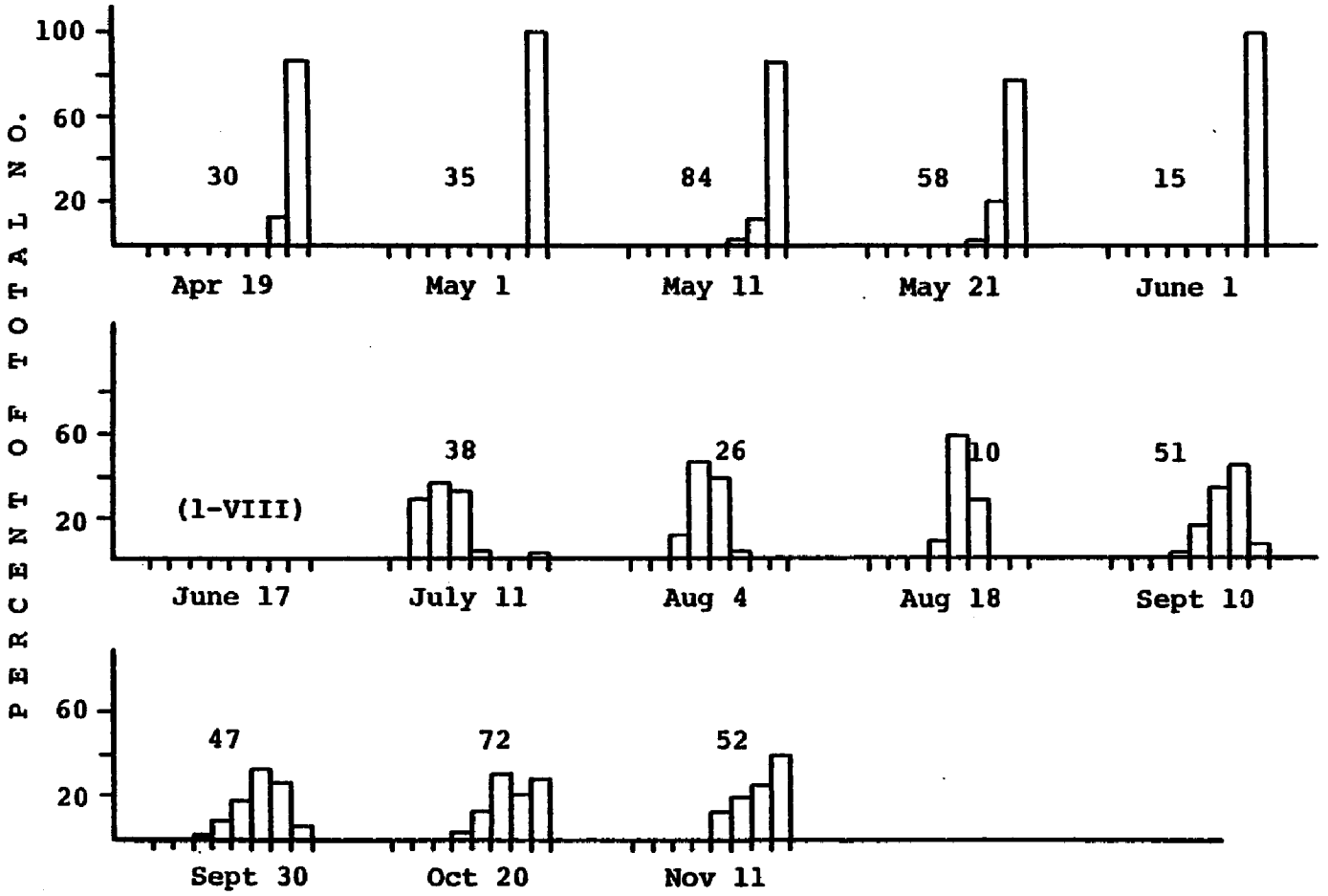

Figure 24. Distribution of stages in the 1978 garden population, in percent of total number caught. Total animals = number above each date; eight subdivisions per date = stages I through VIII.

instars I were collected in 1978. In fact, the collections in mid-June of 1978 yielded a single specimen, an adult female. It is most likely that the absence of first instars can be attributed to differential behavior: first instars may prefer deeper soil strata, and would therefore be obtained from soil samples to a depth of 8 cm (1976 data), but not from the upper 1 to 2 cm examined in the board collections. Furthermore, first and second stages have a short duration at higher temperatures and a large proportion of them might be undergoing ecdysis at that time and so be inaccessible to the collector.

Table 25. Total numbers of P. inconstans extracted from garden soil samples in 1976.

	Number extracted							
Date	3/26	4/15	5/6	6/8	7/2	8/13	9/16	10/1
total no.	4	21	6	191	169	43	59	5

B) The Woodlot Population:

For a clear presentation of stage distribution of the P. inconstans population, the results from all sampling techniques were combined (qualitative hand-collecting, and quantitative hand-sorting and funnel extraction). The total numbers thus obtained were respectably high (Table 27). Dates were combined, but only if they were not more than 4 days apart.

Starting with October 1978, Figure 25 illustrates the structure of

Table 26. Total numbers of P. inconstans captured from cryptozoan boards in the garden site, 1978.

Date	4/19	5/1	5/11	5/21	6/1	6/17	7/11	8/4	8/18	9/10	9/30	10/20	11/11
total no.	30	35	84	58	15	1	37	26	10	51	47	72	52

Table 27. Total numbers of P. inconstans obtained from Baker woodlot, all sampling methods combined.

1978

Date	10/10	10/24	11/3	11/10
total no.	232	142	178	436

1979

Date	3/8	3/18	3/23	4/16	4/29	5/15	5/31	6/6	6/26	7/14	8/9	8/25	9/13	10/10	11/5	11/17
total no.	41	152	358	587	296	68	272	152	215	224	164	304	350	326	447	418

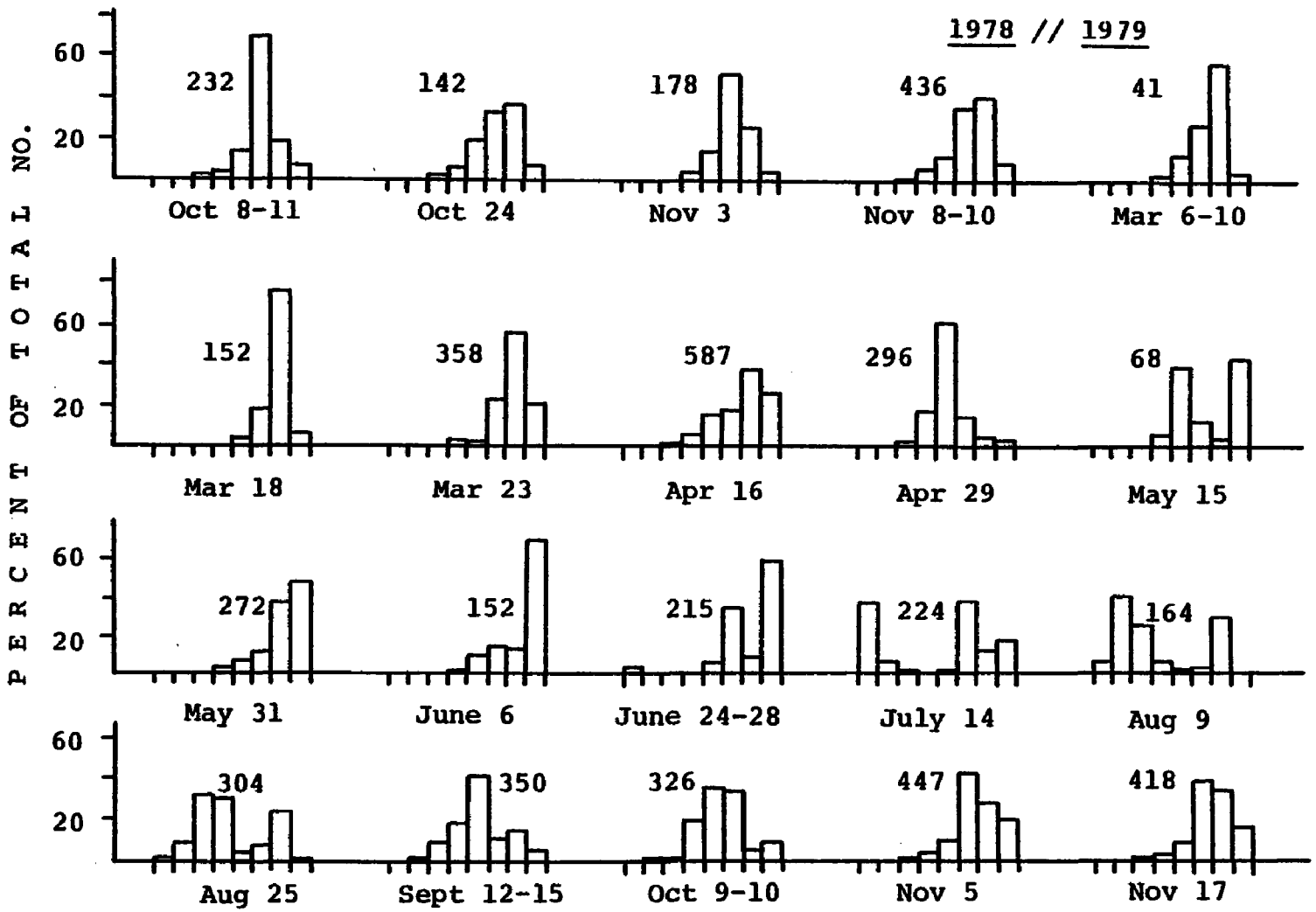

Figure 25. Distribution of stages in the woodlot population. Numbers above histograms = total number of animals; eight subdivisions per date = stages I through VIII.

the woodlot population. From October to November of that year, there was little evidence of advancement in the population. Occasional third instars were present; IV and adults occurred in low numbers; the bulk of the population consisted of VI and VII. No individuals smaller than III were found.

In early spring of 1979, the stage distribution was reminiscent of that recorded the previous fall, with possibly a higher frequency of VII (75% of the population on March 18). In late March to mid-April, the proportion of adults rose to 24%, only to fall again to 3% on April 29: the sudden appearance of an instar V peak on that date (60%) is not entirely explainable, but there is a possibility that fourth instars completed a spring molt to instar V at that time.

At this point one might consider the problem of molting- and therefore inaccessible - individuals in the population. The distinction between freshly molted and older individuals can not be clearly made in young instars. The first three are white; IV is only faintly pigmented; pigmentation, though variable, becomes more and more pronounced from then on. Subadults and adults have about the same coloration, but freshly molted individuals do show lighter pigmentation for a few days following ecdysis, particularly in the penultimate segment of adults.

Because darkening of the integument following a molt is gradual but relatively rapid, recognition of very recent molts is subject to some error. However, this kind of circumstantial evidence was recorded for hand-collected P. inconstans in the spring of 1979 (Table 28) and was found to enhance interpretation of the data illustrated in Figure 25:

On March 23 (Figure 25) the proportion of adults in the population began to increase; at that time, 17% of the males and 23% of the females appeared to have molted very recently (Table 28).

On May 31 (Figure 25) the percentage of adults had again doubled, and the percentage of recently molted individuals was even higher than in March (Table 28).

On June 6, the adult population reached a high of 64%, and contained 23-28% freshly molted animals.

As might be expected, data for subadults were similar to those for adults. Spring and early summer are apparently the times of a major maturation push through subadults to adults.

To return now to Figure 25: by early June, fourth instars were sparse, and adults constituted 64% of the population. By late June, the new generation had appeared, clearly offset from the generation of the previous year: II, III and IV were lacking, V were virtually non-existent, and adults were still prominent.

Table 28. Frequency of occurrence of recent molts, in percent of the total number examined.

	Total no. and (% recent molts)		
Instars exam.	March 23	May 31	June 6
VII females	45 (22.2)	46 (30.4)	19 (21.1)
VII males	55 (25.5)	22 (13.6)	
VIII females	47 (23.0)	53 (37.7)	57 (28.1)
VIII males	24 (16.7)	24 (33.3)	39 (23.1)

Table 29. Results of mark-recapture program for adult P. inconstans in the garden site.

Date marked	no. marked	no. recapt.	dates recapt.	days mark-recap.
Apr. 16	10	1	Apr. 30	14
19	6	0	Apr. 29	10
23	8	2	May 3, 10	10-17
29	17	3	May 3, 10	4-11
30	8	3	May 7, 10	7-10
May 3	8	2	May 7, 18	4-15
7	25	5	May 10, 18, 19	3-12
10	19	4	May 14, 19	4-9
14	15	1	May 29	15
18	9	0		
23	13	1	May 29	6
29	9	1	June 6	6
June 4	-	-		
17	1	0		
July 7	-			
18	-			
31	-			
Aug. 10	-	NO ADULTS FOUND		
16	-			
20	-			
Sep. 5	-			
15	3	0		
25	1	1	Oct. 16	21
Oct. 8	2	0		
16	5	1	Oct. 26	10
26	13	3	Nov. 11, 20	16-25
Nov. 11	22	0		
TOTALS	194	28 (14.4%)		

Spring 1979: 0 recaptured (of 31 collected)

Adult life appeared to be brief, however. Their numbers dwindled in July, not to reappear until September. At that time instars I and II had disappeared, and the numbers of IV, V and VI were replenished during the fall growth period. In November, VI and VII formed the bulk of the population. The proportion of adults was quite high then -

Table 30. Results of mark-recapture program in the garden site for subadult *P. inconstans*.

Date marked	no. marked	no. recapt.	dates recapt.	days mark-recapt.
Apr. 16	-	-		
19	2	0		
23	4	1+1 twice	May 7, 10, 14	14-21
29	-	-		
30	-	-		
May 3	-	-		
7	4	3	May 10, 18	3-11
10	1	0		
14	-	-		
18	2	0		
19	-	-		
23	5	0		
29	-			
June 4	-			
17	-			
July 7	-			
18	-			
31	-	NO SUBADULTS FOUND		
Aug. 10	-			
16	-			
20	-			
Sep. 5	-			
15	17	0		
25	4	0		
Oct. 8	8	1+1 twice	Oct. 16, 26	8-18
16	5	1	Oct. 26	10
26	5	0		
Nov. 11	16	1	Nov. 20	9
TOTALS	73	11 (15.1%)		

Spring 1979: 0 recaptured (of 9 collected)

whether the relatively low numbers encountered in early spring were a result of overwinter mortality must be left to speculation.

C) Mark-recapture program:

Mark-recapture programs are normally used to obtain population parameters such as survival, recruitment and life stage distribution. In the garden site, such a program was performed in order to answer two more specific questions:

a) does the adult population present in the spring survive through the summer? Or, alternatively, is there an overlap between post-reproductive adults and the newly-molted autumnal population of adults?

b) Can advancement of subadults to adults te documented seasonally by the disappearance of marked individuals?

The detailed results are given in Tables 29 and 30. As witnessed by several nil-recaptures, and by the relatively low over-all recapture rate (14 to 15 %), the program was not totally successful.

Intervals between marking and recapturing dates are of particular interest. For adults (Table 29) they may be interpreted in two ways. First: in spring and early summer, marked individuals were recaptured after a maximum of 17 days. Independent of time of marking, adults thus would not be found again after approximately two weeks had passed. This makes it highly unlikely that the last spring-marked individuals (in May) would be found again in September - about eight weeks later.

An alternative interpretation (supported by longevity observations in the laboratory) would be that these short time intervals indicate a continuous, gradual die-off of adults throughout spring and early summer; that the summer gap in the adult population indeed represents total mortality; and that in the fall replenishment of the adult contingent takes place through maturing individuals belonging to the

year's new recruits.

There is evidence to support the latter interpretation. Of all recaptured individuals (adults and subadults) 79% were found under the same boards they had originated from, and only 21% were found under neighboring boards (at most two boards away). In the garden site, the species seemed to exhibit little horizontal mobility, and emigration thus would add little bias; adult disappearance could indeed be best explained by mortality. Further corroboration is furnished by the similar seasonal occurrence patterns of subadults and adults in the garden population in 1976 and in the woodlot population in 1979.

Few subadults were found, and even fewer were recaptured (Table 30). It is likely that nil-recaptures in the case of subadults indicate exuviation, both in spring and fall. Evidence of graduation at these times was also found in the woodlot population (see Section 3.3.) as well as in the garden population, as discussed earlier.

Several authors have addressed themselves to the validity of mark-recapture techniques (McLeod, 1958; Turner, 1960; Greenslade, 1964; Ericson, 1977), but their search for bias concerned quantitative population parameters not included in the goals of the present study. In general it may be said that the mark-recapture program was, in itself, not conclusive. But the phenological data obtained for P. inconstans in the field support the tentative conclusions drawn from the program, just as the recapture results lend credence to the interpretation of sampling results.

3.4. Sex ratios in field populations

Figure 26 summarizes the sex ratios observed in the garden (1976 and 1978) and in the woodlot populations (1978-79); all stages from IV upward were included in the data. Records from the garden population were not entirely reliable because of relatively small sample sizes: seasonal variability in sex ratios ranged from 50 to 85% females in 1976, and 33 to 80% in 1978.

In the woodlot population, the percent females was relatively more constant (range over all dates: 37-66%), frequently around 50%. This would support the conjectures discussed in Section I.3: that the young possess a sex ratio of about 1:1, and that any sex-specific differences in mortality are not drastic, if indeed they exist.

Considering only the adult garden population (Figure 27) in 1978, there was some evidence of a seasonal difference in sex ratios: females appeared to prevail in the spring, males in the fall.

Using the much more ample adult material collected in Baker woodlot (Figure 28), a trend similar to that in Figure 27 could be seen. The percent females remained high through spring and summer (60 to 75%). In September and October the proportion of females dropped to about 25% - possibly because males tend to mature slightly faster than females.

But early maturation of males became apparent only for a short time; by mid-November the sex ratio was again close to unity. A shorter duration of the penultimate stadium in males would ensure insemination of females as soon as they matured. The sperm storage capacity of the species would then enable those females to produce

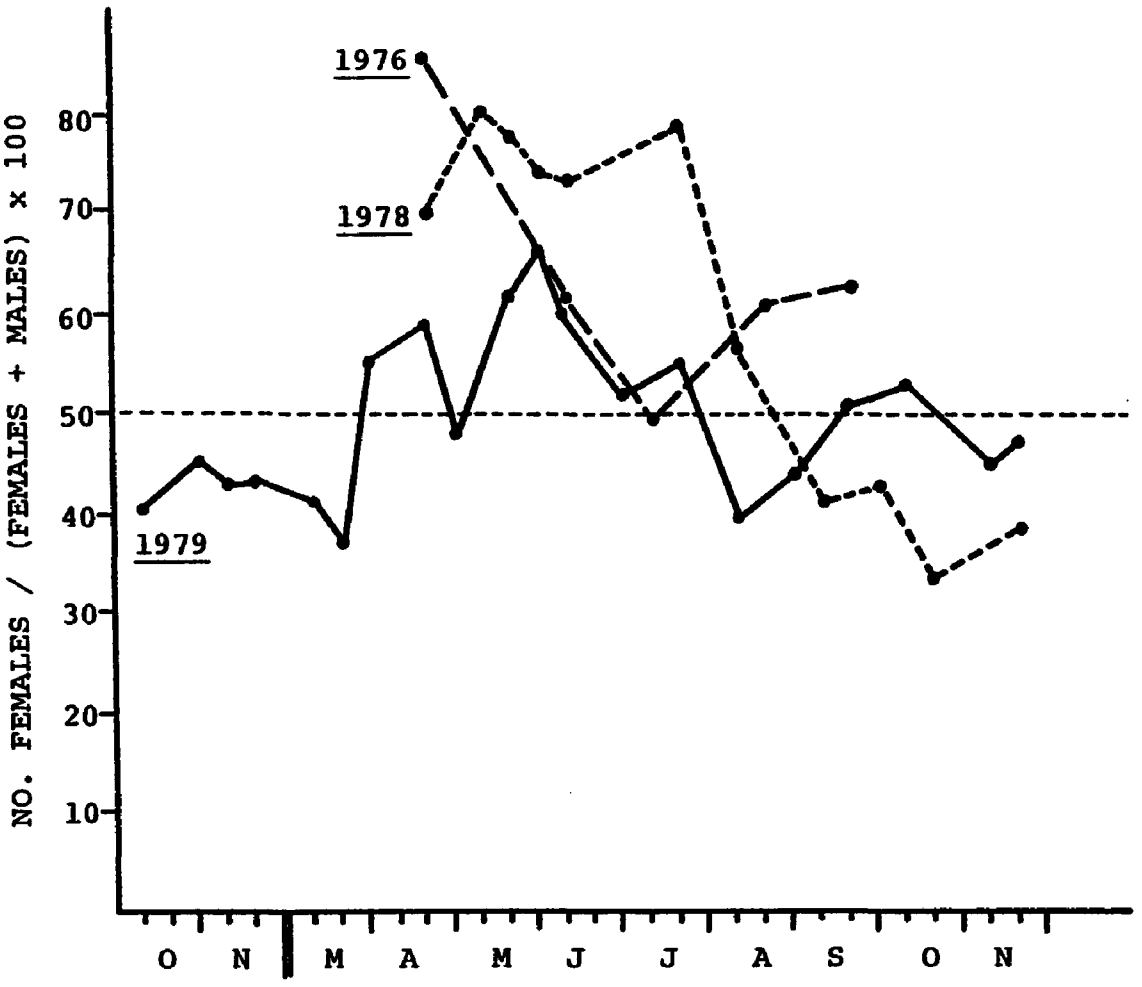

Figure 26. Percent females, of all stages IV through VIII, in the garden (1976, 1978) and the woodlot (1979) populations; where possible, data were summarized at 10-day intervals.

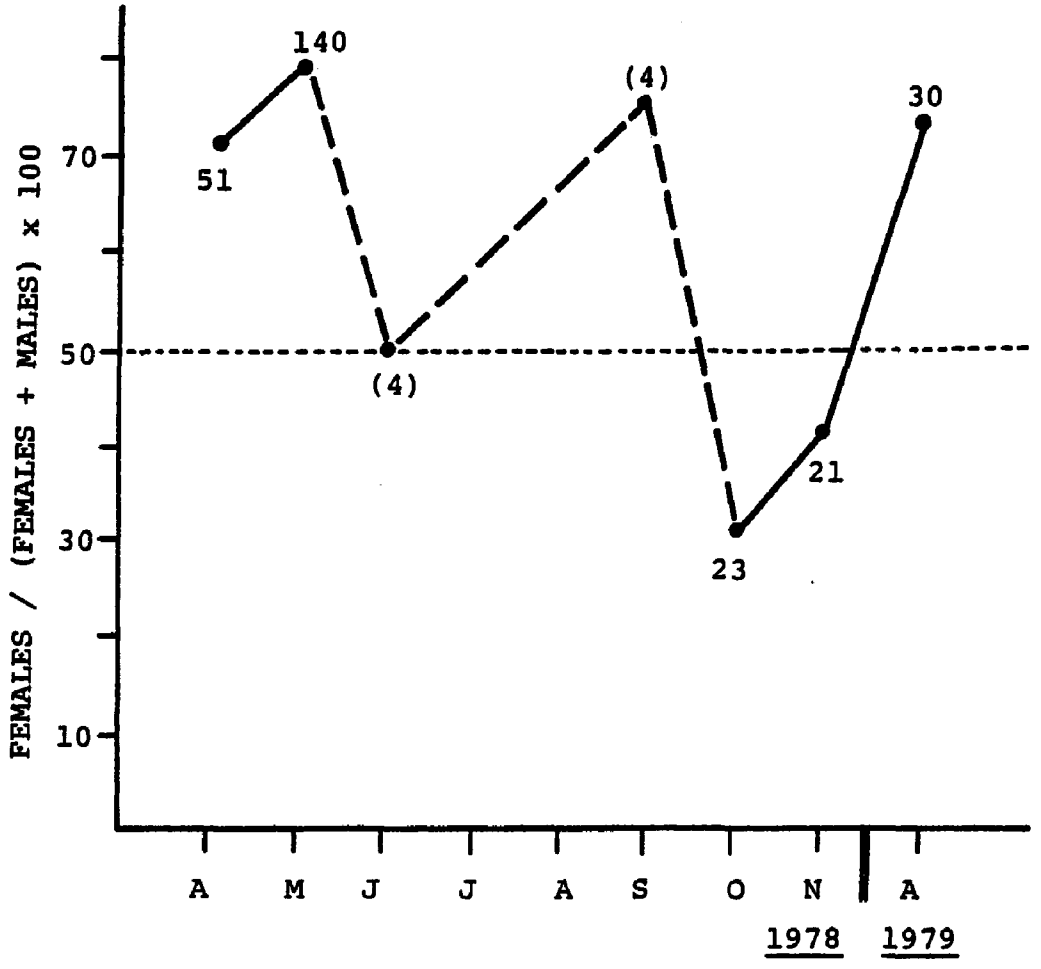

Figure 27. Percent females among adults in the 1978-79 garden population. Numbers are total numbers captured per month.

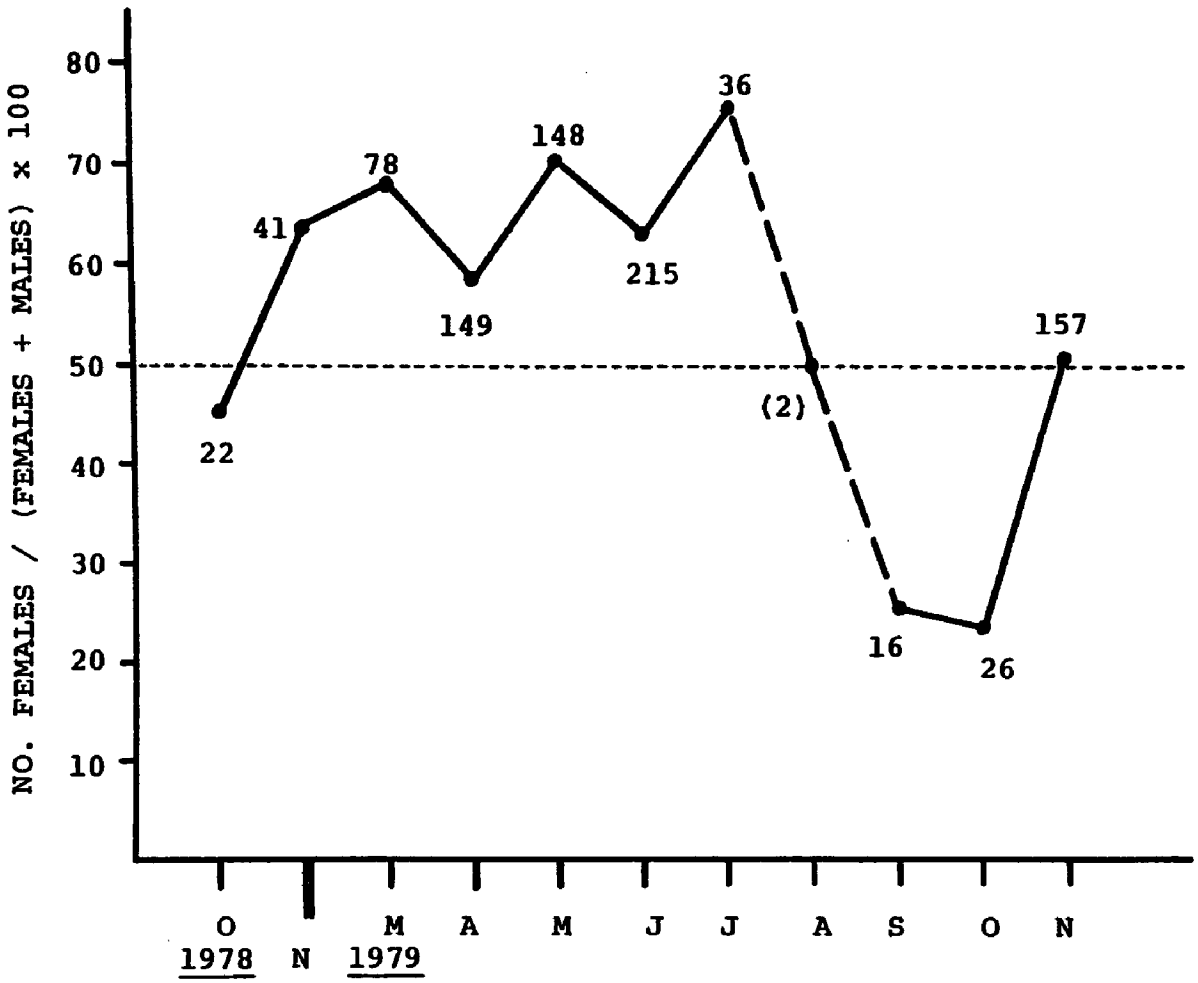

Figure 28. Percent females in the adult woodlot population, summarized per month.

viable eggs as soon as spring temperatures were conducive to it, without need for further mating.

3.5. Aggregation, distribution and density

A) Aggregation in samples:

Blower (1970) found that Polydesmus spp. in a British woodlot were much more compactly aggregated than iulids in the same habitat at various times of the season. In the present study, numbers of P. inconstans extracted from litter samples were high enough to merit calculation of variance/mean ratios as indices of sample aggregation. A X^2 test for small samples (Elliott, 1973) was used to evaluate population dispersion in comparison with a Poisson series, where

$$X^2 = s^2(n-1)/\bar{x}.$$

Table 31 details the results. Compared to a chart of 5% significance levels (Elliott, 1973), all values in Table 31 lay far beyond 5% critical values. Conclusions drawn for P. inconstans populations thus agreed with those drawn by Blower (1970) for other polydesmids. Dispersion was highly aggregated, irrespective of time of year. And aggregation was independent of population stage structure, i.e. it was no more pronounced at the time of yearly recruitment than at any other time. Even when the majority of individuals in the population had reached instars IV to VII (October 9, November 17), they were distinctly aggregated.

B) Distribution and density:

Considering only the litter-inhabiting segment of the woodlot

Table 31. LOW litter samples from Baker woodlot: evaluation of dispersion (aggregation in samples) of P. inconstans by X^2 test.

Date	no. of samples	$\bar{X}$/sam.	S^2	X^2
Apr 29	10	28.1	470.7	150.8
May 31	10	9.4	47.6	45.6
June 24	10	13.0	214.2	148.3
July 12	15	9.3	75.7	114.3
Aug 9	15	7.7	79.9	144.7
Aug 25	15	6.7	40.9	85.8
Sept 12	15	9.8	326.0	465.2
Oct 9	15	11.9	239.1	282.0
Nov 17	15	6.1	42.5	97.1

population (Table 32), differences between LOW and HIGH areas became clear. P. inconstans reached remarkably high densities in the rich litter strata of depressions: the maximum estimate was 450/m^2, on April 29. HIGH samples contained contrastingly few animals; estimated densities ranged from 4.8/m^2 in May to 38.4/m^2 in July.

Clearly, accumulated litter (see Table 23 for litter depths) with its properties of moisture retention and food availability, supported larger populations of P. inconstans. The standard errors of estimated densities were frequently large (e.g. April 29, June 24, September 12),

Table 32. Estimated densities of P. inconstans per m^2 of litter.

	Estimated no./m^2 ± S. E.	
	LOW	HIGH
Apr 29	449.6 ± 109.8	(no samples)
May 31	150.4 ± 34.9	4.8 ± 4.8
June 24	208.0 ± 74.1	8.0 ± 4.7
July 12	148.3 ± 35.9	38.4 ± 21.2
Aug 9	123.7 ± 36.9	30.9 ± 12.9
Aug 25	106.7 ± 26.4	28.8 ± 9.5
Sep 12	157.0 ± 74.6	(no samples)
Oct 9	189.9 ± 3.9	34.1 ± 0.6
Nov 17	98.1 ± 1.7	11.7 ± 0.4

indicating that the species was not evenly distributed through the sample units. However, standard errors were small in October and November, suggesting that aggregation tendencies may vary seasonally.

Soil core data reinforced the horizontal distribution pattern noted in litter samples. Table 33 shows LOW sample totals and means/sample unit of 20 cm^2. HIGH areas (Table 34) yielded few animals; over the entire season, only seven samples contained P. inconstans (of 200 samples total).

Density values for the soil-inhabiting population were purposely restricted to the surface area of one sample unit. The large number of

samples containing zero individuals made any estimates per m^2 highly unreliable. Thus the 0-8 cm subsamples on July 12, with a mean of 2.25 individuals/20 cm^2, would yield an estimated density of 1125 individuals/m^2 - a figure made totally unbelievable by three years of hand-collecting and sorting experience. Here again, aggregation played a role: of the 45 individuals in the July 12 samples, 19 (all instar I) wer extracted from one single soil core.

Differential distribution of P. inconstans with depth could thus not be assessed with accuracy. The only meaningful comparison would have involved densities/m^2 in each vertical habitat subdivision - an estimate possible for litter, but precluded for soil samples by the method employed.

Table 33. Number of animals extracted from soil core subsamples in LOW areas.

	0 - 8 cm		8 - 15 cm	
	total no.	mean/ 20 cm^2	total no.	mean/ 20 cm^2
May 31	11	0.55	6	0.3
June 24	20	1.0	11	0.55
July 12	45	2.25	9	0.45
August 9	7	0.35	1	0.05
November 17	3	0.15	2	0.1

Table 34. Number of animals extracted from soil core subsamples in HIGH areas.

	0 - 8 cm		8 - 15 cm	
	total no.	mean/ 20 cm^2	total no.	mean/ 20 cm^2
May 31	2	0.1	0	0
June 24	0	0	1	0.05
July 12	3	0.05	0	0
August 9	2	0.1	0	0
November 17	0	0	1	0.05

4. CONCLUSION

The stage distribution of P. inconstans populations was remarkably similar in different years and different sites. In contrast to longer-lived polydesmids (Blower and Gabbutt, 1964; Blower, 1969) or to those iulids possessing a life span of more than three years (Blower and Gabbutt, 1964; Blower and Fairhurst, 1968), there was little if any overlap between successive generations.

By designating the 1978 population of Baker woodlot as generation 0, population development could easily be described. Generation 0 reached maturity in fall of 1978 and spring of 1979. These adults

reproduced from May to late July, then died. Their offspring, generation I, rapidly grew to instars VI and VII, and some reached VIII late in 1979. In the spring of 1980 the remainder of generation I would reach maturity and, come May, would begin to produce generation II eggs.

Onset of egg-laying was not directly observed. The first eggs were probably laid in early May, when daytime soil and litter temperatures frequently exceeded 10°C. In the laboratory, 10°C allowed mating as well as the production of viable eggs, and oviposition frequency increased rapidly at temperatures above 10°C, indicating that field temperatures in May were indeed conducive to reproduction.

Given a reproductive period lasting from May to late July, an estimated 6 to 8 broods could be produced per female (based on temperature-dependent oviposition frequencies of 8 to 14 days). Females surviving through the breeding period would therefore lay a total of 300 to 500 eggs each, but some of these eggs were almost certainly destroyed by fungal attack and oophagy.

First instars appeared in early June in the garden, and in mid-June in the woodlot. Given diurnally fluctuating temperatures, an embryonic development time of 4 to 6 weeks in the field compared well with developmental rates observed in the laboratory: 4 to 6 weeks correspond to a time span intermediate between those recorded at 10° and 15.5°C constant temperature.

Growth was rapid at 15.5° and 21°C in the laboratory, supporting field evidence of fast maturation of the new generation from June to October. Adults collected in the fall conceivably may have been generation 0 (post-reproductive) individuals. But the inability to

locate any adults from late July through August in three different years furnished evidence to the contrary. Adults do not molt. All the more reason why their disappearance may best be ascribed to mortality rather than to deep vertical migration (the only other alternative). Stephenson (1961) also found no adults of Brachydesmus superus from August to October; he suggested that males died after mating, females after oviposition.

Fall-maturing adults thus consisted of individuals hatched the same year. They reproduced the following spring and completed their life cycle in approximately 12 months. There was no indication of iteroparity which, in iulids, is evidenced by continued molting and survival of adults through more than one breeding season (Blower, 1969; Blower and Fairhurst, 1968; Baker, 1978b). Similar interoparous behavior has been documented for other litter invertebrates as well. The isopod Tracheoniscus rathkei (Brandt) has a maximum life span of 2 to 3 years in the field (McQueen, 1976; Snider, in press). Brought into the laboratory, at temperatures ranging from 15.5° to 26.6°C, the species maintains iteroparity: up to four breeding periods are distinctly separated by non-breeding growth periods, and the number of young produced increases with age (Snider, in press). P. inconstans did not behave this way. Fecundity decreased with age, and all females died at the end of one, uninterrupted, reproductive period. Both observations indicated semelparity.

Population densities were relatively high in the woodlot. In pine forests, Rubcova (1967) found more than 15.6/m^2 (all diplopods included). For Glomeris marginata, 50/m^2 represents a high density (Bocock et al, 1967). Gist and Crossley (1975) gave a summer density

of 14 diplopods/m^2 in a Liriodendron forest. Only Bornebusch (1930), working in oak woods, arrived at a high estimate of 433 diplopods/m^2.

P. inconstans was distributed unevenly in the woodlot. That population size varies greatly between localities has also been noted by Spaull (1976), by Dunger (1978) for diplopods in grasslands, and by Bornebusch (1930) for total millipedes in three different forest sites. In P. inconstans, differential horizontal distribution could be qualitatively correlated to litter thickness and moisture. Litter fulfilled the dual function of food and cover. The quantity of litter available in palatable, moist condition also determined the characteristics of the animals' micro-habitat.

Uphill locations were drier, warmer, and poorer in food resources (judging by the quantity and state of the litter present). According to Manton (1956) polydesmids are inefficient burrowers and depend on existing crevices for movement. In low-lying areas, crevices allowing vertical movement away from unfavorable climatic conditions would have been provided by the thick, loose litter and crumb layer. In uphill areas, P. inconstans would have had to escape unfavorable surface conditions by taking recourse to the soil with its relative lack of food. it is conceiveable that the persistence of sparse uphill populations was aided by the presence of refugia such as half-buried branches, sheaves of dead bark, and logs.

5. SUMMARY

1) Polydesmus inconstans Latzel 1884 was reared in the laboratory

at constant temperatures of 10°, 15.5°, 21° and 26.6°C. Culture chambers consisted of clear plastic jars with snap-on lids. A plaster-charcoal substrate, overlain by periodically replenished duff, rotten wood and soil, was used as medium. Yeast was added as food.

2) Mating and construction of egg and molting chambers were described.

3) Qualitative accounts of oophagy by other millipede species, and of predation by beetles and centipedes, were given. Carabids and their larvae were shown to be of potential importance in the control of millipede populations. The centipede Tidabius tivius consumed first instars of P. inconstans, but preferred Collembola as food.

4) Duration of the stadia increased with successive stadia as well as with decreased temperature. Stadial durations at 15.5°C were virtually equal to those at 21°C. Differences between the sexes did not become apparent until stadium VII, which lasted significantly longer in females.

5) Sex ratios of progeny produced in culture approximated 1:1.

6) Immatures survived equally well at 15.5° and 21°C, both males and females showing survival percentages between 90 and 100%. Survival was lower for the first two instars at 10°C. 26.6°C resulted in close to 100% mortality of all instars tested (I through VI).

7) The relationship between adult longevity and temperature appeared to be linear between 10° and 21°C. 26.6°C decreased average longevity to approximately 60 days. Males survived longer than females at 10°C (285 vs. 212 days mean) and at 15.5°C (218 vs. 176 days mean).

8) A maximum of 22 ovipositions per female were recorded. Intervals between ovipositions increased with successive egg layings. At 21°C, 7-10 days elapsed between ovipositions, compared to 11-16 days at 15.5°C and 25-30 days at 10°C. The number of eggs laid increased through the first few ovipositions at all temperatures, then underwent a steady decline. Fecundity was lowest at 10°C and highest at 21°C, a temperature suggested to be near-optimal: high ovipositon frequency coupled with a large number of eggs per ovipostion allowed for the highest of all reproductive rates observed.

9) The reproductive biology of field-collected females was compared to that of females reared from egg to adulthood at constant temperature. Both types of females were kept under identical conditions, at 21°C. The results showed that laboratory stock could be used to obtain valid data on the potential of the species.

A maximum total number of 1106 eggs were recorded for one female. On average, females produced 500 to 700 eggs in a life time. Laboratory-reared, isolated females showed the highest mean number of ovipositions (14), the largest mean total number of eggs (9695) and the longest duration of the reproductive period (116 days).

Provenance and past history (laboratory vs. field) had fewer significant effects on reproductive biology than specific rearing

conditions (females in isolation vs. females paired with males). As a rule, both types of isolates laid more eggs and lived longer than their paired counterparts.

10) Viability of eggs did not differ significantly between 15.5° and 21°C (94% and 92% respectively), but was reduced to 85% at 10°C. Females kept in isolation showed greatly decreased egg viability only after the first 8 to 10 ovipositions. Sperm storage capacity was thus effective during the time of highest fecundity.

11) Populations of P. inconstans were studied in two field sites: a home garden (1976 and 1978) and a deciduous woodlot (1978-79), both in the vicinity of Michigan State University campus. Qualitative data on seasonal stage structure were obtained in both sites. The woodlot population was also sampled quantitatively for population density and spatial distribution.

12) Stage structures of the populations were similar in the three years of study. Eggs were laid from May through July by generation 0, which died out after reproducing. Hatching of generation I began in June and ceased in late August. By October, the bulk of the population had reached instars V, VI and VII, and a small proportion of this generation I had graduated to adults by November. The majority did not reach maturity until the following spring, to give rise to generation II, and then to die.

The life cycle in the field encompassed one year. Laboratory observations on the species' reproductive pattern supported the

conclusion that P. inconstans was semelparous.

13) The P. inconstans population in the woodlot was relatively dense. Estimates varied with the season. For low areas (depressions at the bottom of slopes) densities of about 100 to 200 individuals/m^2 were obtained. In uphill areas, densities reached about 30/m^2. These values concern only the segment of the population inhabiting litter and duff. Due to inadequate sampling procedures, estimates for densities in the soil could not be obtained.

Differential densities were qualitatively correlated with litter thickness, moisture and temperature measurements in the two locality types (low depressions and uphill areas).

14) Nematodes and mites were found to be ectoparasites on P. inconstans in the woodlot. Nematode infestation appeared to be negligible. Mites were encountered more frequently, and their occurrence on 2318 live millipedes was recorded. Degree of parasitization varied through the season. Overall, 2.7% of the population were parasitized (range 0.4% to 7.8% on given dates of examination). Most affected animals carried a total of 1 to 4 mites, and instars VII and VIII were found to be the most frequent hosts.

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