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ASPECTS OF THE BIOLOGY

OF

SELENOCOSMIA STIRLINGI HOGG

(ARANEAE, THERAPHOSIDAE)

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A thesis submitted for the degree of Doctor of Philosophy Zoology Department, Monash University

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ABSTRACT

This thesis reports on a study of growth determination in the Australian theraphosid <u>Selenocosmia</u> <u>stirlingi</u> Hogg.

In particular, the effects of food availability, temperature and photoperiod on growth and development were assessed by measuring changes in size and weight. Laboratory and field experiments were performed with juvenile spiders, primarily from instars III to V.

The general biology of the spiders was examined in the laboratory, and field studies were undertaken to provide information on the temperature and rainfall at the field site and on spider activity patterns.

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CHAPTER 1

INTRODUCTION

1.1 OVERVIEW OF THE RESEARCH

This thesis reports on the growth biology of the Australian theraphosid <u>Selenocosmia stirlingi</u> Hogg. In particular, the growth of early instars is investigated, with laboratory experiments designed to assess the roles of food supply, temperature and photoperiod in determining growth and development. Several parameters were used to characterise the growth process and to reveal the strategies and development involved.

Details of the biology of these spiders, such as identification of the first freeliving stage, adult sizes, feeding, moulting and mating bahaviour and so on, were acquired through the observation of specimens collected in the field and maintained in the laboratory. Such information provided a necessary foundation for the design of the experiments mentioned above, and the interpretation of the experimental results.

A study of the field ecology of <u>Selenocosmia stirlingi</u> at Coombah (New South Wales) was undertaken to reveal details of the annual activity patterns of the spiders, the temperatures and prey availability. These details were used to determine realistic limits for the temperatures tested in the laboratory, and to relate the laboratory findings to the spiders in their natural setting.

In this chapter, the nature of growth and development in spiders is reviewed with attention to the effects of environmental variables. A summary of the research, described in the following chapters, is also provided.

1.2 ARTHROPOD GROWTH AND DEVELOPMENT

1.2.1 <u>Terminology</u>

In order to avert any confusion, I have taken <u>growth</u> to mean the increase in size or weight which occurs during an animal's life, and <u>growth rate</u> as a measure of this increase per unit time. <u>Development</u> on the other hand, has been used to refer to transition through certain stages (e.g. from an egg to a juvenile), and <u>developmental rate</u> as the time taken to reach or pass through such stages in a given period of time.

1.2.2 The Processes

It is generally accepted that although arthropods possess some regions of extensible cuticle, growth is achieved by successive replacement (moulting), owing to the presence of a large inextensine cuticular exoskeleton (Wigglesworth 1939, Hackman 1971, Neville 1975, Richards 1951). On the other hand, Bordereau (1982) contends that cuticular expansion without moulting is not unusual and cites many examples, such as abdominal expansion in arachnids. However, with a few exceptions (e.g. physogastry in termite queens), such expansion appears limited, since many of the animals he cites also moult (e.g. lepidopterous larvae) to achieve growth, major rejuvenation and/or formation of new cuticular structures.

1.2.3 <u>Regulation</u>

Control of growth and development in spiders, as with other arthropods, has been demonstrated to be regulated by hormones released from the brain (Krishnakumaran & Schneiderman 1970, Bonaric 1976, 1977a, b, 1978, 1979, 1980a, b, 1981, 1982, Bonaric & De Reggi 1977, Bonaric & Juberthie 1980, Juberthie & Bonaric 1980, Prasad & Kulshrestha 1980,

Juberthie 1983), but the factors stimulating the brain are less well understood. Bonnet (1926, 1930, 1932, 1933, 1934, 1938), in studying a large number of species, concluded that temperature and the amount of food received could influence the total number of nymphal instars, the length of the development period and longevity. In addition, he and others drew attention to the "coefficient individual" or genotype, which causes spiders hatching concurrently from a single egg sack and reared under apparently identical conditions, to exhibit great variation in growth and development. Browning (1941) also concluded that humidity and light conditions influence spider development, probably basing this conclusion, in part, on observations of growth determinance in insects.

The following sections describe the ways in which each of these external variables have been found to influence the growth and development of spiders, and the methods used to measure or regulate these variables and to quantify the spiders' responses.

1.3 <u>REVIEW OF CHANGES IN SPIDER GROWTH AND DEVELOPMENT PRODUCED</u> <u>BY ENVIRONMENTAL FACTORS</u>

1.3.1 Effects of Food Availability

The rate at which food is supplied influences growth and development in spiders through its effects at several levels. The efficiency with which prey are killed and consumed is affected by the rate of supply, with different responses recorded for different species (Witt <u>et al</u>. 1978, Kajak 1978). In addition, the basic metabolic demands of a spider have been shown to respond to changes in food availability (Anderson 1974, Tanaka & Itô 1982). These various responses are necessarily interconnected as the absolute metabolic demands and preferred food intake are related to spider size, which in turn depends on its growth (Haynes & Sisojević 1966, Robinson & Robinson 1970, Breymeyer & Jóźwik 1975, Kajak 1978, Witt <u>et al</u>. 1978, Eberhard 1979).

1.3.1.1 Effects of Food Availability On Feeding

Regardless of the rate of food supply, no spider has been observed to eat all the prey provided over an extended period, even when the rate of food supply resulted in impaired growth or development (Turnbull 1962, 1965, Hagstrum 1970a, Kajak 1978, Eberhard 1979, Hardman & Turnbull 1980). Furthermore, elevated rates of food supply, while producing increased consumption rates, have been shown to result in a decrease in the efficiency of food utilization (i.e. the amount consumed/amount supplied) according to power functions in various species (Kajak 1978). Turnbull (1962) found that the percentage of prey captured fell as the supply increased, while the overall consumption increased. The total dry weight of food extracted from each prey item was generally sustained at constant levels within each stage (except stage 1), regardless of the supply rate. In spite of this moderating influence, the rate of food supply still had a positive effect on the rate of food consumption. Spiders ingest the liquified, predigested contents of their prey (Turnbull 1973, Foelix 1982). Owing to this, Edgar (1971) and Workman (1978) emphasised that for spiders, excretion forms an almost negligible component of their energy budget and estimates of assimilation efficiency from 80% to 100% were not uncommon (Célériér 1971, Steigen 1975, Humphreys 1978).

In general, increases in the rate of food supply result in increased rates of prey capture, but at ever decreasing rates (Kajak 1978). Similarly, increases in the rate of prey capture produced increased rates of consumption, but at ever decreasing rates owing to diminishing consumption efficiency (Turnbull 1962). Therefore, simple factor alterations (e.g. x2 or x3) to the rate of food supply were not directly reflected in the food intake, although there was a positive correlation.

Through investigation of the impact of spiders as predators on prey populations (with the possible application to agricultural practises or simply the understanding of ecological systems), attempts to extend the understanding of these feeding phenomena have been made through studies of hunger (i.e. the amount of food required to satiate a spider after a period of deprivation) (Haynes & Sisojević 1966, Miyashita 1968a, b, Nakamura 1968, 1972, 1977, Hardman & Turnbull 1980). These studies have basically resolved the mean rates of food supply into the periods devoid of prey and those when prey was present. The duration of the period of food deprivation has been shown to effect positively the occurrence of feeding behaviour (Hardman & Turnbull 1980), the total number of prey killed (Haynes & Sisojević 1966), with an upper limit to the increase (Nakamura 1968, 1977), and the efficiency of prey consumption (Haynes & Sisojević 1966). In general, the level of hunger increased with the duration of the food deprivation, but at an ever decreasing rate, approximately following Holling's (1966) equation (Hardman & Turnbull 1980). Within each instar, Miyashita (1968b) and Haynes and Sisojević (1966) found post-ecdysial peaks in food consumption (except for adult males) and also peaks immediately following oviposition (Haynes & Sisojević 1966, Vlijm & Richter 1966). The amount of food consumed after a post-ecdysial fast was proportional to the duration of the fast, with the difference between the post-fast, post-ecdysial consumption and the normal post-ecdysial intake required "...for the recovery from exhaustion by hunger..." (Miyashita 1968b, p. 337). A post-ecdysial period of limited food supply postponed the feeding peak, and resulted in no increase in total consumption, as an energy deficit was not produced (Miyashita 1968a). So food consumption was not only a function of the rate of food supply, but also its temporal patchiness, with periods of fasting resulting in increased feeding activity.

1.3.1.2 Effects of Food Availability on Metabolism

Food availability and feeding have also been demonstrated to affect the basic metabolic rates of spiders and, via such processes, to influence growth and development.

In many species, starvation produced a depression in metabolic activity. Anderson (1974) recorded a 32% to 40% decrease in 0_2 consumption during the first 14 to 30 days of starvation, followed by the maintenance of depressed levels for extended periods in <u>Lycosa lenta</u> and <u>Filistata hibernalis</u>. Although the starved spiders lost weight, Anderson (1974) recorded no associated changes in their activity patterns. In <u>Pardosa astrigera</u>, there was an increase in the metabolic rate over the first two days of starvation, which was followed by depressed rates similar to those observed by Anderson (1974), Itô (1964), Miyashita (1969) and Tanaka & Itô (1982).

Elevated rates of metabolism, up to three-fold have been associated with feeding behaviour (Ito 1964, Hagstrum 1970b), and in times of food shortage (in contrast to Anderson's (1974) observations), Ford (1977) found that metabolically expensive foraging behaviour was curtailed. Increased 0₂ consumption (up to thirteen-fold (Hagstrum 1970b)) has also been associated with ecdysis and, to the extent that food availability affects the number of instars (see Section 1.3.1.3), the lifetime energetic costs of ecdysis will also be affected.

1.3.1.3 Effects of Food Supply on Growth and Development

Increased adult weights and/or sizes have been directly correlated with increased food supply (Turnbull 1965, Miyashita 1968a, Wise 1975, Vollrath 1983), and increased rates of weight gain with elevated rates of consumption (Turnbull 1962). Most studies provide information on overall trends or make crude quantitative

explanations. However, thorough quantitative analyses have been provided by Turnbull (1962), based on weight changes in each instar of <u>Linyphia</u> <u>triangularis</u> with variation in food consumption, and by Miyashita (1968a), who examined size increases related to discrete levels of food supply. Turnbull (1962) found a direct linear relationship between the rate of weight gain and the rate of food consumption, and the total weight gained within an instar increased with increasing food consumption at an ever decreasing rate.

There appeared to be a maximum level of growth (weight gain) which could be achieved within each stage before a moult occurred. Low levels of food were only sufficient to satisfy maintenance costs (as suggested by food debts discussed in Section 1.3.1), and higher levels were required to produce weight gains. While there were also direct linear relationships between the rates of development and the rates of food consumption (the slopes of which declined with each successive stage), in contrast to weight gains, development (moulting) was found to continue slowly even in the absence of feeding.

Miyashita (1968a) found that decreasing the rate of food supply reduced the overall size increase (carapace width) in each instar and the final adult size. Size differences were also influenced by the number of nymphal instars prior to maturation (see below), with additional instars at lower feeding levels, at least partly, compensating for the slower growth rates. Thus, spiders from different feeding regimes could reach the same adult size if those from the lower feeding levels underwent more moults than those at the higher levels.

The most commonly reported developmental response to an increase in food availability is a reduction in instar duration or an increase in the rate of transition through an instar (Browning 1941, Deevey 1949, Turnbull 1962, 1965, Hagstrum 1970a, Vollrath 1983). Although increased food

supply increased the rate of development and adult weight in <u>Agelenopsis</u> <u>potteri</u>, this spider consistently matured in only seven stages (Turnbull 1965) and <u>Linyphia triangularis</u> in five stages (Turnbull 1962). Male <u>Nephila clavipes</u> were also found to mature in a fixed number of instars, but females underwent one more moult on a "poor" diet than they did on a "rich" diet (Vollrath 1983). In contrast, <u>Lycosa tinsignata</u> matured in instar VI, VII or VIII (Miyashita 1968a) and <u>Latrodectus mactans</u> males and females required 4 to 8 and 7 to 9 moults respectively to mature (Deevey 1949), in proportions which were directly related to the rates of food supply. Apparently, different species respond differently to variations in food supply in terms of both growth and development strategies.

In addition to assessing the effects of different rates of food supply, some attention has also been directed to the influences of diet compositon. Failure of Lycosa tinsignata to mature on a diet consisting solely of Drosophila sp. led Miyashita (1968a) to conclude that such a diet was nutritionally deficient. Alternatively, Turnbull (1962) had no such developmental problems with Linyphia triangularis reared on a similar diet. Peck and Whitcomb (1970) reported improved rates of development, maturation and survival in Chiracanthium inclusum when the diet of Drosophila melanogaster was supplemented by different kinds of prey. Prey was provided on an item basis rather than by weight or calorific value, so the results they obtained may, at least in part, have reflected greater absolute rates of supply. The calorific values of Tribolium sp. larvae, Tenebrio sp. larvae, young crickets and houseflies were measured by Breymeyer and Jóźwik (1975) and Drosophila sp. by Edgar (1971) to yield the following results: 2.4, 3.2, 1.0, 1.3 and 1.1 calories/mg respectively. So in terms of energy content, prey species may not be

equivalent, and furthermore, different parts of prey may similarly differ in nutritional accessibility and/or value (Haynes & Sisojević 1966, Greenstone 1979), and spider's may consume them accordingly (Robinson & Robinson 1976).

Differences in growth and development associated with food supply have also been assessed in terms of fecundity. Larger females (associated with higher rates of food supply) tend to lay more eggs (Petersen 1950, Kessler 1971, 1973, Kiritani & Kakiya 1975, Wise 1975, 1976, 1979) or heavier eggs (Turnbull 1962) than smaller females. These phenomena have been partly attributed to greater abdominal capacity (i.e. more space for extra or bigger eggs), and partly to the enhanced ability of larger spiders to catch and eat more food. Estimation of the rate of food supply on the basis of egg production (e.g. Eberhard 1979) may be unreliable, as egg sack production has been recorded under conditions of starvation (Miyashita 1968b, Anderson 1974).

1.3.1.4 Summary of Food Supply Effects

Variations in the quality and quantity of available food have been shown to have direct effects on spider growth in terms of size increases, weight gains and development, and the rates of each of these. The influence is achieved though changes in the rates of prey capture and consumption, consumption efficiency, foraging activity, and basal metabolic demands. For each of these component effects (and undoubtedly others) considerable variation has been observed, but in spite of this the overall trends of increased and/or more rapid growth and development with increased food supply have been well established.

1.3.2 Effects of Temperature

In spiders, temperature has been shown to have no effect on absolute growth (Jones 1941, Workman 1978), but to have a direct influence on the rates of both growth and development and the metabolic processes and feeding behaviour on which they depend (Browning 1941, Jones 1941, Turnbull 1962, Haynes & Sisojević 1966, Horner & Stewart 1967, Anderson 1970, Hagstrum 1970a, b, Peck & Whitcomb 1970, Anderson 1974, Eskafi <u>et</u> al. 1977, Workman 1978, Van Praet & Kindt 1979, Stewart & Martin 1982).

Peck and Whitcomb (1970) found that Chiracanthium inclusum grew more quickly at 90 degrees F (32 degrees C) than at 76 degrees F (24 degrees C) and Hagstrum (1970a) found that between 12 and 30 degrees C, increasing temperature reduced the average minimum instar duration of Tarentula kochi by 1.65 days/degree. Hagstrum (1970a) also found that the durations of instars of spiders in the field were shorter than estimated on the basis of air temperature, but differences in food supply and the microclimate in which the spiders lived may have affected his findings (see Section 1.4.2.3). The time taken by Agelena naevia to pass through five instars was more than doubled by a 10 degree C increase in temperature (Jones 1941). A similar two-fold decrease in the instar durations of Tegenaria atrica from 20 to 30 degrees C was used by Browning (1941) to interpolate the rate of development for an intermediate temperature. Workman (1978) and Eskafi et al. (1977) state that, rates of growth and development have been shown to have a logarithmic dependence on temperature when examined over a sufficient range, rather than a direct linear relationship. This is not surprising as the rates of growth and development no doubt depend on the overall metabolic rates, which have been widely demonstrated to have a logarithmic dependence on temperature (Anderson 1970, Hagstrum 1970b, Anderson 1974, Stewart & Martin 1982).

Constant high temperatures, while accelerating growth, have also been found to cause greater mortality (Jones 1941, Peck & Whitcomb 1970). At the other extreme, <u>Tarentula kochi</u> ceased to moult (i.e. develop) at 10 degrees C (Hagstrum 1970a), <u>Loxoceles</u> sp. below 15 degrees C (Horner & Stewart 1967) and <u>Chiracanthium inclusum</u> at 45 degrees F (7 degrees C) (Peck & Whitcomb 1970). These observations indicate that there are both upper and lower limits to the direct influence of temperature on growth and development and their rates. Overwintering spiders (at low temperatures) have also been observed to lose no weight while refusing food (Turnbull 1962, Haynes & Sisojević 1966, Hardman & Turnbull 1980, Stewart & Martin 1982).

Spiders grown in conditions where the temperature oscillated diurnally with a controlled range about a known mean value, were found to grow more quickly than those reared at a constant temperature equal to the mean (Jones 1941, Workman 1978). Workman's (1978) explanation of these observations was that, as the underlying relationship between growth rate and temperature was a logarithmic dependence (within certain limits), the arithmetic mean of a temperature range would not represent the middle of the range in terms of the effect on growth rates. Thus the studies to date had not actually tested the effects of fluctuating temperature against the appropriate mid-range value, which he suggested would be the integrated mean.

In summary, temperature has been shown to have a direct influence on the rates of growth and development within certain limits which differ between species. Between these limits the rates are believed to have a logarithmic dependence on temperature, which would result in a sigmoidal relationship over the whole non-lethal range.

1.3.3 Effects of Moisture Availability

Spiders drink from freely available water, but Parry (1954) demonstrated that they could also exert a substantial suction to extract moisture from the soil. In contrast, Constantinou and Cloudsley-Thompson (1983) demonstrated that several species of therophosids were unable to restore a physiological moisture deficit from atmospheric moisture in unsaturated air (60% to 85% RH). They observed small weight increases when the spiders were transferred from 20% RH to higher humidities, which were attributed to the adhesion of moisture to body setae. Although atmospheric moisture may not be available to spiders, its effects on growth and development have been investigated.

Jones (1941) reared Agelena naevia at controlled constant relative humidities ranging from 45% to 93% RH and fluctuating conditions of 40% to 64% RH and 24% to 36% RH. She found little variation in absolute growth, although the rate of growth was slightly higher at 93% RH than at 45% RH. The main influence of humidity was in moderating the effects of temperature on mortality. At low relative humidity, mortality increased greatly with increasing temperature, while at high humidities, there was only a slight increase in mortality with increasing temperature. This interaction was also found by Eskafi et al. (1977) in terms of the rates of weight loss and longevity of Loxoceles rufus deprived of food; both were enhanced by combinations of higher temperatures and lower vapour pressures. Peck and Whitcomb (1970) found 10% RH to be a critical level of humidity below which Chiracanthium inclusum could not survive, and indeed at 45% RH considerable stress was evident, particularly in early instars. Although growth was not affected by humidity in early instars, the faster growth of later instars at 60% RH compared to 93% RH could not be explained by the authors. In contrast, in the fourth instar of Tegenaria atrica the rate of development increased with decreases in the

saturation deficit, from 23.13 mm Hg (3-4% RH) to 16.36 mm Hg (30% RH) to 8.25 mm Hg (65% RH) (Browning 1941).

In general, the most pronounced effect of atmospheric moisture availability appears to concern survival rates in relation to increasing temperature, with the possibility of some influence on the rate of growth and development, but little on their absolute levels.

1.3.4 Effects of Light Conditions

In studies on <u>Chiracanthium inclusum</u>, Peck and Whitcomb (1970) showed that reducing the photoperiod from 14 to 10 hours during development reduced the growth rate. Alternatively, spiders reared under constant conditions of 10 h light grew more quickly in most instars (except instar III) than at 14 h light, and seemed to suffer no negative effects when reared in total darkness. Hagstrum (1970a) found that the final moult of <u>Tarentula kochi</u> collected from the field in September would not occur until the photoperiod dropped to 10 h light. Suspended development at 12 h light would immediately recommence when the photoperiod was reduced, indicating the influence of photoperiod as a developmental gate.

Preferential feeding of <u>Pardosa astrigera</u> during daylight was observed by Hardman and Turnbull (1980), while <u>Tetragnatha montana</u> and <u>Dolomedes</u> <u>fimbriatus</u> were primarily active and foraging in the evening and at night (Horn 1969). Where food supply is limited, the number of hours available for feeding, whether in light or dark, could have a significant effect on the growth and development of certain spiders.

Relatively little is known about the full range of possible effects, however, the photoperiod, or changes in photoperiod could be important in the regulation of growth processes.

1.4 REVIEW OF EXPERIMENTAL PROCEDURES

Studies of the effects of environmental factors on growth and development in spiders involve the measurment or regulation of environmental factors, and estimation or quantification of the resultant growth and development. The parameters conventionally used to measure growth and development in spiders and the methods used to regulate or measure the environmental variables under consideration are described below.

1.4.1 Measurement of Growth and Development

As with other arthropods, the cuticular exoskeleton of spiders consists largely of rigid parts joined by flexible anticulations and extensible inter-segmental membranes. For example, Miyashita (1968a) found that in Lycosa tinsignata there was no significant change in the carapace width measured just after ecdysis and three days later. In contrast the highly extensible abdomen in Araneae provides the capacity for expansion or contraction necessary to accompdate changes in nutritional and hydration status within each instar (Anderson 1974). Measurement of growth requires estimation of body size or some other productive output (e.g. eggs). Determination of development requires the recognition of specific stages within the animal's life.

In spiders, there has been considerable debate about the developmental stages in embryonic growth (e.g. Vachon 1957, 1958, Peck & Whitcomb 1970, Emerit 1984), while in contrast, the transition through nymphal stages is clearly marked by ecdyses. In many spider species, attainment of sexual maturity is a terminal stage, but in some species, the females may continue to grow and moult for many years (e.g. Main 1957, 1978, Baerg 1958, Baerg & Peck 1970, Seymour 1979). The following sections described

the parameters commonly used to estimate body size and development in spiders.

1.4.1.1 Growth Quantification

The overall size of a body can theoretically be determined by its volumetric displacement, or its mass (or weight). For regular shaped objects, one or more linear parameters can be used to estimate the volume when its measurement is not possible or practical. This is the principle underlying the use of linear parameters to measure overall spider size. If the shape is not constant (e.g. where allometric growth occurs), measurement of several linear parameters may reveal where the changes in shape occur. The linear parameters most commonly used to estimate the overall size of spiders are as follows:

- (i) Body length (Vellard 1934, Baerg 1958, Murakami 1983);
- (ii) Cephalothorax or carapace length (Jones 1941, Petersen 1950,

Robinson & Robinson 1978a, Stradling 1978, Toft 1980);

- (iii) Cephalothorax or carapace width (Chew 1961, Dondale 1961, Eason & Whitcomb 1965, Horner & Stewart 1967, Miyashita 1968a, b, Hagstrum 1970a, b, 1971, Peck & Whitcomb 1970, Anderson 1974, Humphreys 1976, Robinson & Robinson 1978a, Stradling 1978, Workman 1979, Jocqué 1981, Murakami 1983, Vollrath 1983);
- (iv) Abdomen length (Jones 1941, Stewart & Martin 1982);
- (v) Abdomen width (Anderson 1974, Stewart & Martin 1982);
- Lengths of legs (Vellard 1934, Baerg 1958, Robinson &
 Robinson 1978a, Vollrath 1983);
- (vii) Leg span (Vellard 1934, Baerg 1958, Murakami 1983, Vollrath 1983);

- (viii) Fang lengths or widths (Stradling 1978) and
- (ix) Eye tubercle width (Stradling 1978).

Owing to the enormous extensibility of the abdomen, its measurement has more recently been used in conjunction with other parameters to estimate the nutritional condition in relation to size, rather than to characterize the size of the instar (Anderson 1974). The precision of size estimations based on the span or lengths of legs would be less than those based on the measurement of body parts contained on, or composed of, a single piece of rigid cuticle.

As body weight (live or dry) can be easily measured, and it has often been the preferred parameter for the estimation of overall body size (Petersen 1950, Turnbull 1962, 1965 Miyashita 1968b, Hagstrum 1970a, b, Edgar 1971, Anderson 1974, Breymeyer & Jóźwik 1975, Wise 1975, 1976, Eskafi <u>et al</u>. 1977, Kajak 1978a, Robinson & Robinson 1978a, Workman 1978, Eberhard 1979, Greenstone & Bennett 1980, Stewart & Martin 1982, Tanaka & Itô 1982, Vollrath 1983). As rigid cuticular parts do not change size significantly during an instar (Miyashita 1968a), and weight changes can be substantial, the different estimations of overall size provide qualitatively different information .

Kessler (1971, 1973), Wise (1975, 1976, 1979) Eberhard (1979) and Workman (1979) have also used fecundity as an indicator of growth in adult females, as a large proportion of their acquired weight is reflected in egg production.

1.4.1.2 Quantification of Development

Investigations of development in spiders have been largely concerned with passage through nymphal instars and the attainment of maturity. Instar duration (Browning 1941, Jones 1941, Deevey 1949, Turnbull 1962, 1965, Miyashita 1968a, b, Peck & Whitcomb 1970, Edgar 1971) and the number of instars (Deevey 1949, Peck & Whitcomb 1970, Edgar 1971, Robinson & Robinson 1978a) have commonly been used to quantify development and its rate. These measures can be expressed in various ways to provide the desired form of information. Jones (1941) and Peck and Whitcomb (1970) also examined the transition of spiders from the egg to the freeliving nymphal stages.

Chaetotaxy, the stage-specific presence or distribution of certain setae, has also been used with mixed success as a technique for quantifying development in amenable spider species (Peck & whitcomb 1970, Randall 1978, Stradling 1978).

1.4.2 Quantification or Control of Environmental Variables

Quantification of environmental variables involves decisions about the precise limits within which the variables are to be examined and the resolution or precision with which they can be controlled or measured.

1.4.2.1 Estimation of Field Food Availability

Under field conditions, the levels and/or species composition of naturally occurring potential prey have been estimated by sweep-netting of appropriate vegetation (Turnbull 1966, Kajak 1978, Murakami 1983) and by observing spiders feeding, to identify their catch (Hagstrum 1970b, Kiritani & Kakiya 1975). Prey or accumulated remains caught in spider's webs, or remains discarded beneath the webs (or kept in burrows) have also been used to estimate the quality and quantity of prey captured in the field (Main 1956, Kuenzler 1958, Turnbull 1962, 1965, Chew 1961, Wise 1975, 1979, Murakani 1983). Use of two or more procedures provided information on the degree to which prey was selectively captured in terms of size or species composition (Kajak 1978, Murakami 1983).

Alternatively, potential prey numbers were counted before and after the spiders were confined within a test area to estimate the proportion or quantity captured (Dąbrowska-Prot 1966, Dąbrowska-Prot <u>et al</u>. 1968, Łuczak & Dąbrowska-Prot 1966, Clarke & Grant 1968, Hagstrum 1970a). Humphreys (1975) used the relationship between guanine and nitrogen to estimate food assimilated in the field.

The estimates of available food have been described in various terms: "fruit-fly equivalents" (Wise 1975, 1979), sizes and numbers of particular insects (Murakami 1983), acceptable insect taxa (Hagstrum 1970b) and the total biomass of potential prey or the biomass of dominant prey taxa (Kajak & Stejgwiłło-Laudańska 1968, Kajak 1978).

The impact of different rates of food supply on growth and development under field conditions was assessed by Wise (1975, 1976, 1979), who supplemented the natural levels he had estimated at specific rates.

1.4.2.2 Regulation of Food Supply in the Laboratory

The manipulation of food availability is undoubtedly less difficult under laboratory conditions and various procedures have been used to test different aspects of the effects of food supply on growth and development.

The rate of food supply is often expressed as the number of prey items (e.g. <u>Drosophila</u> sp., <u>Musca</u> sp., <u>Tenebrio</u> sp. or Culicidae) provided per unit time (Browning 1941, Deevey 1949, Miyashita 1968a, b, Peck & Whitcomb 1970, Krishnakamuran & Scheiderman 1970, Tanaka & Itô 1982, Vollrath 1983) or the weight of prey per unit time (Turnbull 1962, 1965, Kajak 1978, Hardman & Turnbull 1980). Where the effects of food supply were not specifically under investigation, prey was generally supplied in excess or at levels deemed to be sufficient to satisfy the demand (Jones 1941, Hagstrum 1970b, Edgar 1971, Breymeyer & Jóźwik 1975, Workman 1978).

In some cases, the number of prey captured was estimated some time after feeding (Turnbull 1962, 1965, Haynes & Sisojević 1966, Miyashita 1968b, Kajak 1978, Hardman & Turnbull 1980) and the remains or cadavers weighed to calculate the amount of food ingested (Turnbull 1962, Edgar 1971, Workman 1978).

In order to standardise the units used to quantify the rate of food supply and the growth of the spiders, equations expressing the generalised relationships between individual prey items, their live or dry weights and/or their energy content have often been derived.

Rather than maintaining constant rates of food supply, in some cases, the rate was adjusted as the spider grew and was supplied at rates determined on the basis of spider weight or size classes (Workman 1978) or according to instar (Browning 1941, Miyashita 1968a). Turnbull (1965) carefully compared the effects of constant rates of food supply throughout development with the effects of food supplies which were altered after specific instars.

Comparisons of monospecific or varied diets have been made (Peck & Whitcomb 1970, Miyashita 1968a, Breymeyer & Jóźwik 1975), but attempts to equate them have been somewhat thwarted by the differences in weight, size and nutritional composition (see Section 1.3.1.3).

Prey was generally supplied live, but anaesthetized prey items were also found to be accepted by spiders in early developmental stages (Browning 1941, Deevey 1949).

1.4.2.3 Measurement of Field Temperature

Assessment of field temperatures involves two main factors: the position in the environment where the temperature was measured in relation to the niche occupied by the spiders, and the instrumentation employed. The apparatus used for estimating ambient air temperatures was generally

not described (e.g. Chew 1961, Dąbrowska-Prot <u>et al</u>. 1968, Stradling 1978, Minch 1979b), as it was for the following microclimate measurements. Hagstrum (1970a) used a thermohydrograph 12 inches (30 cm) above the ground and two thermistor probes at the litter surface and one inch (2.5 cm) below the surface. The microclimates within the bodies of <u>Geolycosa</u> <u>godeffroyi</u> and within its egg sacks were monitored by Humphreys (1974), by implanting a fine thermocouple within the cephalothorax connected by fine leads to an external reference and implanting temperature transmitters into egg sacks. The relationship of spider body temperature to air temperature was similarly measured by Robinson and Robinson (1978b) in connection with spider orientation in the web.

1.4.2.4 Regulation of Laboratory Temperature

Spiders reared in the laboratory have been generally maintained at one or more constant temperatures, in temperature controlled cabinets, incubators or air conditioned laboratories (Browning 1941, Jones 1941, Turnbull 1965, Haynes & Sisojević 1966, Miyashita 1968a, b, Hagstrum 1970a, b, Krishnakumaran & Schniederman 1970, Peck & Whitcomb 1970, Anderson 1974, Eskafi et al. 1977, Workman 1978, Baert 1980, Greenstone & Bennett 1980, Hardman & Turnbull 1980, Tanaka & Itô 1982, Constantinou & Cloudsley-Thompson 1983, Vollrath 1983). The effects of temperatures oscillating diurnally over specified ranges were also examined by Jones (1941), Hagstrum (1970a), Peck & Whitcomb (1970) and Workman (1978). Alternatively, no special arrangements have been made to control the temperature, and spiders were reared in the laboratory where diurnal and seasonal variations were experienced (Deevey 1949, Turnbull 1962, Edgar 1971, Breymeyer & Jóźwik 1975, Kajak 1978). The control for the effects of temperature in these studies was the simultaneous execution of experiments. Where other factors affected the rates of growth and

development, the total number of day degrees experienced by individual spiders may have varied considerably, possibly compounding or neutralising the effects of the other factors under investigation (Murdoch 1971).

Extremes of temperature were also used in the running of laboratory experiments. Low temperatures were sometimes used to mimic overwintering conditions (e.g. 2 degrees C (Hardman & Turnbull 1980), 4 degrees C (Turnbull 1962), 16 to 18 degrees C (Stewart & Martin 1982), 40 degrees F (4.4 degrees C) (Haynes & Sisojević 1966)) or to kill experimental subjects (e.g. -6 degrees C (Witt <u>et al</u>. 1978), -80 degrees C (Wise 1979)). Dehydration of specimens for the determination of percentage body water or dry weight was sometimes achieved with temperatures from 60 to 110 degrees C (Hagstrum 1970a, Kiritani & Kakiya 1975, Eskafi <u>et al</u>. 1977, Workman 1978, Wise 1979, Hardman & Turnbull 1980, Murakami 1983).

1.4.2.5 Estimation of Field Humidity

Assessment of the availability of moisture in the field has often been confined to description of the overall climatic conditions, for example "tropical" (e.g. Robinson & Robinson 1978a, Stradling 1978, Eberhard 1979) or "arid" (e.g. Chew 1961, Main 1978, Cloudsley-Thompson 1983). In contrast, Gray (1968) and Humphreys (1975) measured the humidity of air within spider burrows and the moisture present in the surrounding soil, to provide high resolution and information about the microenvironment surrounding the spiders. The apparatus used for measuring humidity included cobalt thiocyanate papers which have humidity-specific colours (Solomon 19 45)or changes in electrical resistance of specialised sensors (Gray 1968, Humphreys 1975b).

1.4.2.6 Regulation of Moisture in the Laboratory

Careful manipulation of the humidity in which spiders were reared was carried out by Jones (1941), using a modified version of Shelford's (1929) humidistat (cited in Jones (1941)), and others who used specific salt solutions (e.g. $CaCl_2$, NH_4SO_4 , KCl) to regulate atmospheric humidity (Peck & Whitcomb 1970, Eskafi <u>et al</u>. 1977, Constantinou & Cloudsely-Thompson 1983). Humidity was measured with a hygrometer (Browning 1941), wet and dry thermistors (Eskafi <u>et al</u>. 1977) or thiocyanate impregnated papers (Constantinou & Cloudsley-Thompson 1983). In many cases no comment was made concerning either the atmospheric humidity or the supply of moisture for drinking.

Drinking water, which inevitably contributed to the humidity in the spider's container and was therefore excluded by Jones (1941), has been most commonly supplied in a dampened wad of cottonwool or filter paper (Haynes & Sisojević 1966, Breymeyer & Jóźwik 1975, Workman 1978, Hardman & Turnbull 1980, Tanaka & Itô 1982), in dampened plaster of Paris (Turnbull 1962, Edgar 1971) or with water-filled vials plugged with cottonwool (Deevey 1949, Miyashita 1968a, b, Peck & Whitcomb 1970). Larger species were sometimes provided with free water in small dishes (Stradling 1978, Stewart & Martin 1982) and burrowing species with damp soil (Main 1957, Anderson 1974, Humphreys 1975a).

Desiccators were used in some instances to remove body moisture to obtain measurements of dry weight (e.g. Turnbull 1962).

1.4.2.7 Evaluation and Control of Light Conditions

In field based studies, assessment of the photoperiod has usually been restricted to consideration of seasonal changes, which in most cases, are inseparable from temperature. Egg laying, growth, development, mating and diapause have all been correlated with the seasons (e.g. Main 1957, Baerg 1958, Eason & Whitcomb 1965, Humphreys 1976, Kurihara 1979, Minch 1979b).

Under laboratory conditions, the photoperiod has been regulated to 16L:8D (Miyashita 1968a, b, Workman 1978, Greenstone & Bennett 1980, Hardman & Turnbull 1980, Tanaka & Itô 1982), 12L:12D (Jones 1941, Hagstrum 1970, Anderson 1974), 10L:14D (Hagstrum 1970a, Peck & Whitcomb 1970), 14L:10D (Peck & Whitcomb 1970) and continuous darkness (Browning 1941, Krishnakumaran & Schneiderman 1970, Peck & Whitcomb 1970). Regulation of photoperiod and/or light intensity (Jones 1941, Miyashita 1968a, b) has been achieved with light globes (often fluorescent, or shielded to reduce heat output) regulated by a time clock or photoelectric cell. Haynes and (1966) Sisojević/were careful to diffuse the light to avoid clustering of prey, and Turnbull (1962) shuffled the position of cages within the laboratory to randomise light conditions with respect to the experimental spiders.

1.5 SUMMARY OF THE RESEARCH DESIGN

This section reviews the choice of the spider for this study, and the aspects of its growth and development which were investigated.

1.5.1 Species Selection

Theraphosid spiders have a number of attributes which were appropriate for this study, although the precise nature of some of these only became apparent after work had commenced.

<u>Selenocosmia</u> <u>stirlingi</u> was selected because of the large number and size of its young, its extensive distribution and its reported abundance (Salanitri, pers. comm.). The importance of these criteria is detailed below.

Previous work on other species has shown that later instars cannot be reliably identified on the basis of size or weight (e.g. Turnbull 1962, Miyashita 1968a), and patterns of growth and development may be sexually dimorphic as maturity approaches. Therefore, it was considered necessary to commence the experiments with spiderlings of the first freeliving stage. These were collected from maternal burrows in the field during the breeding season.

Most Australian theraphosids are large spiders (Main 1964, 1976, Clyne 1969, Mascord 1970, 1978, 1980) which produce large eggs, which in turn develop into large embryos and large spiderlings. Precise measurements of weight can be obtained from very small spiders. As it was also intended to detect subtle differences in linear size parameters, it was considered necessary to minimise the systematic error associated with these size measurements by using large spiderlings. <u>Selenocosmia stirlingi</u> met this criterion, emerging from the egg sack as large spiderlings, aproximately 5 mm long and 20 mg in weight.

To minimise genetic variability within experiments, large litters were required, but the number of spiderlings which could be housed and cared for was not unlimited. The litters of <u>Selenocosmia stirlingi</u> are of sufficient size to satisfy a compromise between these requirements and limitations.

Within Australia the family Theraphosidae ranges from the extensive arid centre of the continent, through seasonally wet areas in the north, to the tropical, coastal regions of Queensland (Main 1964, 1976, Clyne 1969, Mascord 1978, 1980). These environments provide a great diversity of temperatures, seasonality and availability of food and moisture, which have all been considered important in determining spider growth and development. <u>Selenocosmia stirlingi</u>, while not occurring over this entire range, is the only species found in its southern extremes (ca. 36 degrees S) and, although the precise northern limits of its range are not known, it has been collected in areas which are either tropical or seasonally wet

(Kotzman, unpubl. data). Owing to the potential habitat variety and its geographic accessibility, <u>Selenocosmia stirlingi</u> was considered to be suitable for the intended study.

Specimens were collected from a field site established 5 km south of Coombah (N.S.W.) for most of the laboratory studies, although <u>Selenocosmia</u> sp. from Cairns (North Queensland) were also used.

Identification of the adult specimens collected was primarily based on comparison of this material with the extant type material of Australian theraphosids and the original (and subsequent) published descriptions. The specimens from Coombah were considered to be <u>Selenocosmia stirlingi</u> Hogg, but as there was some doubt about the specimens from Cairns, they have been conservatively referred to as <u>Selenocosmia</u> sp. Specimens from both populations will be lodged with the Museum of Victoria for future reference.

1.5.2 Objectives

The main aim of this study was to examine how growth and development were affected by measurable environmental factors which have previously been found to be important, and to assess the extent to which these factors, when taken together, accounted for the individual variation noted in previous work. In these investigations, it was considered necessary to examine the general biology of the spiders and the environment from which they were collected. Furthermore, it was intended to examine the extent to which the size increase at ecdysis could be predicted on the basis of prevailing environmental conditions and preceding weight changes in the spiders. These findings were to be extrapolated to field conditions in order to predict the number of instars required for individuals to reach maturity, the adult size and the time period involved.

1.5.2.1 Growth Measurement

To provide insight into the conversion of weight gains within instars to size changes at ecdysis, dual estimations of body size were made. Live weights were used in preference to dry weights or calorific values as the continued survival of the specimens was required and conversion via standard equations (as used by Turnbull 1962 and others) would have introduced additional error or noise component to the results. The estimation of overall body size using sclerotised body parts (on whole specimens or exuviae) provided static instar size estimations. The fangs are virtually indestructible body parts which can be measured on whole specimens (with some difficulty), and in contrast to the carapace or cephalothorax, are almost always recovered on exuviae for easy measurement, as was noted by Stradling (1978). In order to test for the possibility of allometric fang growth (which was not found by Stradling 1978), where possible, the cephalothorax lengths and widths and curved fang lengths were also recorded. The development of cuticular buds on the internal surface of the epigastric furrow was also assessed by measuring these buds when the abdominal cuticle of the exuviae could be recovered and untangled.

Documentation of the duration of the instars studied also provided information on the rates of growth (size and weight) and the rate of development.

1.5.2.2 Regulation of Environmental Variables

Owing to the involved nature of the effects of food availability on growth and development of spiders through prey capture, ingestion and metabolic demands, and the feeding behaviour of these spiders (see Section 2.5) it was decided to measure only the rate of food supply. The overall effects would therefore represent the integrated influence of all the

component effects and their associated variation. As the live weight of the spiders might be expected to respond most closely to the live weight of the prey (including the moisture component), this weight parameter was used. The levels at which prey were supplied were initially determined arbitrarily, as no suitable information was available for theraphosids of this size. The primary concern was that the levels should not all fall into the category of "excess".

The temperatures tested in the laboratory were within the range recorded in the soil in the field, although temperatures below 20 degrees C were avoided by and large owing to time constraints. It would have been desirable to measure the body temperatures of spiders in the field (c.f. Humphreys 1974), but as this was not possible, and these spiders were nocturnal, soil temperatures provided the best approximations.

Photoperiods approximating mid-summer and mid-winter at Coombah were used to test their effects, as it seemed possible that feeding patterns might have been sensitive to these light conditions.

The effects of humidity on growth have been reportedly mixed, slight or absent, and the spider's burrow is unlikely to be less than saturated (see Gray 1968, Humphreys 1975b). For these reasons, and to minimise mortality, the spider's jars were provided with sufficient moisture to maintain humidities of approximately 100% RH. Condensation within the jar was used as an indicator of the humidity.

1.5.3 Thesis Structure

Having reviewed previous work on growth and development of spiders in Chapter 1, Chapters 2 and 3 provide respectively introductions to the biology and to the field ecology of <u>Selenocosmia stirlingi</u>. The experimental materials and methods, results and discussion follow in Chapters 4, 5 and 6. Chapter 7 provides a summary of the overall conclusions.

CHAPTER 2

GENERAL BIOLOGY

2.1 INTRODUCTION

This chapter describes aspects of the general biology of <u>Selenocosmia</u> <u>stirlingi</u> from Coombah (N.S.W.), largely obtained from more than four years of observation of individuals kept in the laboratory. The reasons behind the choice of this species for the study were outlined earlier (Section 1.5.1). Part of the information, such as eating behaviour, was used in the design and running of the experiments described in later chapters, while part was derived from them and from field observations. Little attempt has been made to analyse the observations statistically, as they are mostly of a case-study nature and not generally amenable to such treatment. Reference is made to observations of other theraphosid spiders.

2.2 EGGS AND LITTERS

Five female <u>S</u>. <u>stirlingi</u> were collected at Coombah with many offspring and a recently evacuated egg sack, and another five females (also from Coombah) made egg sacks in the laboratory. The eggs were ca. 3.5 mm in diameter and pale yellow. The eggs of <u>Eurypelma californica</u> were also pale yellow, but were probably smaller than those of <u>S</u>. <u>stirlingi</u>, as these spiderlings had a body length of only 4.2 mm at the time of emergence (Baerg 1929, 1958), compared with 5.5 mm (18.3 mg) for

<u>S. stirlingi</u>. Although it is widely accepted that some eggs will fail to develop and emerge as spiderlings, due to death or canibalism, estimates of egg number can be made on the basis of litter size (i.e. the number of spiderlings found with the female). The sizes of litters, for which weight and/or size data were also available on the mothers, are described in Table 2.1. It should be recognised that these litter sizes represent minimum values, as the number of eggs failing to complete development or spiderlings which had already dispersed, were not known. These Australian theraphosids produce somewhat fewer, larger young than the two North American theraphosids. <u>Eurypelma californica</u> was capable of producing 631 - 1,018 eggs (Baerg 1929, 1958) and <u>Phormictopis cancerides</u> produced 200 -300 eggs (Petrunkevitch 1934).

2.3 EMERGENCE FROM THE EGG SACK

Nothing had emerged from two of the laboratory-made egg sacks within 21 to 29 days of production, at which time they were being devoured by the female and were opened and found to contain embryos about to undergo their first moult. Spiderlings emerge from the egg sack through a single hole (Figure 2.1a), and although Petersen (1950) suggested that the female must form this opening for the spiderlings to emerge, this was not observed in these spiders. The spiderlings moult once within the egg sack and leave the first exuviae there (Figure 2.1b), thus emerging as second instar nymphs equivalent to Vachon's pre-nymph (Peck & Whitcomb 1970, Foelix 1982). Only once were they collected in the field at this stage (offspring of MK36) with sparse pellage, no claw tufts, little pigment and an apparent inability to feed (Figure 2.2b). Petrunkevitch (1934) observed that <u>Phormictopis cancerides</u> also emerged at this stage of development. The second instar spiderlings soon moulted into instar III (within about 5 days) and at this stage were fully formed, freeliving

<u>Table 2.1</u>.

Data on adult females and their litters for <u>Selenocosmia</u> spp.

Spider number	Provenance	Cephalothorax length (mm)	Fang length (mm)	Weight (g)	Number of offspring	Mean weight of offspring (mg +/- SE)
MK36	Coombah	14.4*	6.3	-	227	18.3 <u>+</u> 0.34
MK34	ff	17.0	7.6	-	214	19.3±0.16
MK37	11	-	-	4.742	167	19.3±0.19
MK28	11	-	-	4.937	84	20.3±0.68
MK71	11	13.3	5.9	2.970	112	22.5 <u>+</u> 1.09
MK69	11	16.6	-	5.658	193	19.1 <u>±</u> 0.41
MK54	Chillagoe	18.5	-	-	78	-
MK53	11	18.5	7.9	-	139	-
MK78	Cairns	18.2	8.5	-	63	21.2±1.51
MK79	11	17.5	7.5	-	26	1/.6 <u>+</u> 1.26

* Calculated from a fang found in the burrow according to the equation in Section 5.2.1.

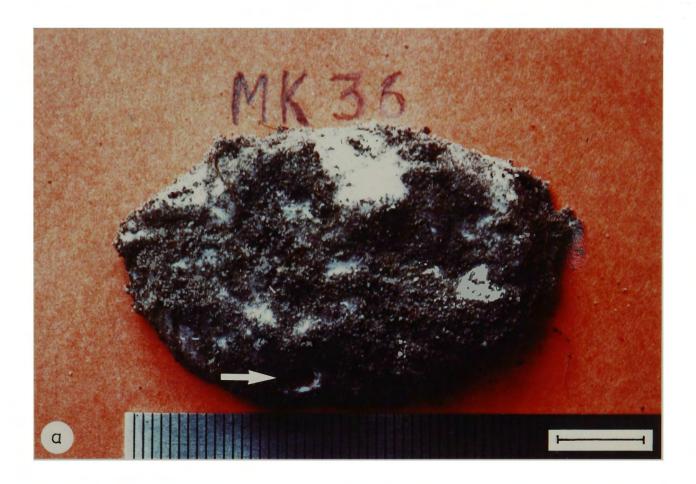
Figure 2.1.

An egg sack of <u>Selenocosmia</u> stirlingi.

(a) The intact egg sack; the arrow indicates the position of the exit pore through which the spiderlings had departed.

(b) The opened egg sack containing the instar I exuviae.

Scale bars: 10 mm.



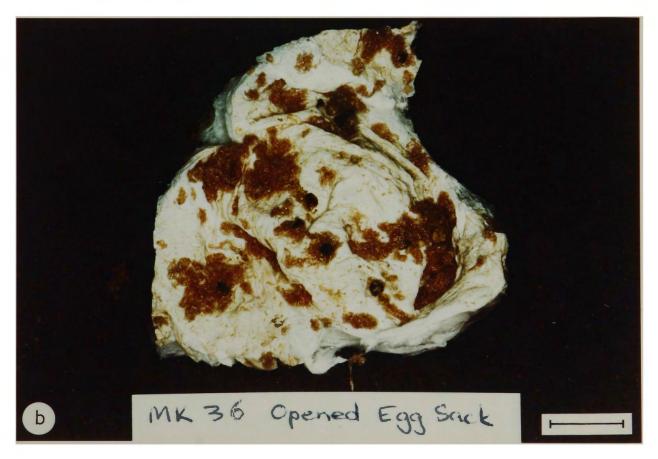


Figure 2.2.

Spiderlings of <u>Selenocosmia</u> <u>stirlingi</u>.

(a) Instar II.

(b) Instar II with peripheral darkening characteristic of an imminent ecdysis.

(c) Instar III.

Scale bars: 10 mm.



spiderlings (Figure 2.2c). The first instar exuviae collected from within the egg sack could easily be distinguished from the somewhat similar second instar exuviae (often found in the burrow) by the presence of bifurcate chelicerae (Figure 2.3a) (Grassé 1949, Bristowe 1954) and toothed tarsal claws. Examination of embryos (Figure 2.3b) revealed that these morphological changes occurred at the first ecdysis.

2.4 MOULTING

Before the moult, the body of the spider began to darken as the old cuticle was reabsorbed and the new cuticle formed beneath it (Deevey 1941, Browning 1942, Stewart & Martin 1982). This was particularly noticeable on the legs and abdomen of the early instar spiders (see Figure 2.2b), and could be used to recognise an impending moult in these stages. In some instances, but by no means always, spiders about to moult spin a low hammock or cradle of web on which they lie (Figure 2.4). The sequence of events involved in ecdysis has been described in detail by Baerg (1929), Petrunkevitch (1934), Minch (1977) and Stewartand Martin (1982) for other theraphosids, and was essentially the same for S. stirlingi. The initial split around the margins of the carapace was achieved with the spider lying on its dorsum. Having rolled onto one side, the carapace was detached except for the dorsal half of the pedicle, which usually remained connected to the abdominal cuticle. The abdominal cuticle split antero-laterally, in line with the lateral margins of the new carapace, and ecdysis proceeded (Figure 2.5a-c): cephalothorax first, then chelicerae, legs and abdomen. With ecdysis completed, the spider remained on its dorsum, gently flexing its legs and fangs (Figure 2.5d), before rolling over and moving away from the bed (Figure 2.4). The time taken to complete ecdysis gradually increased from less than one hour for instar III to more than several hours for mature females.

Figure 2.3.

Photomicrographs of the chelicerae of juvenile Selenocosmia stirlingi.

(a) Exuvium of instar I.

(b) Wholemount of instar I just prior to ecdysis.

(c) Exuvium of instar II.

Scale bars: 200 µm.



Figure 2.4.

A moulting bed (arrow), exuvium and newly ecdysed spider (right).

Scale bar: 10 mm.

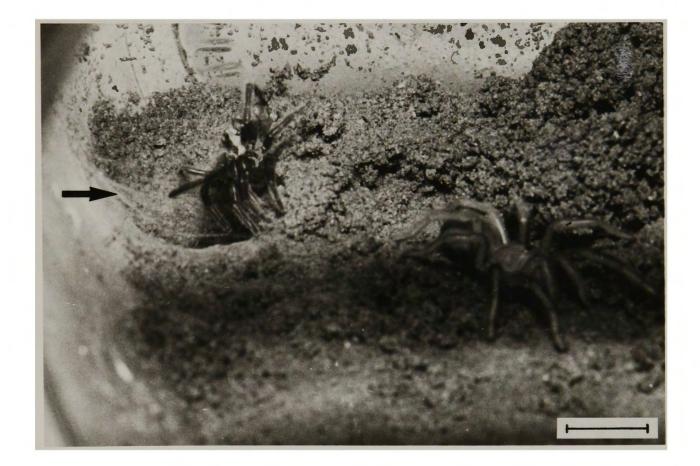


Figure 2.5.

The sequence of events in ecdysis for an instar II juvenile of <u>Selenocosmia stirlingi</u>, from shortly after lifting of the carapace (a) and extraction of the appendages (b and c), to completion of the process (d).

Scale bars: 4 mm.



If the exuvium was not removed within 24 h of ecdysis, it was often macerated in to a pile of cuticle chips by the spider, and only fang measurements could then be made. The reasons for this behaviour were not clear, especially as it was not invariable and did not appear to be related to other factors such as temperature, moisture levels, food availability or pathology. Dondale (1965) observed <u>Philodromus rufus</u> consuming moulting fluid and dissolved proteins from fresh exuviae as a first meal, and this may have been the motivation underlying exuvium maceration by <u>S</u>. <u>stirlingi</u>. As with <u>P</u>. <u>rufus</u>, removal of the exuvium appeared to cause no ill effects to <u>S</u>. <u>stirlingi</u> under laboratory conditions.

2.5 FEEDING

Field observations suggested that <u>S</u>. <u>stirlingi</u> fed nocturnally. However, in the laboratory, prey were readily taken in daylight, under bright artificial light (both incandescent and fluorescent) and during periods of total darkness. This suggested that in the presence of food, feeding was not necessarily prevented by illumination, although it is possible that the tendency to feed was reduced. Regardless of the conditions, not all the prey killed were consumed immediately, and indeed when the spider and the prey were of similar sizes, some were consumed intermittently over several days.

When juveniles were maintained in groups, they were observed feeding together on one prey item. They also adopted this feeding pattern with prey captured by their mother. In the laboratory, one ailing female killed a katydid on which her offspring fed, while she retreated to a corner of the container and died without eating. Deevey (1949) noticed that anaesthetized prey were only acceptable to juvenile <u>Latrodectus</u> <u>mactans</u> up to instar V, which may be related to a natural phenomenon of

feeding on prey captured by siblings or parents or it may simply represent a shift from carrion to exclusively live prey.

While spiders are known to extract liquefied contents of their prey (e.g. Turnbull 1962, 1973, Haynes & Sisojevic 1966, Peck & Whitcomb 1970, Edgar 1971, Foelix 1982), their powers of mastication have only been occasionally reported (Turnbull 1965, 1973). <u>S. stirlingi</u> possess well developed cheliceral teeth, and adults are capable of reducing adult cockroaches (Figure 2.6a) to balls of cuticular chips (Figure 2.6b). In addition, partially consumed mealworms (<u>Tenebrio</u> sp.), presumably containing digestive juices from the spider, would sometimes sink into the substrate (sand) even before feeding was completed. Thus, it was not possible to make meaningful estimates of the discarded prey remains or to determine precisely when the meal was completed, nor to calculate the quantity of food consumed.

Murakami (1983) suggested that there is an optimum prey size for each spider and Decae <u>et al</u>. (1982) refer to a limited size range of acceptable prey. A small experiment was conducted to establish the influence of mealworm size on feeding. Twenty-eight spiderlings were divided randomly into 4 equal groups, supplied with mealworms belonging to different size classes and the weight changes of the spiderlings recorded 24 h later (Table 2.2). Where weight was lost, it was typically 1 to 2 mg, however, weight gains (which were interpreted as indications of feeding) generally exceeded 4 mg. The mealworms in group 1 were not eaten by any spider.

These results, in conjunction with observations that adult spiders eat small mealworms (>10 mg), confirmed that there was a restricted size range of acceptable prey items for these spiderlings, and indicated that 15 to 25 mg mealworms would be appropriately within this range for the growth experiments on early instars.

Figure 2.6.

Food processing by adult <u>Selenocosmia</u> <u>stirlingi</u>.

(a) A <u>Periplaneta americana</u> as a prey item.Scale bar: 10 mm.

(b) Cockroach "rejectamenta" following feeding. Scale bar: 5 mm.



<u>Table 2.2</u>.

Weight changes of instar III spiderlings of <u>Selenocosmia stirlingi</u> over 24 h, associated with the provision of different sized mealworms.

Group	Mean spider wt. (mg)+/-SE	Mean wt. Lost (mg)	Mean wt. Gained (mg)	Percentage gaining >1 mg wt.		n mealworm gth Weignt) +/-SE(mg)
1	22.1±0.45	1.2	0.1	0	25	107.7±7.56
2	22.9±0.42	1.3	4.2	42.9	21	59.7±1.69
3	23.5 <u>+</u> 0.69	1.1	6.5	28.6	14	32.7±1.14
4	22.1±0.37	0.0	4.7	100.0	11	8.9 <u>+</u> 0.64

Spiders refuse food for a period of time, once the moult cycle has commenced and prior to ecdysis (Baerg 1938, Haynes & Sisojević 1966, Miyashita 1968b, Hardman & Turnbull 1980, Stewart & Martin 1982). Evidence of an imminent ecdysis (darkening of the cuticle, see Section 2.4) was used in conjunction with body weight measured daily, in order to estimate the length of this fasting period in instars III to V. The data (Table 2.3) show that there was a progressive decline in the percentage of spiders which gained weight as the meal time approached the ecdysis. The reduction in sample size (and associated accuracy) in the 3 and 4 day categories reflected the increasing difficulty of recognising the imminent ecdysis at these times. In spite of these limitations, the amount of food available within a given instar was subsequently calculated to exclude food provided on or after 3 days before the ecdysis, as fewer than 50% of spiders gained weight from such meals. In contrast, Stewart and Martin (1982) recorded pre-ecdysial fasts of up to 34 days in adult Dugsiella hentzi, suggesting that the fasts extend in length as the spider becomes older and larger.

2.6 DEHYDRATION

When atmospheric humidity has been low, and a source of moisture was not available for drinking, dehydration of the spider could result. The probability of a full recovery from dehydration depends on the severity of the moisture deficit. Mild dehydration can be reversed simply by providing drinking water by moistening the sand in the jar containing the spider. In slightly more extreme cases, a puddle of free water appears to be needed in order for the spider to rehydrate itself. Whether this simply provides a larger source, or one which is more easily used, or a combination of the two, is not known. It was sometimes necessary to confine the spider in a dish 10 to 15 mm deep in water overnight to effect

Table 2.3.

The number and proportion of spiderlings of <u>Selenocosmia</u> spp. (instar III to VIII) gaining weight when feeding preceded ecdysis by one to four days.

	Time	Before	Ecdysis			
	(days)					
-	1	2	3	4		
Number of Cases	68	64	27	7		
Number Gaining Weight	3	14	11	4		
Percentage	4.4	21.9	40.7	57.1		

a cure. Dehydration requiring this treatment could be recognised by jerky movements, an apparent inability to extend the legs fully (as noted by Anderson (1974)) and claw-tufts clogged with sand which had not been cleaned away. The clogged claw tufts probably resulted from the demise of the hydraulic system on which they may operate (Ho mame 1957, Rovner 1978). One spider, which could not be revived with the provision of free water, was resusitated by placing its ventral surface (including the mouth) in water, with opposing limbs (e.g. I Left with IV Right) extended in pairs, in an attempt to suck water into the body. The spider recovered completely and was still alive about 2 years later.

2.7 MATURATION

Although no single individual completed development from the egg sack to a reproducing adult during the study, various aspects of the developmental process were revealed.

Using a stereomicroscope to examine the inner surface of the ventral abdominal cuticle under pseudo dark-field illumination (Appendix A), translucent cuticular structures were visible. Small buds of cuticle, thought to be presumptive spermathecae in females, could be found on spiderlings as young as instar III. In males, these structures were retained in this form to maturity (Figure 2.7a). In the later instars (e.g. instar VII illustrated), the males also developed a small, distinctive patch of more dense setae with pronounced sockets anterior to the epigastric furrow between the cuticular levels (Figure 2.7a). In females, the small buds extended and widened from instar IV or V onwards and, providing the exuvium could be collected intact and the abdominal cuticle untangled, the spiders could be sexed from their exuviae quite early in their development (e.g. instar IV). Stradling (1978) noticed similar spermathecal development from instar VI onwards in <u>Avicularia</u>

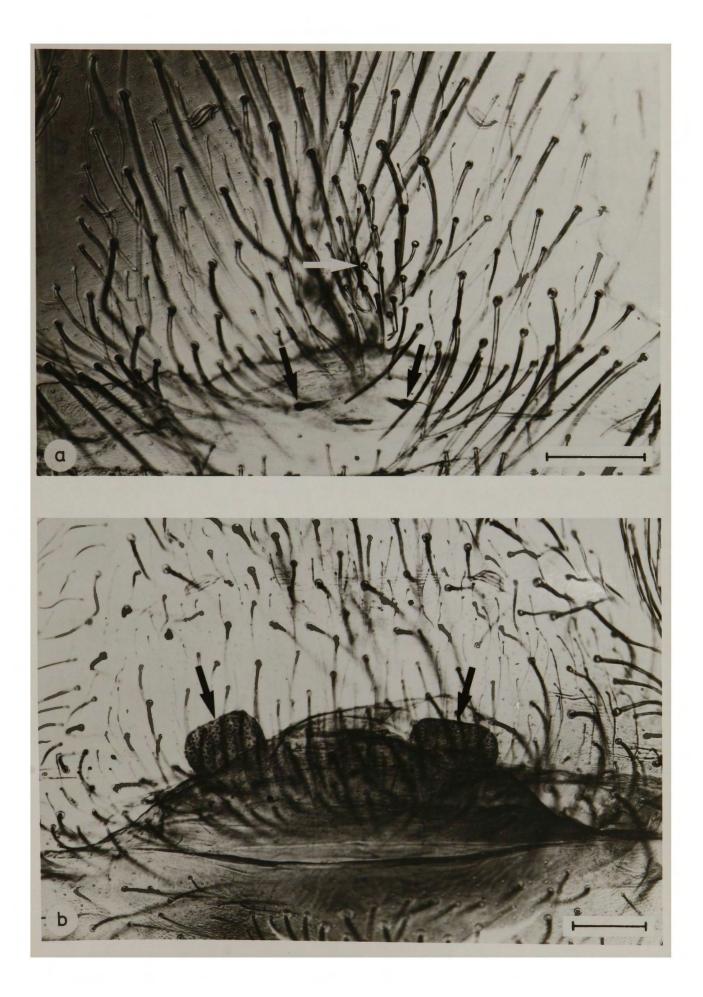
Figure 2.7.

Photomicrographs of the internal surface of the cuticle in the centre of the epigastric furrow of juveniile <u>Selenocosmia</u> <u>stirlingi</u>.

(a) A juvenile male; black arrows indicatecuticular buds, the white arrow, one of thedistinctive setae.

(b) A juvenile female with paired spermathecae (arrows).

Scale bars: 200 µm.



avicularia. Juvenile males of instars IX or older could also be distinguished on the basis of their swollen palpal tarsi (Figure 2.8).

The stridulating organ (which is composed of sets of opposing bristles on the maxillae and basal segments of the chelicerae) began to form in instar VI. Initially, two or three bristles developed on each maxilla and these were used in stridulating behaviour. The hissing sound, typical of stridulation, could not be heard however, possibly due to the small size of the bristles and the high frequencies they would be likely to produce, or simply because the organs were not fully formed.

2.8 ADULT SIZE

In <u>S. stirlingi</u>, as with <u>Avicularia avicularia</u> (Stradling 1978) and other theraphosids (McCook 1887, Baerg 1928, 1958, Stewart & Martin 1982), females continue to moult even when sexually mature. This led to a range of sizes in adult female cephalothorax lengths in <u>S. stirlingi</u> between 13.3 and 17.0 mm. This compares with cephalothorax lengths estimated to be 17.8 to 44.8 mm in <u>A. avicularia</u> (Stradling 1978), and 17.4 to 23.3 mm in <u>Dugsiella hentzi</u> (Baerg 1958). Attainment of sexual maturity represents the terminal stage of growth for males. As only one male specimen was collected at Coombah, sixteen specimens from the South Australian Museum from similar geographic locations were measured (Appendix B). The cephalothorax lengths of these specimens were found to range from 12.2 to 17.6 mm, compared with 15.5 to 18.6 mm for <u>Dugsiella</u> <u>hentzi</u> (Baerg 1938).

2.9 MATING

The following description of mating is based on several encounters observed when male and female specimens were placed together, in pairs, in the same container:

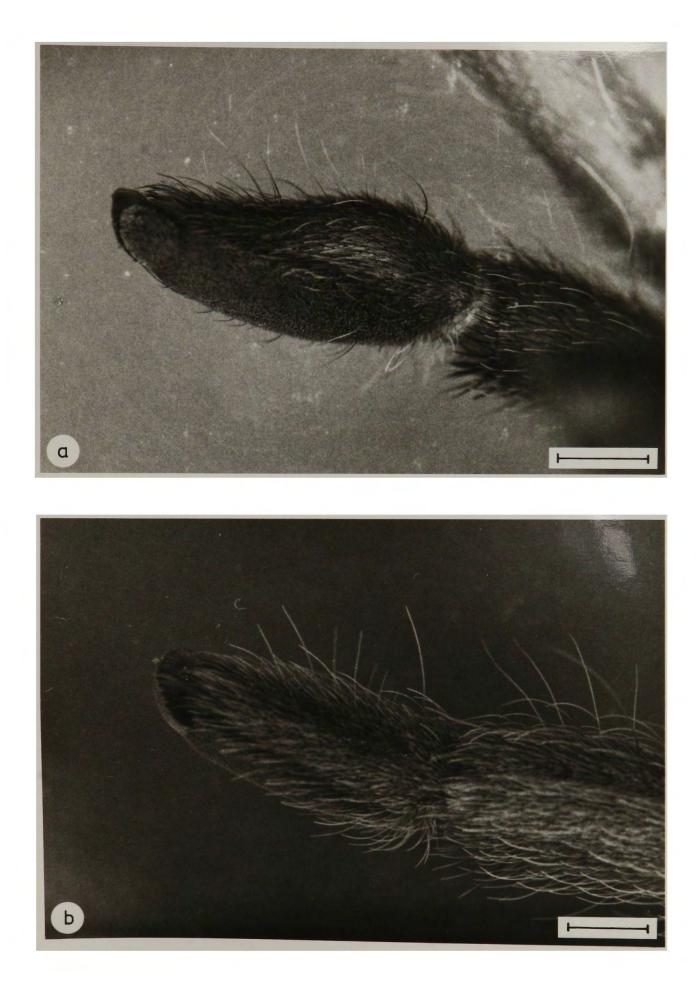
Figure 2.8.

Palpal tarsi of juvenile <u>Selenocosmia</u> <u>stirlingi</u> (instar IX).

(a) A male.

(b) A female.

Scale bars: 1 mm.



Either partner made the initial approach or contact. This caused the male to drum or tap his palps (and sometimes legs I & II) on the substrate, in the air and on to the female, until she stood facing him. The female then adopted an aggressive stance with her palps, legs I and II raised and her body raised to about 60 degrees from the horizontal (Figure 2.9a). If the male then retreated, he soon returned and recommenced drumming. With both spiders in "aggressive" postures, the male advanced, drumming on the female's chelicerae and legs until his first pair of legs was held above her cephalothorax and the second pair interdigitated with either legs I and II or the palps and legs I of the female. The male continued to drum with his palps on the ventral surface of her coxae and in the vicinity of the epigastric furrow, while pushing the female backwards to a more acute angle. Insemination was achieved when one palp was pushed forward and drawn back so that the tip of the embolus entered the female's epigynum (Figure 2.9b). The union lasted for up to 10 seconds during which the sperm were presumably transferred to the spermathecae. Single or multiple insertions using either or both palps (if they were intact) were seen to occur. Mating terminated with the withdrawal of the male or both partners and no participant attacked its mate on any occasion.

In general, there appeared to be little difference between this sequence of events and those described by Baerg (1928, 1958), Petrunkevitch (1911, 1934) and Minch (1979c) for other theraphosids. It should be noted however, that unlike the other species, male <u>S. stirlingi</u> have no spurs on their legs to secure the females fangs during mating. In spite of this, they also escaped unharmed after mating in the laboratory, as with <u>A. avicularia</u> (Stradling 1981). The presence of a male embolus, in a female burrow in the field, suggested that the males did not always escape from the female.

Figure 2.9.

Mating behaviour of <u>Selenocosmia</u> stirlingi.

(a) Pseudo-agressive posture near the commencement of courtship, female left.

(b) In copulo, female right.

Scale bars: 10 mm.



2.10 EGG SACK FORMATION

Egg sack formation by <u>S</u>. <u>stirlingi</u> appeared to follow the general scheme of events described by Baerg (1929, 1938, 1958) for <u>Eurypelma</u> <u>californica</u>. The egg sack was commenced with the formation of a flat disc of thick, white web about 30 to 40 mm in diameter, attached to the substrate at its margins. The eggs were laid as a glutinous mass in the centre and more sheets of web were layered over them (Figure 2.10a). With an action which seemed to mould the web layers together, the female pulled the margins from the substrate with her palps and fangs (Figure 2.10b). She then rotated this oblate spheroid with the long axis in a vertical plane, crimping along the joined edges and then covered it with more web all over to form the completed, spherical egg sack.

2.11 MORTALITY

Apart from dehydration, most spiders died during ecdysis. In such instances, the new, underlying cuticle appeared to be malformed so that it either ruptured during the ecdysis or prevented completion of the process through adhesion to the old cuticle. Similar mortality has been reported elsewhere (Petrunkevitch 1934, Jones 1941, Deevey 1949, Baerg 1958, Turnbull 1962, Peck & Whitcomb 1970), and was observed in spiders which appeared to have developed some pathology during preceeding instars. Some of these developed translucent abdomens, while others developed rusty patches or spots on the dorsal surface of their abdomens. Attempts to treat these conditions with topical applications of antibiotics invariably failed. A number of spiders died from no apparent cause.

Figure 2.10.

Egg sack formation by <u>Selenocosmia stirlingi</u>.

(a) The "sandwich" stage, with the egg massbetween sheets of silk immediately beneath the spider.

(b) Final moulding and holding of the egg sack.

Scale bars: 10 mm.



CHAPTER 3

FIELD STUDIES

3.1 INTRODUCTION

The main rationale for undertaking field studies was to obtain data on the environment of these spiders and their associated activity patterns, in order to relate the laboratory findings to natural conditions. The short duration of field trips and the intervals between them naturally restricted the resolution of detail in these investigations, however in spite of these limitations, much useful information has been collected.

This chapter addresses the physical environment and the activities of the spiders.

3.2 MATERIALS AND METHODS

3.2.1 The field area

Several likely burrows were located on a sand dune, 5 km south of the Coombah homestead (New South Wales), on the east side of the Silver City Highway (136 km north of Wentworth). Excavation confirmed that the occupants were indeed <u>S. stirlingi</u>. As more burrows were located, they were marked with sequentially numbered wooden stakes (60 cm long) which were placed about 150 mm east of the burrow entrance. On the west side of the highway, burrows were also marked (alphabetically), to provide a known

source of spiders for laboratory work, and an area for the field experiments which was adjacent to that part of the field site in which temperatures and spider activities were recorded.

A planimetric map of the burrows and other major features east of the highway was produced with a telescopic level (Fuji Corp.) and a pair of plane tables (Figure 3.1). Owing to the size of the site, shared information from two baselines was superimposed to produce the final map. Spot heights were measured along a series of levelled transects and the contours interpolated between them were tied to sea level with a Special Survey Mark (SSM 3910, lat. = 33° 01⁻, long. = 141° 38⁻, height = 53.759 m) located within the site.

Twice during the study (October 1982 and October 1984), the diameter (to the nearest mm) and depth (to the nearest cm) of each marked burrow were recorded using calipers with a dial (Mitutoyo) or linear vernier scale, and a 1 m length of rubber respectively (see Section 4.2). Assessment of the relationship between the depth of the burrow and its topographic position was estimated using the interpolated contours from the map.

3.2.1.1 Rainfall

Throughout the field study, rainfall data were obtained from a plastic wedge rain-gauge at the Coombah homestead (5 km north of the field site). The records represented the best approximation of the rainfall at the field site, in spite of the highly localised nature of rainstorms in arid areas.

3.2.1.2 Temperature

Solid state temperature sensors (AD590JH) connected to a 4-channel Rustrak strip chart recorder (Galton Inc. U.S.A.), were used to monitor

field temperatures for 24 h during each field trip. Initially two sensors were buried at 25 and 60 cm and left for 6 weeks to settle. On the following field trip, the temperatures of the buried sensors were compared with sensors introduced to similar depths within burrows. As no differences could be distinguished, three sensors were installed in the soil at 60 cm, 20 cm, and at the surface (covered with a film of sand), for the remainder of the study. The temperatures recorded were taken to indicate those experienced by the spiders at those depths in the burrow and to reveal the progressive transfer of heat in the sand diurnally and annually.

3.2.1.3 Assessment of prey availability

On two field trips, six plastic pitfall traps, complete with protective raised lids (100 mm diameter x 200 mm) were set in a line down the slope of the southern sand dune and the accumulated contents examined the following morning. In addition, a note was made of potential prey species seen moving on the surface at night, and of the remains collected from excavated burrows.

3.2.2 Spider Activity

Information concerning the condition of the burrows, observation of their occupants, and any external indications of spider activity were evaluated and recorded during each visit.

Some evidence about the seasonality of male spider activity was obtained from examination of the records accompanying sixteen male specimens from the South Australian Museum (examined for size determination), the specimen collected at the Coombah Homestead, and the type from the British Museum (Natural History) (Appendix B).

3.3 RESULTS

3.3.1 The field area

The map of the field area (Figure 3.1) shows a central swale bordered on the north and south by sandhills and to the east by a claypan (in the foreground of Figures 3.4a and 3.4b). The total relief is a little less than 7 m, although the swale had been somewhat enlarged during nearby road construction, which may also have produced the two northern-most tracks traversing the site. The Silver City Highway lies about 10 m west of the fenceline and runs parallel to it.

The burrows, scattered throughout the site, appear to occur in clusters as well as isolated individuals, although, as the distribution pattern was not specifically in question, no attempt has been made to confirm this with statistical analyses. Burrows are most abundant on the top of the northern sandhill, but are also common throughout the remainder of the site with the exception of the claypan, the very base of the swale and the eastern slopes of the northern sandhill.

3.3.1.1 Burrow location and morphology

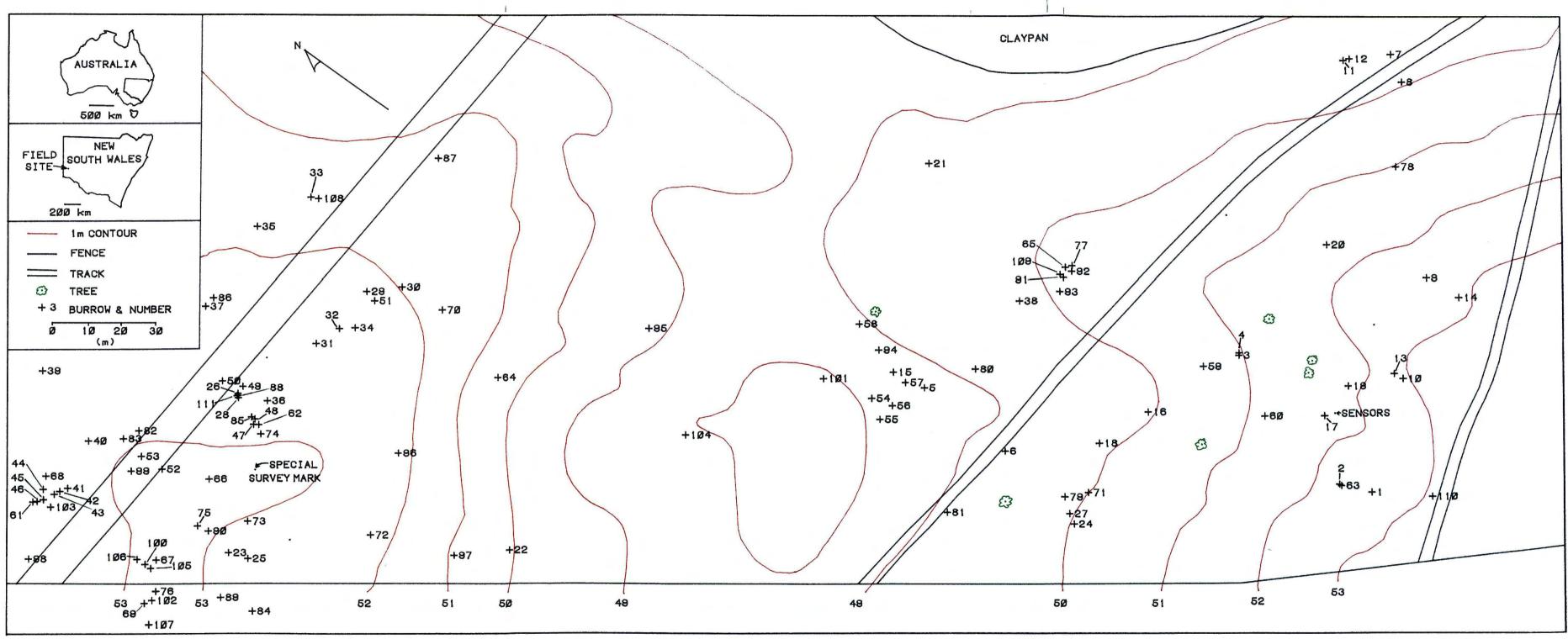
Investigation of the relationship between burrow depths and diameters measured during the study revealed a wide scatter of points and no apparent trends (Figure 3.2a); the highest coefficient of determination value achieved was 0.11 for Y = a + b/X. Similarly, there was a wide scatter of points relating burrow depth to altitude (Figure 3.2b) with the highest coefficient of determination = 0.14 for Y = a + b/X.

3.3.1.2 Rainfall

Representation of the monthly rainfall data (Figure 3.3a) revealed several main features. There was a drought in the first half of the study Figure 3.1.

Planimetric map of the field site, Coombah (New South Wales).

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Figure 3.2.

Burrow dimensions and position at the Coombah field site (New South Wales).

(a) Relationship between depth and diameter.

(b) Relationship between depth and the altitude of the burrow entrance (mid-point between adjacent contours).

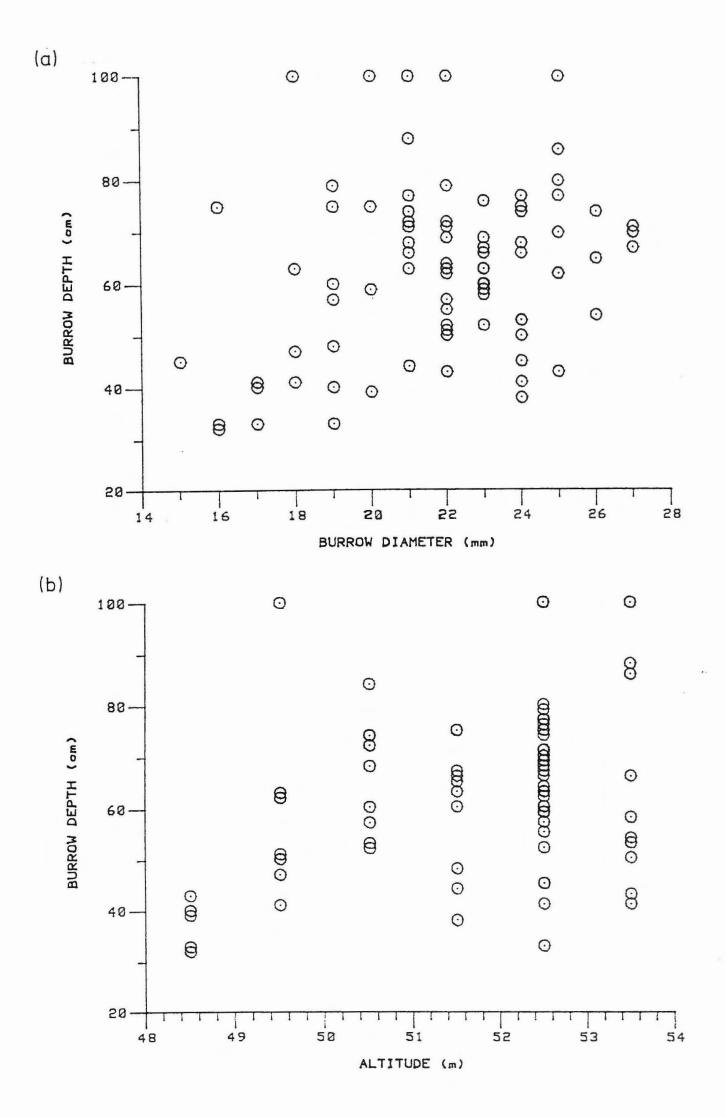


Figure 3.3.

Observations of environmental conditions and spider activity at the Coombah field site (New South Wales). Two abscissae, field trip occurrence (upper) and time (lower) apply to all graphs.

(a) Rainfall from the Coombah homestead;monthly totals.

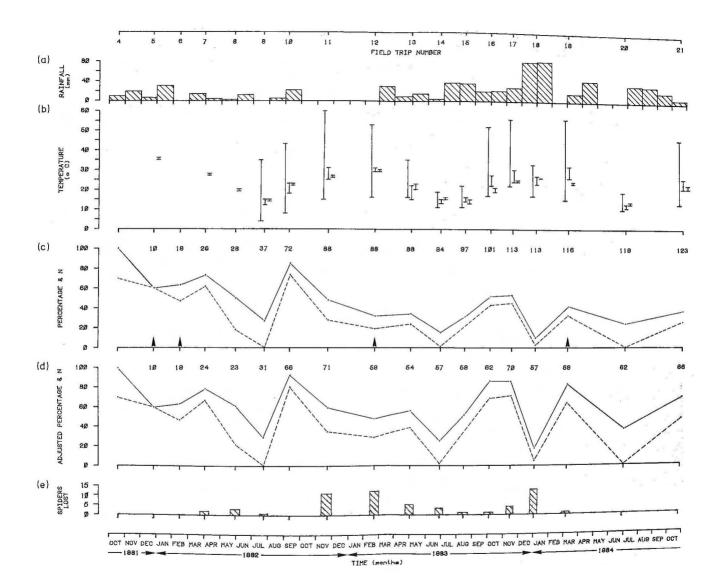
(b) Diurnal temperature excursions; three readings at 60 cm were followed by groups of three reading in the following sequence: surface, 20 cm and 60 cm (from left to right).

(c) Spider activity (arrows indicate juveniles seen in maternal burrows); solid line indicates open burrows, broken line indicates spiders seen.

(d) Adjusted spider activity;solid line indicates open burrows,broken line indicates spiders seen.

(e) Spiders lost from the population.

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which culminated in no rainfall from September 1983 to March 1984 (see Figure 3.4a), which was followed by above average falls over the next 12 months (see Figure 3.4b). Overall the rainfall was typically low (ranging from 130.04 - 408.28 mm annually) and unreliable, with 10 of the 37 months under observation (27%) recording no falls and the six-monthly totals listed below giving a good indication of the variability: 83.06, 46.98, 31.24, 125.97, 270.35, and 137.93 mm.

3.3.1.3 Temperature

The range of temperatures recorded at the surface, 20 cm and 60 cm below the surface on each trip are illustrated in Figure 3.3b. The diurnal and annual ranges were greatest at the surface, less at 20 cm and least at 60 cm. Temperatures exceeded 20 degrees C at the surface in almost all months except once in June, but only from August or October to June at 20 cm and from September to May at 60 cm. Diurnally, maximum and minimum temperatures were achieved 6 and 12 hours after the surface at 20 cm and 60 cm respectively. The summer temperatures of 1983-84 appeared to be somewhat depressed at the time of maximum rainfall. As described in greater detail by Ettershank (1971), warming and cooling of the surface during the day approximated the first half of a sine curve, while after sundown, the temperature declined slowly to a minimum before dawn. In the soil, the diurnal cycles were not distinguishable from even sine curves.

3.3.1.4 Prey availability

Owing to the exceedingly low collection of potential prey (several 4 mm ants) in the traps and the rare observations of potential prey on the surface, the presence of spider (Lycosidae and Theraphosidae), beetle (Dermestidae) and scorpion (<u>Urodacus yaschenkoi</u>) remains with burrow debris were the only indicators of prey consumed in the field and were not analysed in detail.

Figure 3.4.

The Coombah field site landscape (New South Wales). Views west from the claypan on the eastern margin of the site.

(a) September 1982, at the beginning of the drought.

(b) August 1983, following rain.



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3.3.2 Spider Activity

3.3.2.1 Burrow observations

The condition of burrows varied during the study throughout the following range: fully open with trampled grass forming a flange about the entrance (Figure 3.5a), sometimes surrounded by tailings from recent diggings (Figure 3.5b), and very occasionally with a thin film of web across the top or around the mouth; open, but rough around the edges; partially constricted by sand and/or vegetation at or near the surface, sometimes occupied by other spiders (Lycosidae or Theridiidae); visibly blocked with sand and web (Figure 3.6a); or indistinguishable from the surroundings having been blocked with sand, and sometimes partially vegetated. Some burrows were also partially excavated at the surface (Figure 3.6b), although the animal(s) responsible was not identified. The percentage of burrows described as open and the total sample size are illustrated in Figure 3.3c.

By stealthily approaching each burrow at night, it was often possible to see the occupant(s) in the entrance or upper regions of the burrow. These were recorded as "seen", and the percentages are also illustrated in Figure 3.3c. Both curves follow similar patterns, although the absolute percentages of the spiders seen was almost always somewhat lower than those recorded for burrows open. Percentages were consistently low in early winter (June and July) and peaks occurred in spring (September to November) and to a lesser extent in late summer or early autumn (March and April), with levels depressed to some extent over the height of summer. Although new burrows were found within the field area with almost every visit, it is reasonable to assume that spiders were also being lost from the population. Indeed MK34.01 was collected with a parasitic pompilid wasp larva attached to her abdomen. This, and other losses may have

Figure 3.5.

Open burrows of <u>Selenocosmia stirlingi</u> at the Coombah field site (New South Wales).

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(a) Typical appearence.

(b) With tailings produced by recent digging.

Scale bars: 30 mm.



Figure 3.6.

Alternate conditions of <u>Selenocosmia</u> <u>stirlingi</u> burrows at the Coombah field site (New South Wales).

(a) Blocked with a plug of sand and web.Scale bar: 30 mm.

(b) Partially excavated by an unidentifiedclawed animal.Scale bar: 10 cm.



caused the steady decline in all but the lowest activity levels during the course of the study. Examination of burrow closures provided further information concerning this possibility.

The total range of periods of time over which burrows were recorded as closed and subsequently reopened was divided into ten classes and the frequencies of occurrence in each were examined. Although the maximum period was 700 days, most burrows (90.5%) reopened in less than 260 days.

If burrows remaining closed in excess of 260 days were removed from the sample from the time at which they first closed, and percentages of open burrows and "seen" spiders were calculated from the adjusted sample size, two main trends were revealed (Figure 3.3d). Firstly, after the initial year, the population remained fairly steady between 54 and 71 viable burrows rather than increasing. Secondly, although the patterns of activity were essentially unaltered, the peaks of open burrows were sustained at more than 80% (except immediately after the worst of the drought, April 1983), and the maximum percentage "seen" around 62 to 80%, rather than steadily declining.

Furthermore, when the number of burrows removed from the sample is plotted (Figure 3.3e), the distribution is not even throughout the year, but appears to have seasonal maxima from late spring to early summer (November to January) each year. The position of these peaks was partly a consequence of deleting the burrows from the time of first closure and they may have been vacated sometime earlier.

3.3.2.2 Reproduction

Small spiderlings (instars II to IV) were collected for laboratory experiments in December 1981 and February 1983. Others were seen in the entrance of various burrows with their mothers at night on those dates, and also in February 1982 and March 1984.

These results, summarised in Figure 3.3c, suggested that breeding usually occurred in summer. One of the field specimens was seen with young in 1982 and 1983 suggesting that either annual breeding occurred with this spider, or that growth and development were extremely slow.

Only one male spider was found in the field throughout the entire study. This specimen was collected at the Coombah homestead on the first field trip (June 1981), not at the field site itself.

Where available, the collection dates of the preserved museum specimens described earlier (Section 2.8) provided some additional insight into the timing of wandering behaviour in males (Appendix B).

3.4 DISCUSSION

3.4.1 The Field Area

The field site lies in the geological province known as the Murray Basin which is an area almost completely covered in Quaternary deposits (Cunningham <u>et al</u>. 1981). Coombah is situated to the west of the Great Anabranch of the Darling River near a series of lakes and channels which were more active in wetter periods of the Pleistocene (Bowler 1980). The two dunes within the field site were formed from red-brown sand with calcareous layers encountered within 1 m of the surface, while the low lying areas tended to contain more clay (Leeper 1964).

The vegetation was described as a Belah-rosewood community on the classification provided by Cunningham <u>et al</u>. (1981). It was an open form, with several individual trees scattered about 100 m apart and blue bush, grasses and herbs beneath. Clumps of <u>Erimophila</u> sp. ("turpentine bush") boardered the site to the north and south and some individual shrubs were located within it. The ground cover changed dramatically during the study in response to moisture availability and the succession was as follows:

grasses, bare ground with no cover, low herbs, and then taller herbs and spear grasses. Twelve months after the completion of field work, the pasture-type grasses, present at the commencement of the study, were returning to the area.

The relationship between burrow depth and altitude was investigated as it appeared that the latter could be used as a simple approximation of the clay content in the soil: less upslope and more downslope and in the clay pan. From collection of specimens for the laboratory, it was suspected that the higher clay content at the slope margins may have been associated with shallower burrows due to the lower porosity and improved water holding properties in these areas. Analysis of the field population did not support this hypothesis.

The diameter of spider burrows has been directly correlated with the size of the occupant (Decae <u>et al</u>. 1982, Miller & Miller 1984). If this relationship was also true for <u>S</u>. <u>stirlingi</u>, it seemed possible that the larger spiders might also have made deeper burrows, as suggested by Petrunkevitch (1911). Such a trend was not observed in this population, and indeed, in the extremes, one smallish burrow (18 mm) was in excess of 100 cm deep while a larger one (24 mm) was only 40 cm deep.

The rainfall pattern observed during the study is typical of this region and compared well with figures from Menindee, 100 km north-east of Coombah. There the annual falls have ranged from 52 to 766 mm and the mean is 236 mm (Cunningham <u>et al</u>. 1981). The mean annual rainfall over the three years of the study at Coombah was 232 mm.

The consequences of this variable and erratic rainfall appeared to be twofold during the study. The drought of 1982-83 was associated with almost total decimation of the vegetative ground cover and dehydration of the exposed soil surface (Figure 3.4a and 3.6b). It seemed likely that herbivorous insects and arthropod predators also declined, thus reducing

the availability of potential food. In contrast, the heavy rains which followed, late in 1983, had the reverse effect and additionally seemed to correspond with depressed summer temperatures, even at 60 cm.

If it was assumed that 20 degrees C was near the temperature below which growth and development ceased (see Section 5.2.4.1) and metabolic demands (particularly in the absence of food) were minimised, this temperature could be called an "ecological zero". In contrast, 20 degrees C seemed to provide optimum conditions for these processes (see Section 6.5.3.3). Within the burrow (at 60 cm), 20 degrees C was only exceeded for the 9 months from September to May, suggesting a short growing season. However, the highest levels of activity were recorded in September and October, which suggested that the elevated temperatures near the burrow entrance must have been exploited behaviourally in a similar manner to the basking of Geolycosa godeffroyi (Humphreys 1974), to achieve body temperatures above those in the base of the burrow. This would facilitate feeding and growth while avoiding the thermal extremes of summer near the surface. Potential prey at the surface (depending on the moisture and vegetation availability) may also have been more abundant at this time, as the temperature began to increase.

Throughout the study, very little potential food was observed either on the surface or in the pit-fall traps. Remains in the burrow, while providing a definite description of prey which had been eaten, could not be used for quantitative analyses for the following reasons. Firstly, when fresh diggings were observed around the burrow entrance, old egg sacks, exuviae and prey remains were found in the tailings. Under the influence of natural weathering agents this debris was soon dispersed. Secondly, prey items with fewer or smaller indigestible body parts (such as lepidopteran larvae) would be more difficult to collect and subsequently detect, as noted by Hobby (1930, 1940). Finally, such

evidence could only be obtained when the burrow was excavated and therefore destroyed. With the exception of the lycosids, none of the species found in the remains were seen on the surface or in pit-fall traps, indicating the non-comparability of these techniques. This may have been partly due to a temporal displacement between the two sets of observations.

3.4.2 Spider Activity

3.4.2.1 Burrow Blocking

Burrows became blocked as a consequence of the action of natural agents (such as wind and rain) combined with an absence of positive clearing by the occupant, as a result of deliberate plugging by the spider within the top 10 to 15 cm of the burrow or as a consequence of the combined actions of the two. As the end product of combined agents could not be distinguished from natural weathering alone (i.e. no evidence of a burrow opening in an unblemished soil surface), it was only on odd occasions that deliberate plugging was observed. Burrow plugs, formed from leaves and/or sand and web, have been produced by other theraphosids under both laboratory and field conditions (Gertsch 1949), and the plugging technique used by Aphonopelma chalcodes was described in detail by Minch (1979a). Gwynne and Watkiss (1975) describe burrow plugging behaviour of Geolycosa wrightii; however the plugs were formed by blowing or saltating sand grains which were arrested in the top of the burrow. The entrance diameter was constricted with a web collar and the burrow closed off with a single layer of sticky web on which the sand accumulated. This technique appears to differ from the theraphosid technique, which involves the formation of soil and web balls packed together to form the plug (Minch 197%).

Main (1962, 1968) and Gray (1968) have recorded door-sealing in trapdoor spiders associated with seasonal weather conditions and predator avoidance. These factors may also contribute to the behaviour observed in these theraphosids.

3.4.2.2 Burrow conditions

Open burrows were those in which spiders were active or those which had neither been plugged by the spider nor weathered closed, irrespective of the presence or absence of the spider. The difference between the proportion of open burrows and those in which the spiders were seen was probably due partly to this unquantified "presence" factor, and partly as a consequence of failing to see active spiders which were temporarily at lower levels in their burrows.

It is possible that the new burrows located throughout the study (mostly of adult sized dimensions) were newly recruited in the population or opened after prolonged closure. Thus the levels of activity actually declined through the same period or were approaching real levels as the whole population was being revealed. The apparently permanent closure of some burrows suggested that individuals were actually leaving the population. The adjusted values resulted in a more constant population size and sustained activity levels, and could be interpreted as supporting this.

Although one spider closed its burrow for 700 days, the infrequency and short duration of field trips resulted in very poor resolution and this spider, and indeed some of the new recruits, may well have opened and replugged the burrow in the intervening periods. This limitation must be kept in mind when reviewing the trends in activity or apparent losses.

The apparent loss of spiders from the population (as estimated on the basis of sustained burrow closure) may have resulted from death due to old

age, during moulting (as observed in the laboratory), following attack by parasitic wasps, or by migration. One case of parasitism by a pompilid wasp (determination by Prof. H.E. Evans, and Evans 1959) was observed and many have been documented for other theraphosids (Baerg 1958, Minch 1979b). No other direct evidence of death within burrows was recorded. The apparent losses mostly occurred in summer, but as the temperature and moisture conditions varied widely at these times, they were probably not directly responsible.

No evidence (such as massive excavation) was found to suggest that burrows were vacated in favour of new dwellings. However, if migration involved displacement of the occupants of existing burrows, such actions would only have been recorded as losses. It seems most likely that, due to the seasonal coincidence of the losses with production of young and the relationship between the timing of this behaviour, moulting and mating in other species (Minch 1979b, Baerg 1938), mid-summer losses may have largely represented departure of newly matured males. Death during ecdysis could also have accounted for losses occurring at this time.

The spring opening of burrows appeared to correspond to the time when the burrow temperature increased above 20 degrees C. Spiders operating within open burrows prior to this time may well have used elevated temperatures in upper levels (after sunny days) in order to remain active. Minch (1979b) claimed that temperature was not the cue for burrow unblocking as spiders at different altitudes (and hence temperatures) opened their burrows at virtually the same time. Furthermore, Gabel (1972), while suggesting that a drop in temperature caused burrow plugging, observed burrows which remained open even when the nightime temperatures dropped below freezing. Minch (1979b) observed that spiders maintained in the laboratory blocked their burrows somewhat later than those in the field, suggested that perhaps photoperiod, or temperature,

might at least moderate the behaviour. However, photoperiod (or light regime) is generally linked with the annual fluctuations of temperature within the soil, if not with specific temperatures. While these two factors would be difficult to separate under field conditions, laboratory findings revealed that <u>S</u>. <u>stirlingi</u> lost little weight when maintained at or below 20 degrees C, so perhaps a temperature pattern gate (originally suggested by Gabel (1972)) regulates this behaviour, at least in part. In addition, as Minch (1979b) proposed, an internal clock, possibly set genetically or during early development, may regulate the annual activity patterns and might be moderated by photoperiod and/or temperature patterns.

The mid-summer decline in spider activity (December to January) corresponds to the time when temperatures and moisture deficit at the surface are generally most extreme. At this time of the year, Minch (1979b) recorded burrow blocking associated with either egg sack production or moulting (although it was not obligatory) in <u>Aphonopelma</u> chalcodes.

The occurrence of juveniles at Coombah, between late December and early March, supported Minch's (1979b) suggestion that the blocking was associated with reproductive activity. Alternatively, the losses from the population at this time, (which were believed to be maturing males) and the summer-autumn collection of males (in the S.A. Museum collection), suggest that moulting may also occur at this time of the year.

3.5 SUMMARY

The following summary of the field observations is provided. These findings have been limited by the degree of resolution of the field investigations, both in terms of the nature of the data available and the periods between the field trips. In spite of this, the seasonal activity

patterns of the spiders were remarkably consistent with observations of other theraphosids (e.g. Baerg 1958, Minch 1979b). The lowest temperatures occurred in winter in both the soil and at the surface, and were associated with consistently low levels of spider activity. As both the surface and soil temperatures rose in spring, maximum levels of spider activity were observed. During the hottest months, mating and/or reproduction probably occurred within blocked burrows. The peak in the estimated losses from the population, which also occurred at this time, may have been due to maturation of males, or mortality associated with summer conditions or moulting. Activity levels rose slightly in autumn as the temperatures at the surface declined, before dropping to the winter lows.

Temperatures at the surface fluctuated widely, both diurnally and annually, but within the soil, even at only 20 cm, the diurnal excursions were reduced to a maximum of 10 degrees C. At 60 cm, the diurnal excursions were rarely greater than 1 to 2 degrees C. In the soil, the temperature exceeded 20 degrees C from about August to May, during which time surface temperatures generally exceeded 35 degrees C.

Both spider activity patterns and surface temperatures were lower in the summer of the drought-breaking rain, than during the drought year.

CHAPTER 4

EXPERIMENTAL MATERIALS AND METHODS

4.1 INTRODUCTION

This chapter contains details of the materials and methods used for experiments run in the laboratory and in the field. Details of the statistical procedures used to analyse the data are also provided.

4.2 COLLECTION OF SPECIMENS

To obtain live spiders from burrows up to 100 cm deep in porous sand, a specific technique was developed. To prevent infilling and loss of the burrow during excavation, a 1 metre length of 3/16 inch (4.8 mm) diameter spear-gun rubber (Clark-Maples Pty. Ltd.) was carefully introduced into the burrow by gentle twisting and pushing. In this manner, it could be worked to the terminal chamber so that the residual on the surface (subtracted from 1.0 m) indicated the length, and therefore approximate depth, of the burrow. In addition, it gave some indication of the slope and direction of the burrows departure from vertical. Excavation commenced beside the mouth of the burrow and away from its apparent fall. The burrow was carefully opened along its length with the tailings accumulating in the adjacent excavated hole. This was enlarged and deepened as necessary in order to keep its base below the opening burrow, until the terminal chamber was reached. Adult specimens were coaxed into jars while juveniles were collected, often in clusters, with soft forceps (see Appendix C). Debris, such as food remains, exuviae and egg sacks was also collected.

<u>Selenocosmia</u> sp. from near Cairns (N. Queensland) were collected in a similar manner by Michael Trenery and Alan Williamson and airlifted to the Zoology Department (Monash University).

4.3 MAINTENANCE OF SPIDERS

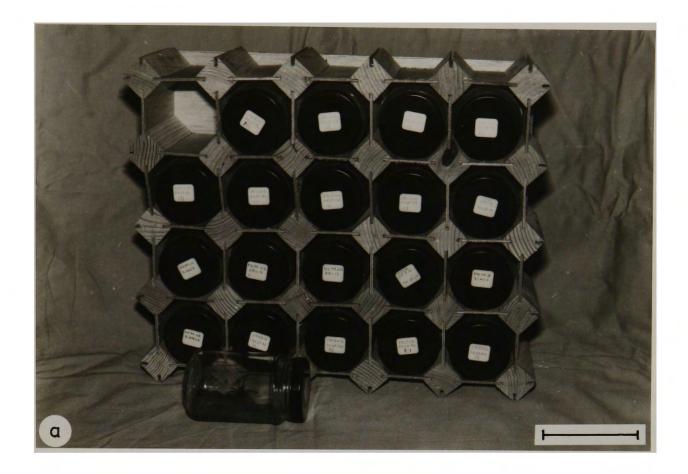
In the laboratory, where the temperature was less than or equal to 20 degrees C, spiders were placed in separate 8 oz Pomade jars (Laboratory Supply Pty. Ltd.) containing 40 g of sand moistened with water. The sand was obtained from the field site, heat sterilised at 100 degrees C for 72 h, and sieved to remove aggregations and larger organic matter. Juveniles were kept for some time with their mother or siblings before being isolated. Each spiderling was then numbered according to the collector and maternal parent; for example MK36.153 referred to spiderling number 153 (selected at random from the litter, except for the last individual) belonging to female number 36 collected by the author. When assigned to an experiment, an additional number was provided to characterise the temperature, feeding level, social condition, light regime or other particulars of the experiment. The jars were stored horizontally in wooden racks to provide the maximum flat surface for the spiders to stand on, to reduce light penetration and with the labels clearly visible (see Figure 4.1). Ventilation was provided by periodically removing the lids (which were intact to exclude marauding ants and to maintain high humidity). As it was needed, water was added to the soil in the jars to keep it moist. The history of each individual was recorded on a system card and included some or all of the following details: initial weight, experiment commencement date, dates and weights of each food item provided, dates and weights at each moult and comments on overall condition.

Figure 4.1.

Housing facilities for spiders maintained in the laboratory.

(a) A wooden rack to hold 16 jars.Scale bar: 100 mm.

(b) A typical jar containing moist sand and a spiderling.Scale bar: 20 mm.





4.4 WEIGHING

Using soft forceps (Appendix C), spiderlings were caught by one or more legs and transferred to a plastic container for weighing (+/- 0.05 mg) (Mettler HK60 balance). When the combination of weight and strength of the spider were too great for this procedure (usually 1.5 g +), the spiders were coaxed out onto the bench and lifted with conventional forceps secured above and below the posterior region cephalothorax, at about the centre of gravity.

Almost all spiders were weighed immediately after collection and where appropriate, at the commencement of each experiment. During the experiments, each individual was weighed either each 14 days (e.g. conditions 1 to 4 in Table 4.1) or within 24 hours of ecdysis (all other experiments, Table 4.1). In the former case, estimates of the weight at and time of ecdysis were made on the assumption of linear weight gains over the intervening days and from the distinct appearance of pre- and post- ecdysial spiders. In some instances, spiders were additionally weighed on each of the 3-4 days preceeding the moult. In all conditions excluding 1 to 4 (see Table 4.1), the exuvium was also weighed separately, so that not only the initial weight for the current instar, but also a final weight for the preceeding instar were recorded. As moisture is lost during ecdysis (Stewart & Martin 1982) and moisture adhering to the exuvium may be lost prior to weighing, the final weight for an instar will be slightly less than the true maximum achieved.

4.5 DETERMINATION OF SIZE

The cephalothorax length and width, curved and straight fang lengths and, on the exuviae of instars greater than IV, the lengths of the cuticular buds on the epigastric furrow were measured (Figure 4.2). The term cephalothorax has been used for measurements on both exuviae and

Figure 4.2.

Positions of the morphometric measurements made on mounted exuviae.

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(a) Dorsal view of the cephalothorax;

i. length,

ii. width.

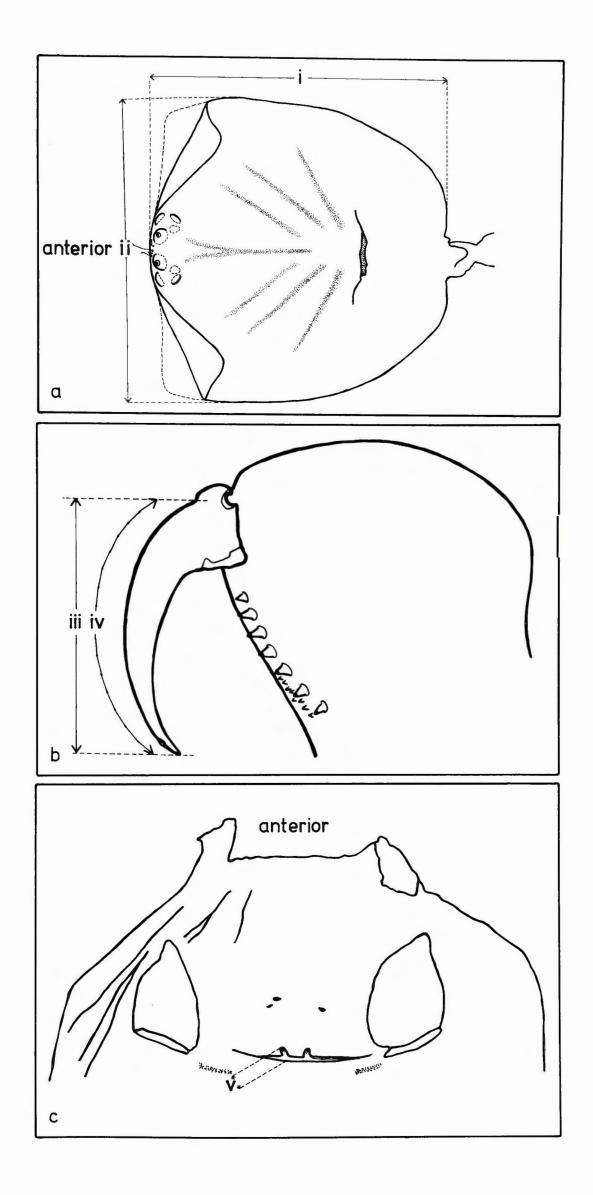
(b) Prolateral view a chelicera;

iii. straight fang length,

iv. curved fang length.

(c) Dorsal view of the ventral abdominal cuticle at the epigastric furrow;

v. cuticular bud or spermathecal length.



whole specimens, as in both cases, the carapace provides the length and width boundaries for this part of the body.

4.5.1 Preparation of Exuviae

Exuviae were stored in 100% ethanol (EtOH), prior to mounting directly onto histological slides in Euparal (Chroma, W. Germany) under coverslips. Infiltration of the EtOH was facilitated in a vacuum chamber (40 mm Hg, >0.5 h). Chelicerae were detached and mounted with the prolateral surfaces uppermost, and the isolated cephalothorax (carapace) with its dorsal surface uppermost. Where applicable, the ventral portion of the abdominal cuticle was lightly stained with Azo Black (in 70% EtOH/H₂O, George T. Gurr Ltd., England) for about 30 s, rinsed with 100% EtOH and mounted under a separate coverslip (10 mm diameter) on the same microscope slide. For instars greater than V, only the chelicerae, cephalothorax and abdominal cuticles were mounted. Each slide was labelled with details of identity, experimental conditions, instar and the date of ecdysis (Figure 4.3).

4.5.2 Measurment Techniques

Using a Leitz projector (Prado) with a rotating objective turret and a 90 degree prism, the mounted exuviae were projected (about 750 cm) on to a Tektronix Inc. flatbed digitizer (Tektronix Model 4956 option 31) coupled to a computer (Tektronix model 4051) (Figure 4.4). After calibration with a standard 1 mm micrometer slide, two magnifications (approximately x46 and x133) were used to measure the previously described parameters and the results (together with the spiders identity number and the instar) were recorded on floppy disc (see Appendix D for the measuring programme). These data were transferred to a Burroughs B7800 mainframe computer and merged with manually entered information on Figure 4.3.

An example of a mounted exuvium on which measurements were made. Microscope slide 25 x 76 mm.

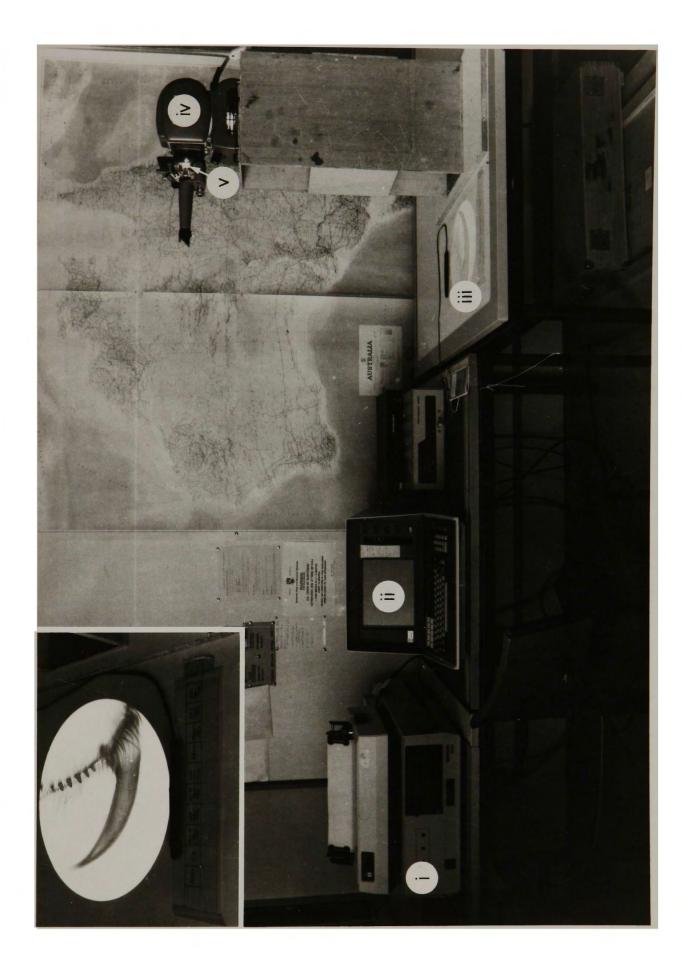
MK71.36 Exurium V 32H15 19. xii. 1983

Figure 4.4.

Apparatus with which the mounted exuviae were measured.

i. Disc drive,
ii. Computer,
iv. Projector,
v. Microscope slide,
iii. Projected image.

Insert: Detail of the projected image and the menu for selection of scale or other functions via the digitizer pad.



weights, instar durations and food supply, to form the total data file (see Appendix E).

By taking multiple measurments of a single subject, the maximum systematic error resulting from defining the boundaries of each structure and accurately positioning the digitizer stylus, was estimated to be +/-0.02 mm. Further error in fang measurements resulted from their tapered shape and consequent divergence from the plane of focus. For fangs 1 or 5 mm long, the degree of underestimation produced by the fang shape was calculated to be in the order of 1.26 to 1.45% (see Appendix F).

Where possible, on large live or preserved specimens, fang lengths and cephalothorax lengths and widths were also measured, with calipers (Mitutoyo) equipped with a dial scale.

4.6 FOOD SUPPLY

Cultures of <u>Tenebrio molitor</u> L. (Tenebrionidae) were maintained at 22 degrees C in open plastic containers containing granulated mouse or kangaroo food pellets (Barastoc Pty. Ltd.). Sheets of newspaper provided shelter and a surface on which to place fresh slices of apple or banana skins for moisture and added nutriment, without promoting fungal growth. Periodically, cultures were synchronised by isolating pupae at 4 degrees C until they were needed. The larvae (mealworms) were sieved from their food medium and sorted to obtain the required sizes. In most experiments, individual mealworms were weighed (Mettler HK60 balance) prior to presentation to the spider. Those not used were returned to the culture boxes. In the food size preference trials described in the previous chapter (Table 2.3), the length of each mealworm was also estimated by linear comparison with a standard metric rule. It should be noted that the extensibility of the mealworms made this a very approximate estimation.

Once provided, food was not removed (for the reasons outlined in Section 2.5) unless its state of decomposition was deemed to be a health risk for the spider. Thus, prey items were available to the spider for capture in the light or dark within 12 hours of supply.

4.7 LABORATORY EXPERIMENTS

Experimental conditions included various combinations of temperature, photoperiod and food availability, for spiders from several litters from both Coombah and Cairns. These combinations, together with the precise details of each experiment, are summarized in Table 4.1, and the methods used to manipulate the conditions are described below.

4.7.1 Manipulation of conditions

4.7.1.1 Food supply

The rate of food supply was primarily regulated by the interval between meals. Under most conditions, the high feeding rate interval ("H" in Table 4.1) was every 7 days and the low feeding rate ("L" in Table 4.1) was every 14 days. In condition 12, higher ("X") and lower ("M") levels were added, in which feeding occurred every 3 or 17 days respectively. With the exception of condition 8, an attempt was made to ensure all meals lay in the size range 15 to 25 mg. However, there was some evidence that in conditions 1 to 4, the sizes were not consistently obtained during the course of the experiment. As condition 9 involved larger spiders, the meal size was increased to 25 to 35 mg, but at the same feeding intervals described above. Apart from condition 5, all meals were weighed so that a mean rate of supply (mg wet weight per day) could be estimated.

Table 4.1.

Details of the conditions manipulated in the laboratory experiments, including the spiders used and the feeding, weighing and measuring protocols employed.

CONDITION NO.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Litter	36	36	34	34	69	69	69	71	71	79	79	79	78	78
Temperature ([°] C)	30	25	30	25	28	28	30	30 32 35	31	28 33	31	31	31	25
Rate of food supply *	H L	H L	H L	H L	X M	H L	H L							
Photoperiod **	S	S	S	S	S	S	S	S	S	S	S	S	S W	S
Instars III-V	+	+	+	+	+	+	+	+	-	+	+	+	+	+
Instar VI-VIII	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Weighed each 14 days	+	+	+	+	-	-	-	-	-	-	-	-	-	
Weighed prior to e cdysis	-	-	-	-	+	+	+	+	+	+	-	+	+	+
Spider & e xuvium weighed at ecdysis	s -	-	-	-	+	+	+	+	+	+	+	+	+	+
Food weighed	+	+	+	+	-	+	+	+	+	+	+	+	+	+
Meals counted	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Spermathecae measured	-	-	-	-	+	+	+	+	+	+	+	+	+	+

* "H" = high, "L" = low, "X" = extra high, "M" = extra low ** "S" = summer (15L:9D), "W" = winter (10L:14D)

4.7.1.2 Temperature

Constant temperatures were maintained within +/- 0.5 degrees C in constant temperature rooms or within cabinets designed specifically for the purpose. In the latter, domestic fan heaters (Goldair model Celsius 22T) were wired to control units so that the fans continuously circulated the air and the heating elements boosted the temperature to preset levels. Cooling was achieved by housing the cabinet in a room at least 6 degrees C below the desired level.

4.7.1.3 Photoperiod

Desired light regimes were obtained using incandescent bulbs (4 x 60 W or 2 x 25 W) on mains powered (240 V AC) mechanical time clocks within the C.T. rooms or cabinets, respectively.

4.7.1.4 Moisture

In all the experiments, the sand in each container was kept moist to provide a source of drinking water and to maintain high humidities (near saturation).

4.7.2 Field Experiments

Three experiments involving the return of juvenile spiders to the field were carried out during the study; two were designed to test the viability of experiments conducted in the field, and the third to assess food consumed in the field and to test laboratory findings under field conditions.

4.7.2.1 Experiment 1

On a grid pattern 3 m x 4 m, 12 holes of 5-7 mm diameter and 150 mm deep were formed by pushing a pointed wooden dowel into the pre-moistened sand. Marking stakes were planted 150 mm west of each hole. Instar III spiderlings (MK36.194 to 205 inclusive) were placed in the tops of the holes and encouraged to enter the artificial burrows. The presence or absence of these spiderlings was checked on successive trips.

4.7.2.2 Experiment 2

Sixteen artificial burrows, 15 mm in diameter, 500 mm deep and scattered over an area of about 100 square metres west of the highway, were constructed with a tube corer. Various sizes of spiderlings of instars V-VII (offspring of MK36 and MK34 from laboratory growth experiments) were released into these artificial burrows. About 7 weeks later, the burrows were excavated and the spiders recovered.

4.7.2.3 Experiment 3

Ninety-two spiders of various sizes and instars from previous laboratory experiments were branded for individual identification. The spiders were anaesthetised with CO₂ and lightly scorched with a fine nichrome wire connected to a variable power supply running at 2 - 2.25 V DC (Figure 4.5a). Brands were applied to the retro-lateral margins of the ventral surface of the coxae of the walking legs (providing 8 possible locations) to produce distinctive combinations (Figure 4.5b). Although this system provided possible 256 combinations, values from 1 to 9 only on each side were used/in a conventional decimal arrangement.

The spiders were randomly assigned to six experimental groups from each available instar. Of these groups, three were returned to the field and three were maintained in the laboratory in a temperature controlled

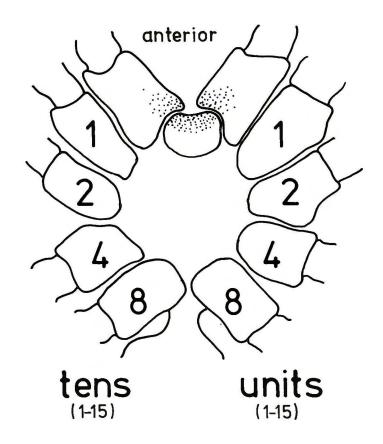
Figure 4.5.

Branding apparatus and the potential numbering sites on the spider.

(a) A nicrome wire "pencil" and variable power source.

(b) Potential brand locations on the ventral surface of the coxae of the walking legs.Each coxa was assigned a specific numeral (when branded), and the sum of these provided the numerical value for each side.





cabinet. So that the field conditions of temperature and light regime could be mimiced in the laboratory, a six week delay was established between laboratory and field-released spiders, and weekly adjustments were made in order to track field conditions. Under both conditions, groups of spiders were provided with no food, a weighed mealworm either during or after each field trip, or a weighed mealworm during or after every alternate field trip. Field released animals were additionally exposed to naturally occurring prey items. Spiders in the groups which were maintained in the laboratory were weighed at each moult and the exuviae collected.

4.7.3 Statistical Analysis

This section outlines the statistical tests used to analyse the data obtained from the laboratory experiments, and the reasons for their choice.

Several different statistical tests based on the principles of analysis of variance (ANOVA) (e.g. t-tests, one-way and two-way ANOVA, linear regression and analysis of covariance) were selected to compare sample means from different experimental conditions or the relationships between variables. These tests are strong, appropriate and robust (Ferguson 1971, Sokal & Rohlf 1969, Wonnacott & Wonnacott 1971, Freund 1973, Zar 1974).

Individual values were compared with sample means (e.g. Section 5.2.4.2) using t-tests (Sokal & Rohlf 1969, p.224) and a calculator (Sharp EL-515), as were pairs of sample means (e.g. Section 5.2.4.1) (Sokal & Rohlf 1969, p.208). Alternatively, means from two or more samples (e.g. Section 5.2.4.2) were compared using one-way ANOVA according to Sokal and Rohlf (1969, p. 232) or, by using the SPSS software package (Nie <u>et al</u>. 1970).

Where experimental design and execution resulted in strict comparability of the independent variables, two-way ANOVA was used to compare sample means within each condition, and to assess any interaction between them, using the SPSS software package (Nie et al. 1970). There are several methods commonly used to accomodate unequal sample size, which causes non-additivity of the sums of squares (Steel & Torrie 1960, Sokal & Rohlf 1969, Zar 1974). The most common methods involve the fitting of constants (in various sequences) or less often the estimation of weighted mean sums of squares, with different results most likely in the event of significant interactions (Steel & Torrie 1960). Different constant-fitting models available with the SPSS software package were applied to the data, and found to yield comparable results in all cases. The results obtained using the "classical experimental approach" are provided in Chapter 5 (Nie et al. 1970). Where significant differences were found between more than two means using ANOVA, Student-Newman-Keul's (SNK) tests were used to determine where the differences lay (Zar 1974, p.151). Where necessary, adjustments were made for unequal sample sizes according to Zar (1974, p.154). As this a posteriori test is somewhat weaker than ANOVA (Zar 1974, p.155), in some cases, significant differences found with ANOVA could not be resolved in more detail by the SNK test.

Of the assumptions underlying the use of ANOVA, homogeneity of variances (or "homoscedasticity") was of the greatest concern here. While Bartlett's test has been favoured in the past, some authors now believe that since it is more sensitive to non-normality than the ANOVA it follows, it may be overly conservative (Zar 1974, p.133). The "quick and dirty" F-max test, based on variance ratios and sample sizes, was used, in spite of its inferior efficiency, because of its simplicity and suitability to the data (Sokal & Rohlf 1969, p.375). Where sample sizes

are equal, Glass et al. (1972) and Zar (1974, p.135) claim that ANOVA is robust to heteroscedasticity, and in such cases, it was therefore not necessary to transform the data. With the remaining cases of heteroscedastic data, the following protocol was used. It was not possible to use Taylor's power series to determine the precise transformation which would restore homogeneity of the variances (Taylor 1961, Elliot 1977), because there were too few means and insufficient degrees of freedom to perform meaningful analyses. As logarithmic transformations often restore homogeneity of variances (and normality) to data (Sokal & Rohlf 1969, p.382), these were used and the ANOVA performed on the transformed data when homoscedasticity was achieved. Where this transformation was not successful, the relationships between the means and the variances were inspected, and according to Glass et al. (1972), the resultant impact on an ANOVA was described. Where a larger mean was associated with a larger variance, the actual probability of making a type-I error (i.e. rejecting the null hypothesis when it is true) became somewhat lower than the nominally set 5% level, that is, the test became more conservative (Glass et al. 1972). Instead of falsely rejecting the null hypothesis 1 in 20 cases, the odds might fall to say 1 in 25 cases. Conversely, where two underlying populations overlapped in their tail regions, and the observed value lay in that region, the likelihood of a type-II error (i.e. accepting the null hypothesis when it is not true) would be increased. This would reduce the probability of detecting subtle differences which would have been significant if the variances had been homogeneous.

In order to characterise the relationship between pairs of variables, simple linear regressions were performed with a Fortran programme adapted from published subroutines by Ettershank (pers. comm.) (Appendix G). Although the underlying assumption of independence was not always strictly

met (e.g. in the morphometric analyses, Section 5.2.1), the method was appropriate for providing equations to describe the relationships, provided that care was taken to use the variables in the arrangement used in the regression for estimations. The strength of the relationships was determined with a coefficient of determination derived from a Pearson product-moment correlation coefficient (Ferguson 1971, p.99). The equality of slopes of the regression lines was assessed using analysis of covariance (ANCOVA) (Sokal & Rohlf 1969, p.450). Where the relationships involved more than one independent variable, stepwise multiple regression from the SPSS software package (Nie <u>et al</u>. 1970) was used, with care taken to avoid nonlinear sections of the relationships or to linearise curvilinear relationships.

Chi-square tests (Zar 1974, p.42) were used to compare observed frequencies with expected frequencies (e.g. with sex ratios, Section 4.5), using a calculator.

Where annotated, the significance of F or Chi-square values are as follows: *** = p < 0.001, ** = p < 0.01, * = p < 0.05. Values of p > 0.05 was considered not significant and labelled NS.

CHAPTER 5

EXPERIMENTAL RESULTS

5.1 INTRODUCTION

This chapter contains the results obtained from experiments carried out in the laboratory and the field. It is divided into two main sections: firstly, preliminary analyses which have a bearing on the experiments and secondly, the experimental results themselves. Details of the statistical analyses used were provided in Section 4.7.3. The relationships investigated apply to spiderlings within the size ranges tested and can only be extrapolated to much larger individuals with caution, since a relationship that may be curvilinear over its entire natural range, may appear linear over smaller intervals.

5.2 PRELIMINARY RESULTS

5.2.1 Morphometric Relationships

In order to test the validity of mean straight fang length as an indicator of spider size, to test for allometry and to provide equations with which missing values could be estimated from those available, comparisons were made between the metric variables measured.

To test for allometry of fang curvature, the relationship between the mean curved fang length (CFL) and the mean straight, tip-to-base fang length (SFL) (Figure 4.2b) of each pair of fangs, was investigated. There were strong linear relationships between CFL and SFL in both the Coombah (r = 0.998) and Cairns (r = 0.997) populations. As there was no

significant difference between the slopes of the simple linear regression lines (F = 0.0195, p >0.90) (Sokal & Rohlf 1969, p.450), the combined populations were plotted and an equation describing the data generated, using simple linear regression (Appendix G) (Figure 5.1).

There was a strong linear relationship between cephalothorax length (CL) and width (CW) (Figure 4.2a) for both the Coombah and Cairns populations (Figure 5.2). The slopes differed significiantly (F = 29.23, p < 0.001). There was a significant difference between the slopes of the regressions of CW on SFL (F = 7.68, p < 0.01) (Figure 5.3) and there was a significant difference between the slopes of CL on SFL (F = 3.86, p < 0.05) (Figure 5.4).

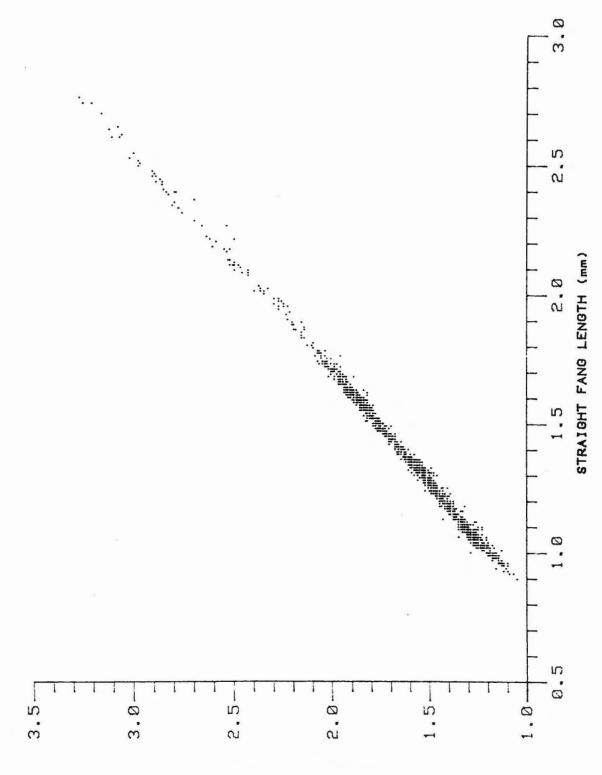
5.2.2 Size-Weight Relationships

The relationships between the initial and final weights recorded for individuals in each instar (excluding offspring of MK36 and MK34, for which such weights were only estimated) and the size of the spiderlings (represented by the mean straight fang length (SFL) (Figure 4.2b)) were investigated. As the natural relationships were found to approximate power functions, they were linearised by logarithmic transformations of both variables for the following analyses. The slopes of the simple regression lines for the Coombah and Cairns populations were significantly different for both initial weight on size (F = 160.3, p < 0.01) (Sokal & Rohlf 1969 p. 450) (Figure 5.5) and final weight on size (F = 213.7, p <0.01) (Figure 5.6). The significance of the differences between the initial and final weights was revealed by examining the weight range calculated for a given size. For a size where SFL = 1.58 mm, a Coombah spider's weight could range from 75.5 mg to 134.5 mg and a Cairns spider's weight from 73.7 mg to 141.7 mg. Conversely, using regressions of SFL on initial and final weights, for a weight of 100 mg, a Coombah spider's size could be estimated at SFLs of 1.43 mm to 1.72 mm and a Cairns spider's

Figure 5.1.

Relationship between the curved and straight fang lengths of <u>Selenocosmia</u> from Coombah and Cairns (instars III to VIII).

y = 0.0406 + 1.1516 x $r^2 = 0.995$, SE = 0.0020 mm, df = 1507.



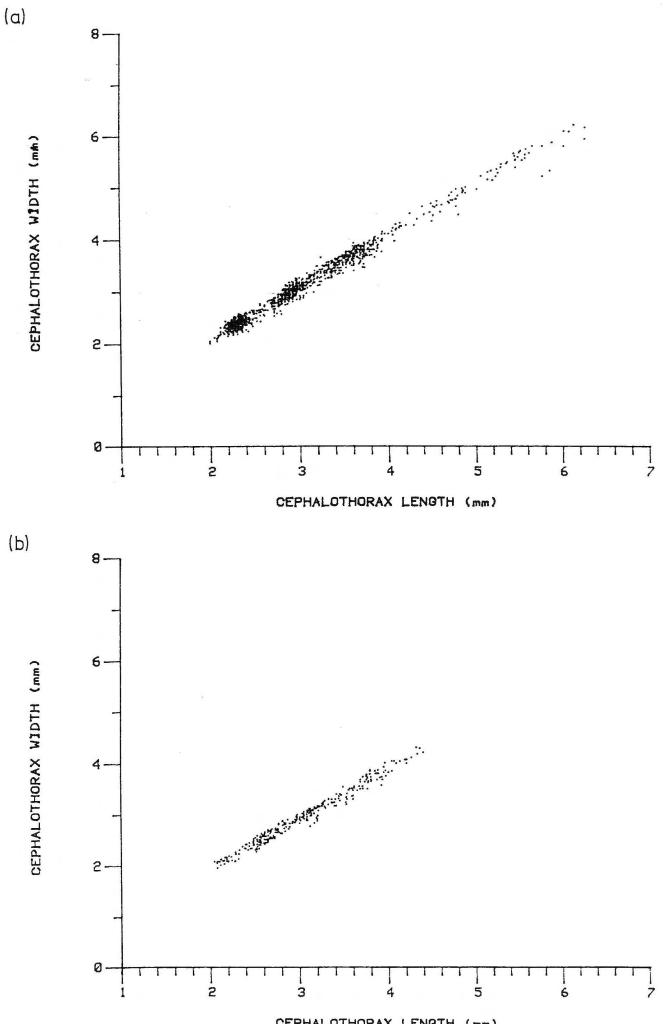
CORVED FANG LENGTH (mm)

Figure 5.2.

Relationship between the cephalothorax width and length for <u>Selenocosmia</u> from:

(a) Coombah (instars III to VI); y = 0.0712 + 1.0070 x r² = 0.983, SE = 0.0040 mm, df = 1077.

(b) Cairns (instars III to V); y = 0.0504 + 0.9497 x $r^2 = 0.977$, SE = 0.0083 mm, df = 305.



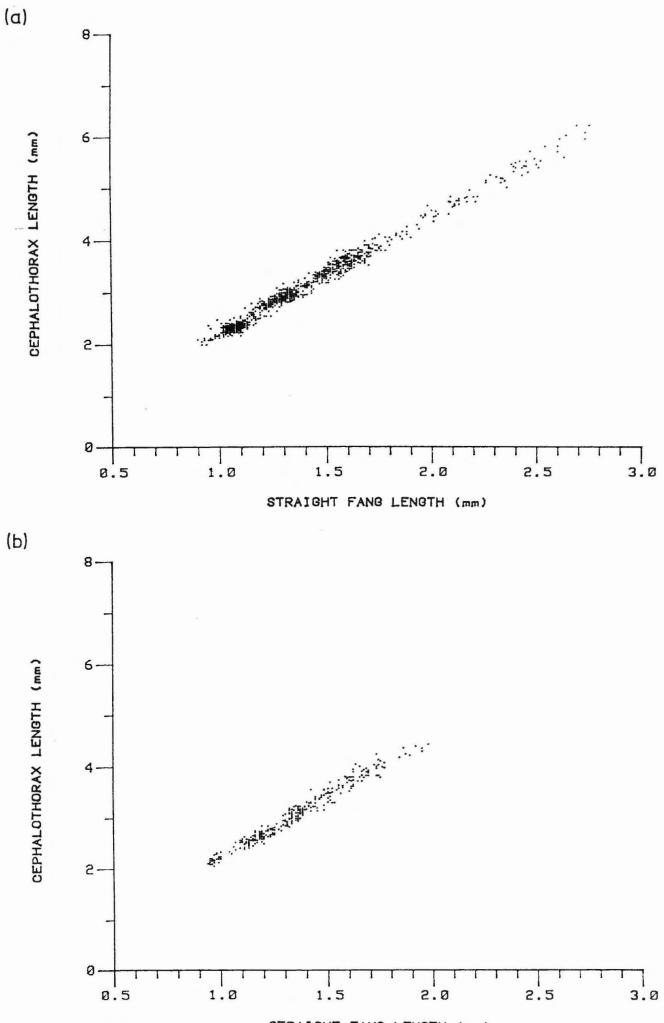
CEPHALOTHORAX LENGTH (mm)

Figure 5.3.

Relationship between the cephalothorax length and straight fang length for <u>Selenocosmia</u> from:

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(a) Coombah (instars III to VIII);
y = -0.1053 + 2.3056 x
r<sup>2</sup> = 0.984, SE = 0.0088 mm, df = 1089.
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(b) Cairns (instars III to V); y = -0.1372 + 2.3547 x r² = 0.970, SE = 0.0235 mm, df = 306.



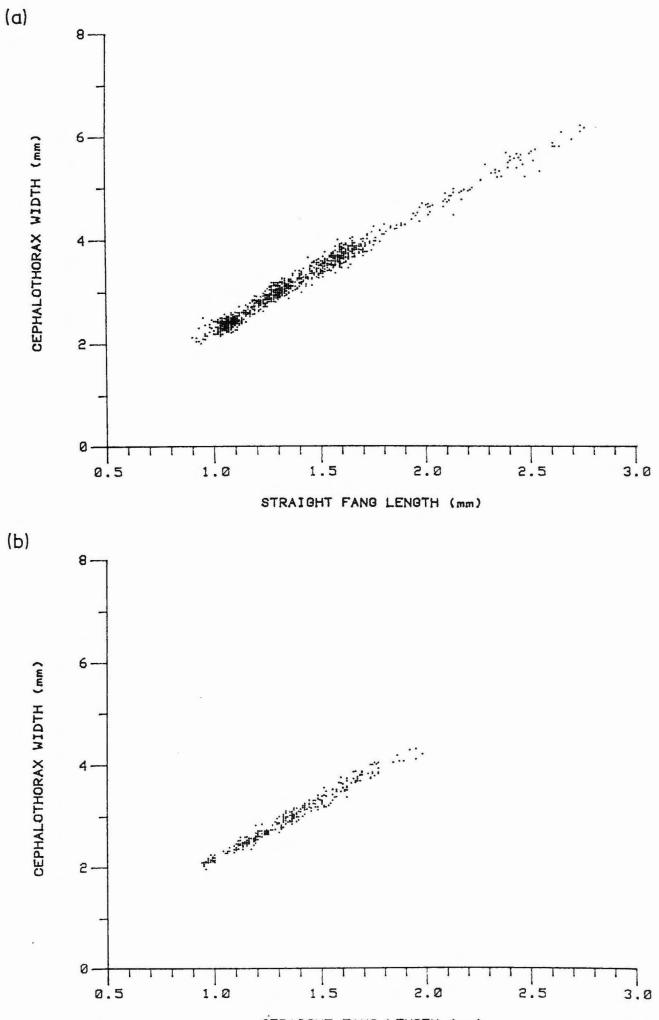
STRAIGHT FANG LENGTH (mm)

Figure 5.4.

Relationship between cephalothorax width and straight fang length for <u>Selenocosmia</u> from:

(a) Coombah (instars III to VIII); y = -0.0584 + 2.3391 x r² = 0.981, SE = 0.0099 mm, df = 1103.

(b) Cairns (instars III to V); y = -0.1193 + 2.2648 x r² = 0.976, SE = 0.0203 mm, df = 308.



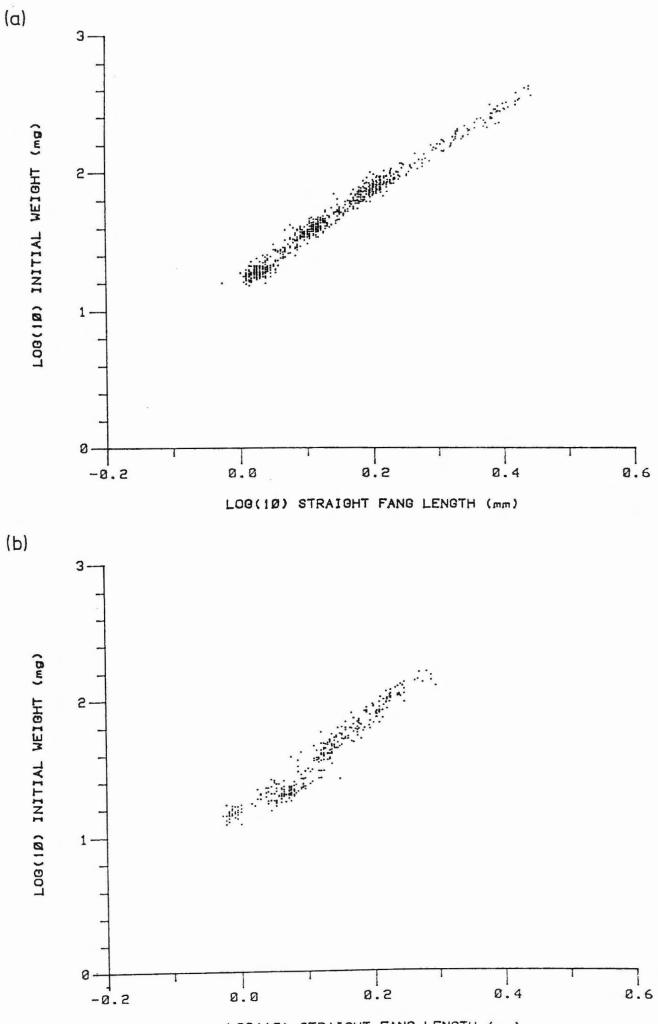
STRAIGHT FANG LENGTH (mm)

Figure 5.5.

Relationship of the initial weight to the straight fang length of <u>Selenocosmia</u> from:

(a) Coombah (instars III to VIII) (offspring of MK36 and MK34 not included); y = 1.2276 + 3.2519 x $r^2 = 0.981$, SE = 0.0168 mg, df = 717.

(b) Cairns (instars III to V); y = 1.1233 + 3.7023 x r² = 0.938, SE = 0.0685 mg, df = 322.



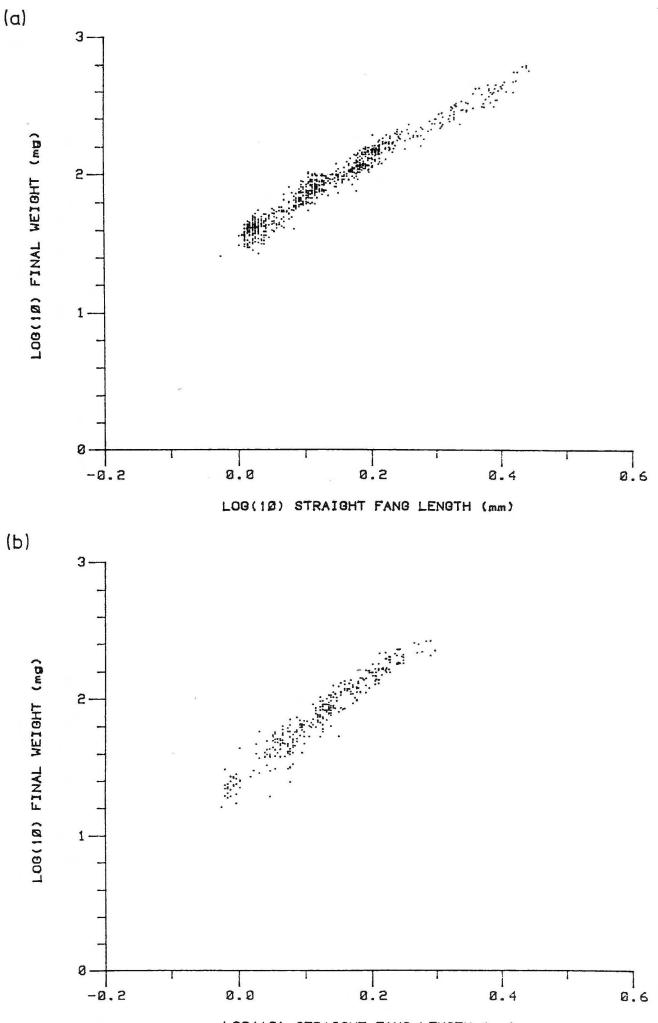
LOG(10) STRAIGHT FANG LENGTH (mm)

Figure 5.6.

Relationship of the final weight to the straight fang length of <u>Selenocosmia</u> from:

(a) Coombah (instars III to VIII) (offspring of MK36 and MK34 not included); y = 1.5566 + 2.8599 x r^2 = 0.962, SE = 0.0213 mg, df = 717.

(b) Cairns (instars III to V); y = 1.4193 + 3.6352 x r² = 0.928, SE = 0.0563 mg, df = 322.



LOG(10) STRAIGHT FANG LENGTH (mm)

size from 1.43 mm to 1.69 mm. As these values approximate the intersection of the two regression lines, the two populations would not be significiantly different.

5.2.3 Estimated Final Weights

The maximum weights recorded for each instar for the offspring of MK36 and MK34 (Appendix E) were estimated on the assumption of linear weight changes between weighings which occurred before and after ecdyses (see Sections 4.1.4 and 4.2.1.1) and are called "estimated weights". These were compared with weights calculated from the equation relating final weight to mean straight fang length for the other Coombah spiders (Figure 5.6a), which are called "calculated weights". The differences between "estimated" and "calculated" weights were not uniform across the different conditions of temperature and food availability (conditions 1 to 4 in Table 4.1) (Figure 5.7). At 25 degrees C, the "estimated weights" were generally greater than the "calculated weights" by a mean of 29.12 mg at the high feeding levels, and 14.41 mg at the lower feeding levels. At 30 degrees C, the "estimated weights" were higher than the "calculated weights" by a mean of 0.95 mg at the high feeding levels, but at the low feeding levels, the "estimated weights" were 11.23 mg lower on average than the "calculated weights".

5.2.4 Commencement Weights

5.2.4.1 Delay Effects

Construction of the temperature-controlled cabinets resulted in a considerable delay between the time at which some of the experimental subjects were collected, and the commencement of the experiments in which they were involved. The effects of spending 6 to 7 months in the laboratory (temperature at or below 20 degrees C) with no food were

Figure 5.7.

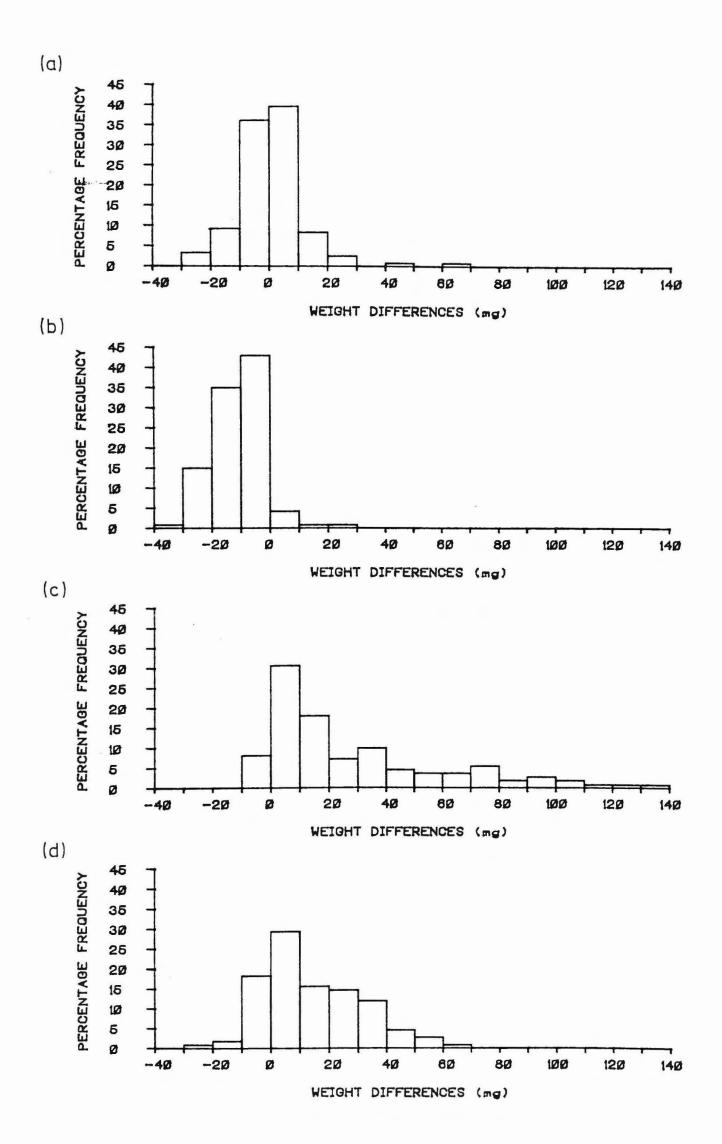
Distributions of the differences between the final weights for instars III to V estimated by interpolation between regular weighings and those calculated from fang lengths for the offspring of MK36 and MK34.

(a) 30 degrees C, high feeding level; $\overline{X} = 0.95$ mg, SE = 13.43 mg, n = 120.

(b) 30 degrees C, low feeding level; $\overline{X} = -11.23$ mg, SE = 7.10 mg, n = 120.

(c) 25 degrees C, high feeding level; $\overline{X} = 14.43$ mg, SE = 98.96 mg, n = 110.

(d) 25 degrees C, low feeding level; $\overline{X} = 29.12 \text{ mg}$, SE = 98.96 mg, n = 111.



investigated in terms of commencement weights (for spiderlings assigned to conditions 6, 7 and 8, see Table 4.1) and altered growth patterns (for spiderlings assigned to condition 6). The latter effects are described as comparison 5 and are dealt with in Section 5.3.5.

Comparison of spiderling weights at the time of collection and when the experiments commenced (6-7 months later) using one-way ANOVA (Sokal & Rohlf 1969, p.208) revealed that there was a significant decrease in the weights of the offspring of MK71 from $\overline{X} = 22.5$ mg to $\overline{X} = 20.9$ mg (F = 10.494, p < 0.001), but no significant change in the weights of the offspring of MK69 (F = 0.427, p > 0.05), with a mean of 19.1 mg.

5.2.4.2 Weight Distributions of the Litters

At the commencement of the experiment, the distributions of spiderling weights for each litter were examined (Figures 5.8 and 5.9), in order to identify and eliminate any individuals which may have eaten (and therefore were significantly heavier than their siblings), and to establish similarities and differences between the litters. Using t-tests (Sokal & Rohlf 1969, p.224), the following individuals were found to be significantly heavier than their siblings, with p < 0.001: MK76.061 (t(df = 98) = 5.928), MK79.057 (t(df = 107) = 5.225), MK79.094 (t(df = 107) = 3.410), MK78.015 (t(df = 55) = 4.049) and MK78.029 (t(df = 55) = 4.740) (Figures 5.8 and 5.9).

One-way ANOVA (Nie <u>et al</u>. 1970) revealed that there were significant differences between the initial weights of the litters (F = 29.858, p < 0.001), with the weights of offspring using a Student-Newman-Keul test: MK79 < (MK69 = MK36) < (MK71 = MK78 = MK34).

5.2.5 Mortality

During the experiments, the majority of the spider deaths (80%) occurred before the completion of instar III (Table 5.1). While survival

100.

Figure 5.8.

Weights of <u>Selenocosmia stirlingi</u> from Coombah at the commencement of the laboratory experiments (instar III). The arrow indicates an individual whose weight was significantly greater than its siblings.

(a) Offspring of MK36;
 X = 19.6 mg, SE = 1.074 mg, n = 80.

(b) Offspring of MK 34; X = 21.5 mg, SE = 0.319 mg, n = 80.

(c) Offspring of MK69; $\overline{X} = 19.2 \text{ mg}$, SE = 0.535 mg, n = 120.

(d) Offspring of MK71; X = 20.9 mg, SE = 0.296 mg, n = 99.

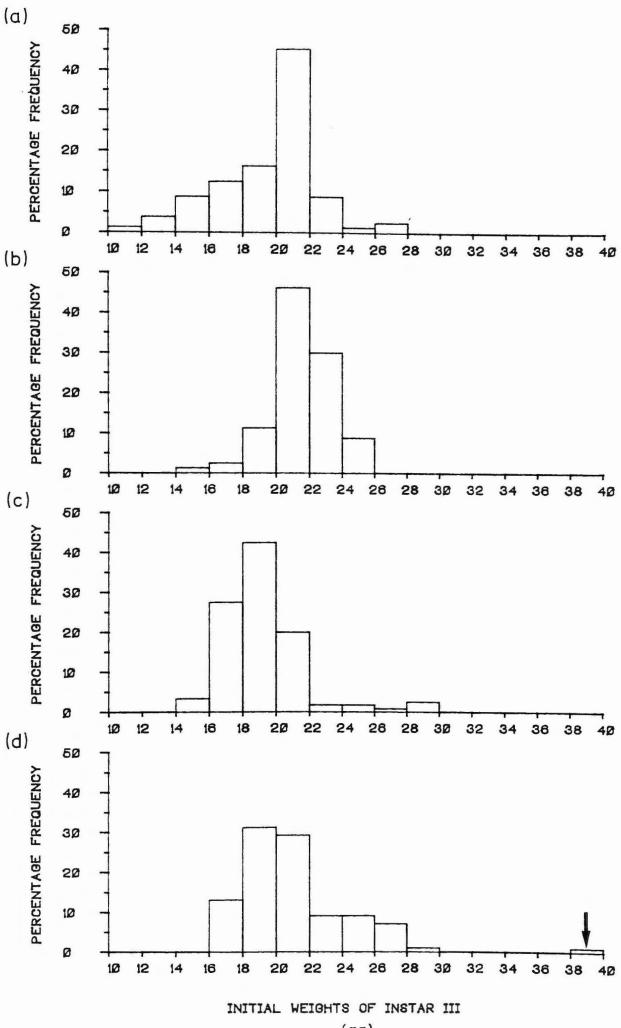
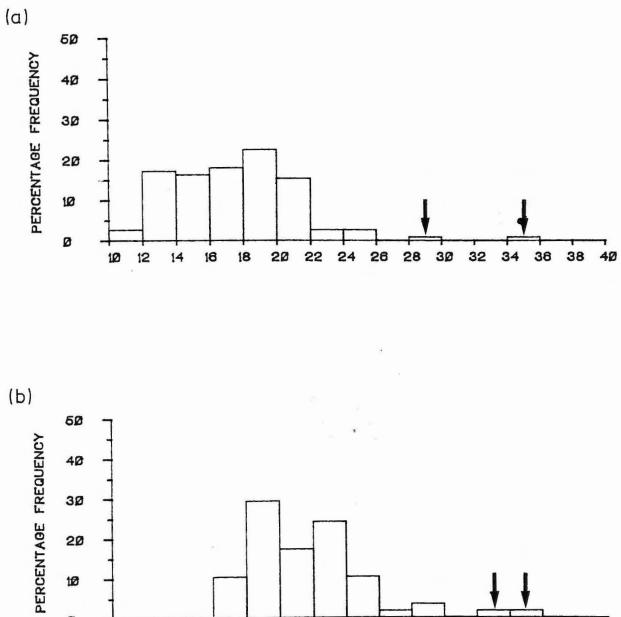


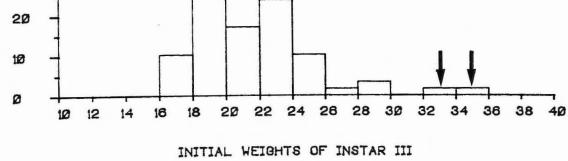


Figure 5.9.

Weights of <u>Selenocosmia</u> sp. from Cairns at the commencement of the laborarory experiments (instar III). The arrows indicate the individuals whose weights were significantly greater than their siblings.

(a) Offspring of MK79; $\bar{X} = 17.3 \text{ mg}$, SE = 0.322 mg, n = 110.





(mg)

<u>Table 5.1</u>.

Mortalities of the different spider litters during the laboratory experiments.

		Deaths in Instar			
Litter	Total Number	III	IV	V	Total
мк36	80	0	3	2	5
МК34	80	1	1	1	3
мк69	120	9	0	0	9
MK71	100	5	0	0	5
MK79	110	37	3	2	42
MK78	58	20	0	0	20
Totals	548	72	7	5	84

was generally high in the litters from Coombah (94%), those from Cairns experienced very high mortalities, accounting for 69% of all deaths.

5.2.6 Food Supply

For each litter of spiders used in the experiments, the rates at which food was supplied (mg per day live weight) were compared, both among the designated feeding levels and among the temperature conditions using two-way ANOVA (Nie <u>et al</u>. 1970). Significant differences existed between the two designated feeding levels ("H" and "L") for the offspring of MK36 (F = 643.98, p < 0.001), MK34 (F = 1090.84, p < 0.001), MK69 (F = 1159.15, p < 0.001), MK71 (F = 4154.85, p < 0.001) and MK78 (F = 3880.41, p <0.001) (Table 4.1); and for the offspring of MK79 (F = 618.95, p < 0.001) and with a Student-Newman-Keul test (SNK) (Zar 1974, p.151): "X" > "H" > "L" > "M" (Table 4.1 and 5.2).

The designated feeding levels were not significantly different under different temperature conditions for the offspring of MK69 (F = 0.105, p > 0.05), MK71 (F = 1.407, p > 0.05), MK79 (F = 1.582, p > 0.05) and MK78 (F = 0.016, p > 0.05). Nor was there significant interaction between the designated feeding levels and temperature and the rate at which food was supplied to the litters. However, the rate of food supply within each designated feeding level differed significantly among the temperatures for the offspring of MK36 (F = 233.73, p < 0.001) and MK34 (F= 317.17, p < 0.001) and there was significant interaction between these two factors (F_{36} = 14.03, p < 0.001 and F_{34} = 51.07, p < 0.01).

Among the litters, two-way ANOVA (Nie <u>et al</u>. 1970) revealed that the designated levels were significantly different (F = 45.85, p < 0.001) with the rates of food supply from an SNK test as follows: (MK34 = MK36)> (MK79 = MK78 = MK71 = MK69). The relevant mean feeding rates are summarised in Table 5.2.

Table 5.2.

The significantly different groups of rates of food supply (mg/day) achieved in the laboratory experiments.

Group	Litter and	Feeding Levels*					
	(Temperature (degrees C))	"X"	"H"	"L"	"M"		
1	MK34(30)		2.899	1.637	-		
	" (25)	-	4.089	2.142	-		
	мк36(30)	-	2.755	1.572	-		
	" (25)	-	3.785	2.197	-		
2	мк69	-	2.755	1.406	-		
	MK71	-	2.680	1.369	-		
	МК79	3.127	2.853	1.503	1.080		
	мк78	-	2.996	1.546	-		

* (See Section 4.7.1.1)

5.3 EXPERIMENTAL COMPARISONS WITH INSTARS III TO V.

Using combinations of the conditions summarised in Table 4.1, a series of comparisons was made to test the influences of various factors on growth and development, primarily over instars III to IV. The variables used in some or all of the initial comparisons (Sections 5.3.1 to 5.3.12) were as follows: the rate of size increase (i.e. the increase in mean straight fang length (Figure 4.2b)) per day and the rate of weight gain per day during the completion of instars III to V; the time taken from the commencement of the experiments (in instar III) to the completion of instar V; the overall size increase achieved (as the increase in mean straight fang length (Figure 4.2b)) and the overall weight gained over the same period. Where two-way ANOVA was used, unless otherwise stated, there was no significant interaction between the independent variables.

5.3.1 Comparison 1

The effects of two feeding levels ("H" and "L") on the offspring of MK36 at 30 degrees C (condition 1, Table 4.1) were analysed using one-way ANOVA (Nie <u>et al.</u> 1970). The rate of size increase was significantly greater at the higher feeding level ($\overline{X} = 6.303 \mu m/day$) than at the lower feeding level ($\overline{X} = 4.204 \mu m/day$) (Table 5.3). The time taken to complete instars III to V was significantly greater at the lower feeding level ($\overline{X} =$ 119 days) than it was at the higher feeding level ($\overline{X} = 93$ days) (Table 5.4). The increase in size was greater at the higher feeding level ($\overline{X} =$ 0.58 mm) than at the lower feeding level ($\overline{X} = 0.50$ mm) (Table 5.5).

5.3.2 Comparison 2

At 25 degrees C, the influences of the two feeding levels ("H" and "L") on the offspring of MK36 (condition 2, Table 5.3) were analysed using one-way ANOVA (Nie <u>et al</u>. 1970). The rate of size increase was

106.

Table 5.3.

F-values from comparisons (ANOVA) of the rates of size increase over instars III to V of spiderlings under various experimental conditions (*** = p < 0.001, ** = p < 0.001, * = p < 0.05, NS = p > 0.05).

Experimental		Feeding	Temperature	Photoperiod	Delay
Comparison	Condition(s)	Level			
1	1	88.834***		-	-
2	2	82.970***	-	-	-
3	3	158.755***	-	-	-
4	4	7.757**	-	-	-
5	5,6	379.385***	-	_	13.922***
6	6,7	158.057***	19.085***	-	-
7	8	536.318***	6.106**	-	-
8	10,11	49.479***	11.779***	-	-
9	11,12	13.978***	-	-	-
10	13	157.709***	-	0.565 NS	-
11	13,14	141.544***	19.898***	-	-

Table 5.4.

F-values from comparisons (ANOVA) of the time taken to complete instars III to V of spiderlings under various experimental conditions (*** = p < 0.001, ** = p < 0.001, * = p < 0.05, NS = p > 0.05).

Experimental		Feeding	Temperature	Photoperiod	Delay
Comparison	Condition(s)				
1	1	57.103***	_	-	-
2	2	69.476***	-	-	-
3	3	96.067***	-	-	-
4	4	7.251*	-	-	-
5	5,6	256.406***	-	-	2.126 NS
6	6,7	100.224***	8.748**	-	-
7	8	218.383***	5.868**	-	-
8	10,11	2.605 NS	15.385***	-	-
9	11,12	18.608***	-	-	-
10	13	26.580***	-	0.102 NS	-
11	13,14	10.839***	38.170**	-	-

Table 5.5.

F-values from comparisons (ANOVA) of the size increase from instar IV to V of spiderlings under various experimental conditions (*** = p < 0.001, ** = p < 0.01, * = p < 0.05,NS = p > 0.05).

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Experimental		Feeding	Temperature	Photoperiod	Delay
Comparison	Condition(s)	Level			
1	1	18.178***	-	_	_
2	2	0.008 NS	-	-	-
3	3	30.654***	-	-	-
4	4	2.005 NS	-	-	-
5	5,6	69.352***	-	-	17.668***
6	6,7	41.931***	8.499**	-	-
7	8	160.663***	0.449 NS	-	-
8	10,11	36.381***	2.453 NS	-	-
9	11,12	4.327*	-	-	-
10	13	36.557***	-	1.188 NS	-
11	13,14	18.413***	<0.001 NS	_	-

significantly greater at the higher feeding level ($\overline{X} = 3.398 \ \mu\text{m/day}$) than it was at the lower feeding level ($\overline{X} = 2.338 \ \mu\text{m/day}$) (Table 5.1). The time taken to complete instars III to V was significantly greater ($\overline{X} = 223$ days) at the lower feeding level than it was at the higher feeding level ($\overline{X} = 158 \ \text{days}$) (Table 5.4). There was no significant difference in the size increases at the two feeding levels, and the overall mean was 0.53 mm (Table 5.5).

5.3.3 Comparison 3

The influences of two feeding levels ("H" and "L") on the offspring of MK34 at 30 degrees C (condition 3, Table 4.1) were analysed using one-way ANOVA (Nie <u>et al</u>. 1970). The rate of size increase was significantly greater at the higher feeding level ($\overline{X} = 5.526 \mu m/day$) than at the lower feeding level ($\overline{X} = 3.645 \mu m/day$) (Table 5.3). The time taken to complete instars III to V was significantly greater at the lower feeding level ($\overline{X} = 100 days$) (Table 5.2). The increase in size was significantly greater ($\overline{X} = 0.58 mm$) at the higher feeding level than it was at the lower feeding level ($\overline{X} = 0.47 mm$) (Table 5.5).

5.3.4 Comparison 4

At 25 degrees C, the effects of two feeding levels ("H" and "L") on the offspring of MK34 (condition 4, Table 4.1) were analysed using one-way ANOVA (Nie <u>et al</u>. 1970). The rate of size increase was significantly greater at the higher feeding level ($\overline{X} = 2.699 \ \mu\text{m/day}$) than it was at the lower feeding level ($\overline{X} = 2.055 \ \mu\text{m/day}$) (Table 5.1). The time taken to complete instars III to V was significantly greater at the lower feeding level ($\overline{X} = 236 \ \text{days}$) than it was at the higher feeding level ($\overline{X} = 205$ days) (Table 5.2). There was no significant difference in the size increases at the two feeding levels, and the overall mean was 0.51 mm (Table 5.5).

5.3.5 Comparison 5

With the offspring of MK69 reared at 28 degrees C, the influences of a 6 month delay and two feeding levels ("H" and "L") (conditions 5 and 6, Table 4.1) were analysed using two-way ANOVA (Nie et al. 1970). The rate of size increase was significantly greater at the higher feeding level $(\overline{X}$ = 4.990 μ m/day) than at the lower feeding level (\overline{X} = 2.923 μ m/day) and significantly greater in the spiderlings not experiencing a delay (\overline{X} = 4.056 μ m/day) than in the delayed spiderlings ($\overline{X} = 3.561 \mu$ m/day) (Table 5.3). The rate of weight gain was significantly greater at the higher feeding level (\overline{X} = 1.323 mg/day) than at the lower feeding level (\overline{X} = 0.680 mg/day), but no significant difference was produced by the delay (\overline{X} = 1.002 mg/day) (Table 5.6). The time taken to complete instars III to V was significantly greater at the lower feeding level (\overline{X} = 163 days) than it was at the higher feeding level (\overline{X} = 112 days) and no significant difference was produced by the delay (\overline{X} = 137 days) (Table 5.4). The size increase achieved at the higher feeding level (\overline{X} = 0.55 mm) was significantly greater than those achieved at the lower feeding level (\overline{X} = 0.47 mm) and the size increase of the delayed spiderlings (\overline{X} = 0.47 mm) was significantly less than that achieved when grown without a delay (\overline{X} = 0.52 mm) (Table 5.5). The overall weight gained was significantly greater at the higher feeding level (\overline{X} = 147.9 mg) than it was at the lower feeding level (\overline{X} = 110.4 mg), but no significant difference was produced by the delay (\overline{X} = 129.1 mg) (Table 5.7).

Table 5.6.

F-values from comparisons (ANOVA) of the rates of weight gain over instars III to V of spiderlings under various experimental conditions (*** = p < 0.001, ** = p < 0.01, * = p < 0.05, NS = p > 0.05).

Experimental		Feeding	Temperature	Photoperiod	Delay
Comparison	Condition(s)	Level			
5	5,6	674.183***	_	-	3.096 NS
6	6,7	191.408***	19.155***	-	-
7	8	1840.312***	12.057***	-	-
8	10,11	171.337***	6.002**	-	-
9	11,12	45.172***	-	-	-
10	13	140.306***	-	2.008 NS	-
11	13,14	105.946***	7.117*	-	-

.

Table 5.7.

F-values from comparisons (ANOVA) of the weight gained over instars III to V of spiderlings under various experimental conditions (*** = p < 0.001, ** = p < 0.01, * = p < 0.05, NS = p > 0.05).

Experimental		Feeding	Temperature	Photoperiod	Delay
Comparison	Condition(s)	Level			
5	5,6	104.061***	-	-	0.560 NS
6	6,7	38.449***	5.239*	-	-
7	8	306.576***	0.424 NS	-	-
8	10,11	42.768***	5.619**	-	-
9	11,12	5.200**	-	-	-
10	13	23.714***	-	1.384 NS	-
11	13,14	20.644***	0.055 NS	-	-

114.

5.3.6 Comparison 6

The effects of two temperatures (28 degrees C and 30 degrees C) and two feeding levels ("H" and "L") (conditions 6 and 7, Table 4.1) on the offspring of MK69 were analysed using two-way ANOVA (Nie et al. 1970). The rate of size increase was significantly greater at the higher feeding level (\overline{X} = 4.350 µm/day) than it was at the lower feeding level (\overline{X} = 2.237 μ m/day) and it was significantly greater at 28 degrees C (\overline{X} = 3.561 μ m/day) than at 30 degrees C (\overline{X} = 2.711 μ m/day) (Table 5.3). The rate of weight gain was significantly greater at the higher feeding level (\overline{X} = 1.193 mg/day) than it was at the lower feeding level ($\overline{X} = 0.581 \text{ mg/day}$), and it was significantly greater at 28 degrees C ($\overline{X} = 0.958 \text{ mg/day}$) than at 30 degrees C ($\overline{X} = 0.731 \text{ mg/day}$) (Table 5.6). The time taken to complete instars III to V was significantly greater (\overline{X} = 177 days) at the lower feeding level than it was at the higher feeding level (\overline{X} = 119 days) and it was also significantly greater at 30 degrees C ($\overline{X} = 162$ days) than at 28 degrees C (\overline{X} = 142 days) (Table 5.4). The size increase achieved was significantly greater at the higher feeding level ($\overline{X} = 0.51$ mm) than at the lower feeding level ($\overline{X} = 0.40$ mm) and was significantly greater at 28 degrees C (\overline{X} = 0.47 mm) than at 30 degrees C (\overline{X} = 0.42 mm) (Table 5.5). The overall weight gained was significantly greater at the higher feeding level (\overline{X} = 140.3 mg) than at the lower feeding level (\overline{X} = 102.3 mg) and the weight gain was significantly greater at 28 degrees C (\overline{X} = 126.4 mg) than it was at 30 degrees C (\overline{X} = 110.3 mg) (Table 5.7).

5.3.7 Comparison 7

With the offspring of MK71, the influences of three temperatures (30, 32 and 35 degrees C) and two feeding levels ("H" and "L") (condition 8, Table 4.1) were analysed using two-way ANOVA (Nie <u>et al</u>. 1970). The rate of size increase was significantly greater at the higher feeding level (\overline{X} = 4.787 µm/day) than it was at the lower feeding level (\overline{X} = 2.586 µm/day), and temperature also had a significant effect (Table 5.3). Using a Student-Newman-Keul test (SNK) (Zar 1974, p.151), there was no significant difference between the rates of size increase at 32 degrees C and 30 degrees C (\overline{X} = 3.770 µm/day), but they were significantly different to 35 degrees C (\overline{X} = 3.573 µm/day). The rate of weight gain was significantly greater at the higher feeding level ($\overline{X} = 1.241 \text{ mg/day}$) than at the lower feeding level ($\overline{X} = 0.548 \text{ mg/day}$) and was significantly affected by temperature (Table 5.6). Using an SNK test, there was no significant difference between the rates of weight gain at 32 degrees C and 30 degrees C (\overline{X} = 0.927 mg/day), but they were significantly different to 35 degrees C ($\overline{X} = 0.844 \text{ mg/day}$). The time taken to complete instars III to V was significantly greater at the lower feeding level (\overline{X} = 154 days) than at the higher feeding level (\overline{X} = 110 days) (Table 5.4). While the ANOVA indicated that the time taken was significantly influenced by temperature, the SNK test did not reveal any trend in the following means: from 30 degrees C (\overline{X} = 134 days), 32 degrees C (\overline{X} = 126 days) and 35 degrees C (\overline{X} = 137 days), yielding an overall mean of 132 days. Due to an uncorrectable association between the means and variances in these comparisons, the actual probability of a Type-I error was somewhat lower than the nominal 5%, see Section 4.7.3 (Glass et al. 1972). The size increase over the three instars was significantly greater at the higher feeding level (\overline{X} = 0.52 mm) than at the lower feeding level (\overline{X} = 0.40 mm) but there was no significant effect produced by temperature ($\overline{X} = 0.44$ nm) (Table 5.5). The weight gained was significantly greater at the higher feeding level (\overline{X} = 135.8 mg) than it was at the lower feeding level (\overline{X} = 84.5 mg), but temperature had no significant effect (\overline{X} = 110 mg) (Table 5.7).

5.3.8 Comparison 8

Using two-way ANOVA (Nie et al. 1970) and the offspring of MK79, the influences of three temperatures (28, 31 and 33 degrees C) and two feeding levels ("H" and "L") (conditions 10 and 11, Table 4.1) were analysed. The rate of size increase was significantly greater at the higher feeding level (\overline{X} = 3.773 µm/day) than it was at the lower feeding level (\overline{X} = 2.510 µm/day) and it was significantly affected by temperature (Table 5.3). A Student-Newman-Keul test (SNK) (Zar 1974, p.151) revealed no significant differences between 28 degrees C (\overline{X} = 2.608 µm/day), 31 degrees C (\overline{X} = 3.572 µm/day) and 33 degrees C (\overline{X} = 3.406 µm/day) which had an overall mean of 3.281 µm/day. The rate of weight gain was significantly greater at the higher feeding rate ($\overline{X} = 1.099 \text{ mg/day}$) than at the lower feeding rate ($\overline{X} = 0.552 \text{ mg/day}$) and temperature had a significant effect (Table 5.6). An SNK test revealed no significant difference between 28 degrees C $(\overline{X} = 0.841 \text{ mg/day})$, 31 degrees C $(\overline{X} = 0.942 \text{ mg/day})$ and 33 degrees C $(\overline{X} = 0.942 \text{ mg/day})$ 0.855 mg/day) which had an overall mean of 0.886 mg/day. The time taken to complete instars III to V was not significantly affected by the feeding level (\overline{X} = 127 days), but it was significantly affected by temperature (Table 4.4). An SNK test revealed that the time taken was significantly greater at 28 degrees C (\overline{X} = 164 days) than at 31 degrees C and 33 degrees C (\overline{X} = 115 days). The increase in size was significantly greater at the higher feeding level (\overline{X} = 0.45 mm) than at the lower feeding level (\overline{X} = 0.31 mm), but temperature had no significant effect (\overline{x} = 0.39 mm) (Table 5.5). Weight increases over the three instars were significantly greater at the higher feeding level (\overline{X} = 135.7 mg) than at the lower feeding level $(\overline{X} = 73.5 \text{ mg})$ (Table 5.7). Although the ANOVA revealed a significant effect of temperature on weight gain, an SNK test revealed no significant difference between the means at 28 degrees C (\overline{X} = 139.0 mg), 31 degrees C $(\overline{X} = 112.1 \text{ mg})$ and 33 degrees C $(\overline{X} = 93.2 \text{ mg})$, with an overall mean of 111.4 mg.

5.3.9 Comparison 9

At 31 degrees C, the effects of four feeding levels ("H", "L", "X" and "M") (conditions 11 and 12, Table 4.1) were analysed using one-way ANOVA (Nie et al. 1970). The rate of size increase was significantly affected by the feeding level (Table 5.3). A Student-Newman-Keul test (SNK) (Zar 1974, p.151) revealed that there was no significant difference between the two higher feeding levels ("X" and "H"), but they produced significantly greater rates of size increase ($\overline{X} = 4.196 \, \mu m/day$) than at the lower two feeding levels (\bar{X} = 2.376 µm/day), between which there was also no significant difference. The feeding level had a significant effect on the rate of weight gain (Table 5.6). Using an SNK test (Zar 1974, p.151), there was no significant difference within the two higher feeding levels or within the two lower feeding levels, but the higher levels produced significantly greater rates of weight gain ($\overline{X} = 1.185 \text{ mg/day}$) than the lower levels (\overline{X} = 0.556 mg/day). The time taken to complete instars III to V was significantly affected by the feeding level (Table 5.4). An SNK test revealed that the time taken at the lowest feeding level ("M") was significantly greater (\overline{X} = 248 days) than the other three levels ("H" = "L" = "X") (\overline{X} = 120 days). The ANOVA indicated that the feeding levels had a significant influence on the size increase (Table 5.5), but an SNK test found no significant differences between the means at the "X" (\overline{X} = 0.45 mm), "H" (\overline{X} = 0.46 mm), "L" (\overline{X} = 0.34 mm) and "M" (\overline{X} = 0.40 mm) feeding levels with an overall mean of 0.41 mm. Similarly, by ANOVA, the feeding levels also had a significant effect on the weight gained over the three instars (Table 5.7). An SNK test revealed no significant differences between the means at the "X" (\overline{X} = 129.7 mg), "H" (\overline{X} = 135.6 mg), "L" (\overline{X} = 81.4 mg) and "M" (\overline{X} = 103.2 mg) feeding levels with an overall mean of 113.5 mg.

5.3.10 Comparison 10

Using two-way ANOVA (Nie et al. 1970), the influence of mid-summer and mid-winter photoperiods ("S" and "W") and two feeding levels ("H" and "L") (condition 13, Table 4.1) were analysed. The rates of size increase were significantly greater at the higher feeding level ($\overline{X} = 3.898 \ \mu m/day$) than they were at the lower feeding level ($\overline{X} = 1.775 \ \mu m/day$), but no significant difference occurred between the two photoperiod conditions (\overline{X} = 2.918 µm/day) (Table 5.3). The rate of weight gain was significantly greater at the higher feeding level ($\overline{X} = 1.269 \text{ mg/day}$) than at the lower feeding level ($\overline{X} = 0.537 \text{ mg/day}$), but photoperiod had no significant effect ($\overline{X} = 0.931 \text{ mg/day}$) (Table 5.6). The time taken to complete instars III to V was significantly greater at the lower feeding level (\overline{X} = 202 days) than it was at the higher feeding level (\overline{X} = 144 days), but no significant effect was produced by the different photoperiods ($\overline{X} = 171$ days) (Table 5.4). The size increase was significantly greater at the higher feeding level (\overline{X} = 0.56 mm) than at the lower feeding level (\overline{X} =0.36 mm), but photoperiod had no significant effect (\overline{X} = 0.47 mm) (Table 5.5). Due to the uncorrectable association between the means and variances in these comparisons, the actual probability of a type-I error was somewhat lower than the nominal 5%, see Section 3.2.1 (Glass et al. 1972). The weight gained over the three instars was significantly greater at the higher feeding level (\overline{X} = 183.0 mg) than at the lower feeding level $(\overline{X} = 110.6 \text{ mg})$, but photoperiod had no significant effect $(\overline{X} = 149.6 \text{ mg})$ (Table 5.7).

5.3.11 Comparison 11

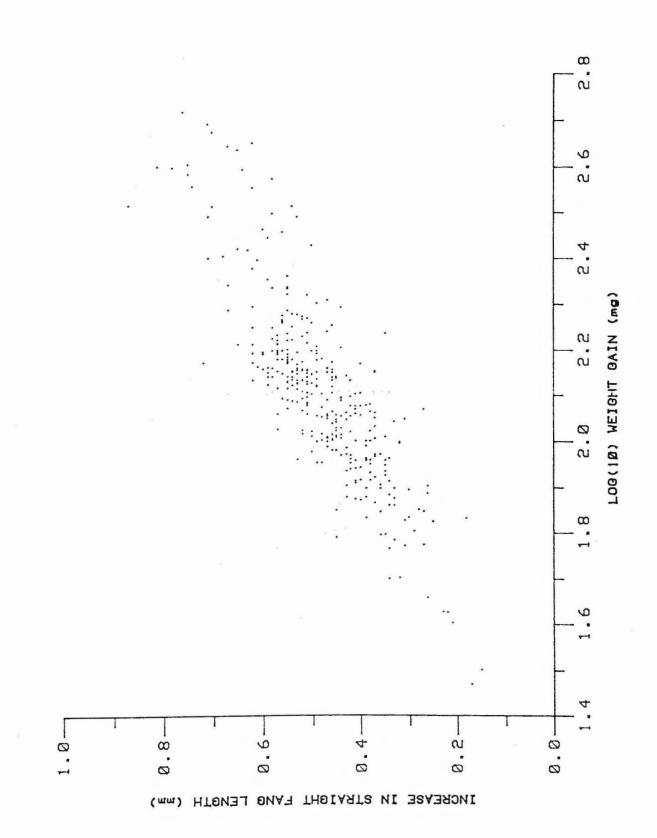
The effects of two temperatures (25 degrees C and 31 degrees C) and two feeding levels ("H" and "L") (conditions 12, 13 and 14, Table 4.1) were analysed using two-way ANOVA (Nie <u>et al</u>. 1970). The rate of size increase was significantly greater at the higher feeding level ($\overline{X} = 3.463$ µm/day) than it was at the lower feeding level ($\overline{X} = 1.877$ µm/day) and it was significantly higher at 31 degrees C (\overline{X} = 2.918 µm/day) than at 25 degrees C (\overline{X} = 2.344 µm/day) (Table 5.3). The rate of weight gain was significantly greater at the higher feeding level ($\vec{x} = 1.154 \text{ mg/day}$) than at the lower feeding level ($\overline{X} = 0.569 \text{ mg/day}$) and it was significantly higher at 31 degrees C (\overline{X} = 0.931 mg/day) than at 25 degrees C (\overline{X} = 0.797 mg/day) (Table 5.6). Significant interaction occurred between feeding level and temperature in terms of the rate of size increase (F = 36.803 p < 0.001) and the rate of weight gain (F = 15.736, p < 0.001). The time taken to complete instars III to V was significantly greater at the lower feeding level (\overline{X} = 207 days) than it was at the higher feeding level (\overline{X} = 156 days) and it was significantly greater at 25 degrees C (\overline{X} = 198 days) than at 31 degrees C (\overline{X} = 171 days) (Table 5.4). The size increase was significantly greater at the higher feeding level (\overline{X} = 0.53 mm) than at the lower feeding level ($\overline{X} = 0.39$ mm), but temperature had no significant effect (\overline{X} = 0.47 mm) (Table 5.5). In spite of this, there was a significant interaction between feeding level and temperature in terms of the size increase achieved. An uncorrectable association between the means and variances in these comparisons resulted in the actual probability of a Type-I error was less than 5%, see Section 4.7.3 (Glass et al. 1972). The weight gained over the three instars was significantly greater at the higher feeding level (\overline{X} = 177.0 mg) than at the lower feeding level (\overline{X} = 119.5 mg), but temperature had no significant effect (\overline{X} = 151.5 mg) (Table 5.7)

5.3.12 Comparison 12

In order to inspect the relationship between the size increase (SI) and the weight gain (WTGN) achieved over instars III to V, a scatterplot of all the spiderlings (except the offspring of MK36 and MK34) was produced (Figure 5.10). The relationship was linearised by transforming

Figure 5.10.

Relationship between size increase and weight gain over three instars, III to V or VI to VIII, for <u>Selenocosmia</u> spp. (excluding the offspring of MK36 and MK34). y = -0.739 + 0.486 x $r^2 = 0.496$, SE = 0.086 mm, df = 201.



the weight gain to logarithms, and a simple regression yielded the following equation (Figure 5.10):

$$SI = -0.739 + 0.486 \log(WT)$$

 $r^2 = 0.496$, $SE = 0.0863 mm$, $df = 201$

Significant improvement in the relationship resulted from the introduction of the rate of food supply (RFS) and temperature (T):

SI = -0.487 + 0.107 RFS + $0.256 \log(WTGN) + 0.0070$ T multiple r² = 0.664, SE = 0.070 mm, df = 201

5.3.13 Comparison 13

The spiderlings from most of the litters were combined and stepwise multiple regression (Nie <u>et al</u>. 1970) was used to calculate the relationships of both the rate of size increase (RSI) and the rate of weight gain (RWTGN) and with the rate of food supply (RFS) and temperature (T). Those spiderlings for which the food was not weighed and the delayed offspring of MK69 were excluded from the analysis. Also, those spiderlings whose growth was not affected by the feeding levels (comparisons 2 and 4), or at temperatures above 32 degrees C were excluded, to exclude nonlinear parts of the relationships. The relationships were as follows:

RSI (mm/day) = -0.00340 + 0.00299 RFS + 0.000147 T multiple r² = 0.666, SE = $0.00084\frac{1}{2}$, df = 284

RWTGN (mg/day) = 3.110 + 1.714 RFS - 0.084 T multiple r² = 0.784, SE = 0.32/, df = 216 Reducing these rates to their component variables, stepwise multiple linear regression on the time taken to complete instar III to V (DUR), the weight gain (WTGN) and the size increase (SI) produced the following equations:

DUR = 514.081 - 10.431 T - 66.155 RFS multiple r² = 0.602, SE = 31.680 days, df = 284WTGN = 1913.378 - 56.350 T + 90.040 RFS

multiple $r^2 = 0.567$, SE = 126.539 mg, df = 284

SI = 0.415 + 0.213 RFS - 0.005 T multiple r^2 = 0.569, SE = 0.066 mm, df = 216

In order to predict the average rate of food supply from known values of the rates of size increase or weight gain and temperature, stepwise multiple regression was used to provide the following equations:

RFS (mg/day) = 0.775 + 202.181 RSI - 0.022 T multiple $r^2 = 0.617$, SE = 0.219 mg/day, df = 284

RFS (mg/day) = -1.305 + 0.455 RWG + 0.042 T multiple $r^2 = 0.781$, SE = 0.221 mg/day, df = 216

5.4 EXPERIMENTAL COMPARISONS WITH INSTARS VI TO VIII

Instar VI spiderlings from condition 8 (Table 4.1) at 32 degrees C were reared through a further three instars (condition 9, Table 4.1) to instar VIII, to test the effects of a change in feeding level on growth and development. Equal numbers of individuals were randomly reassigned to feeding levels to create four groups, whose feeding levels in instars III to V and then VI to VIII were as follows: high then high ("HH"), high then low ("HL"), low then high ("LH") and low then low ("LL"). Analysis of the initial sizes and weights of the spiderlings in these new groups using one-way ANOVA (Nie <u>et al.</u> 1970) and a Student-Newman-Keul test (SNK) (Zar 1974, p.151) revealed the following pattern. The spiderlings from the higher feeding level during instars III to V ("HH" and "HL") were significantly larger (mean straight fang length (SFL) (Figure 4.2b), $\overline{X} =$ 1.92 mm) than those from the lower feeding level ("LH" and "LL") ($\overline{X} = 1.72$ mm) (F = 16.919, p < 0.001) and spiderlings in "HH" and "HL" were significantly heavier ($\overline{X} = 142.2$ mg) than those in "LH" and "LL" ($\overline{X} = 99.6$ mg) (F = 20.773, p < 0.001).

Over instars VI to VIII, the following patterns of growth and development (as outlined in Section 4.3) were revealed, using One-way ANOVA (Nie et al. 1970). Significant differences were found in the rates of size increase (F = 34.966, p < 0.001) and an SNK test revealed that each group was significantly different to the others: "HL" (\overline{X} = 2.454 μ m/day) < "LL" (\overline{X} = 3.003 μ m/day) < "HH" (\overline{X} = 3.966 μ m/day) < "LH" (\overline{X} = 4.956 µm/day). The rates of weight gain were also significantly different (F = 149.905, p < 0.001). An SNK test revealed that while there was no significant difference within each of the later feeding levels, the rate of weight gain was significantly higher in "HH" and "LH" (\overline{X} = 2.551 mg/day) than in "HL" and "LL" (\overline{X} = 1.145 mg/day). A significant difference was found in the time taken to complete instars VI to VIII (F = 0.001) and an SNK test revealed that: "LH" (\overline{x} = 142 days) < 21.661, p "HH" = "LL" (\overline{X} = 193 days) < "HL" (\overline{X} = 250 days). There was no significant difference in the size increases between the groups (F = 2.362), and from an SNK test: "LL" (\overline{X} = 0.61 mm) = "HL" (\overline{X} = 0.61 mm) = "HH" $(\bar{X} = 0.67 \text{ mm}) =$ "LH" $(\bar{X} = 0.69 \text{ mm})$

with an overall mean of 0.65 mm. A significant difference was found in the weight gained (F = 36.006, p < 0.001), with an SNK test indicating that: "LL" = "HL" (\overline{X} = 257.0 mg) < "LH" (\overline{X} = 355.1 mg) < "HH" (\overline{X} = 445.1 mg).

The overall outcome of these patterns of growth and development were revealed in the final sizes and weights of instar VIII. There was a significant difference in the final sizes (F = 11.412, p < 0.001) with an SNK test showing that "LL" = "LH" (\overline{X} = 2.38 mm) < "HL" = "HH" (\overline{X} = 2.57 mm). The final weights were significantly different (F = 37.239, p < 0.001), with an SNK test revealing that "LL" (\overline{X} = 326.3 mg) < "HL" = "LH" (\overline{X} = 421.7 mg) < "HH" (\overline{X} = 577.8 mg).

5.5 SEXUAL DIFFERENTIATION AND MATURATION

The relationship between the lengths of the cuticular buds on the internal surface of the epigastric furrow (Figure 4.2c and Section 2.7) and the size of the spiderling (mean straight fang length (SFL), Figure 4.2b) were inspected in the offspring of MK71 (Figure 5.11a). Individuals on which the cuticular buds were less than, or equal to 0.05 mm, regardless of spider size, were classified as juvenile males. Data from the spiderlings with cuticular buds longer than 0.05 mm (classified as juvenile females) were combined with data from four sexually mature females from Coombah. Following logarithmic transformations of both variables, the relationship between the lengths of spermathecae or cuticular buds and spider size was strongly linear ($r^2 = 0.950$) (Figure 5.11b). The size range of spiderlings with cuticular buds 0.06 mm long, which were deemed to be females in the earliest detectable stage of differentiation, was 1.35 mm to 1.60 mm SFL.

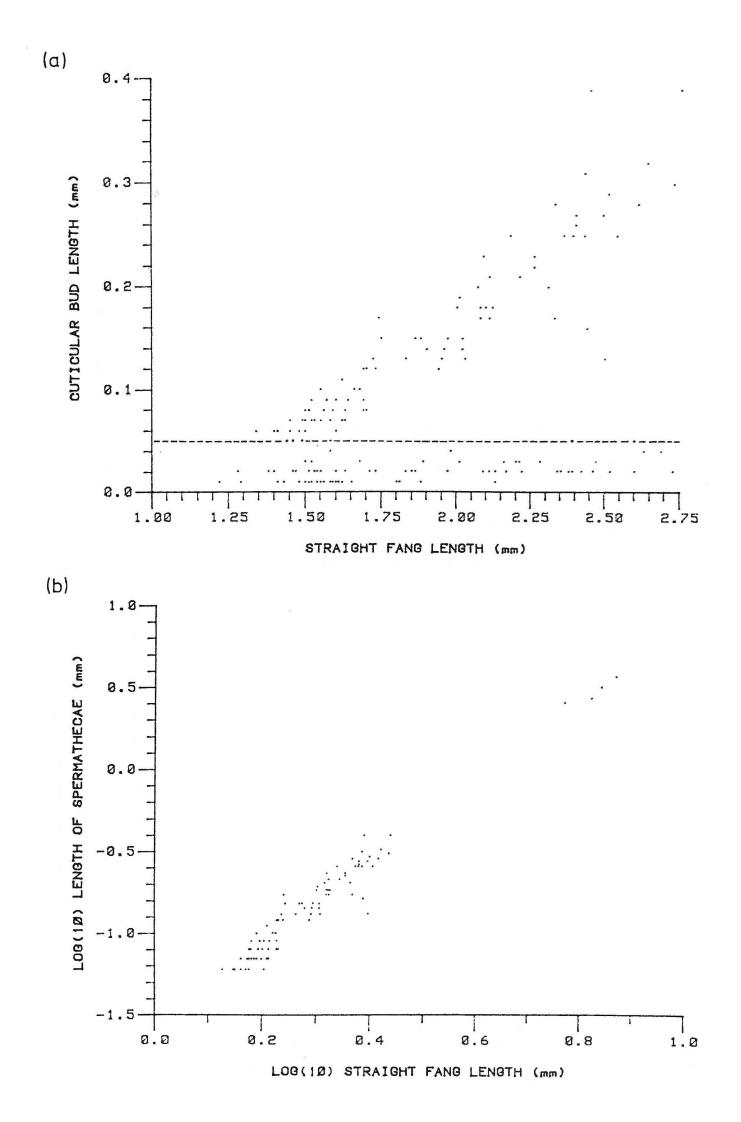
Offspring of MK69 reared in conditions 5 and 6 (Table 4.1) were used to assess the impact of feeding rate on the sex ratio. A Chi-square test (Zar 1974, p.41) was used to test the significance of differences between

Figure 5.11.

Relationships between the cuticular buds (or spermathecae) at the epigastric furrow and spider size, in <u>Selenocosmia stirlingi</u>.

(a) Offspring of MK71 (instars V to VIII); thebroken line marks a cuticular bud length of0.05 mm.

(b) Offspring of MK71 (instars V to VIII) with cuticular buds longer than 0.05 mm and four mature adult females from Coombah (New South Wales); y = -1.568 + 2.494 x $r^2 = 0.975$, SE = 0.058 mm, df = 97.



the observed frequencies of males and females and the expected 0.5. No significant difference was found at the higher feeding level ($\text{Chi}^2 = 0.00$, n = 26, 0.975 \text{Chi}^2 = 4.54, n = 22, 0.025 < p < 0.05). In the following instars, VI to VIII, there were no significant deviations from the expected frequencies of 0.5. The mean sizes of the instar V spiderlings (SFL) was 1.65 mm for those from the higher feeding level and 1.57 mm at the lower feeding level, which puts the latter group within the differentiation size range (see above).

From the offspring of MK69, the smallest and the largest juvenile males and females in instar X were used to determine the relationships between instar number and size (SFL) under constant conditions of temperature and food availability. The relationships were linearised by logarithmic transformations of size (Figure 5.12), and the size ranges of mature males and female (from Section 2.9) were included for comparisons. At the higher feeding level, females were predicted to become sexually mature by instar XII and males between instars X to XII, while at the lower feeding level, females were predicted to mature by instar XIII and males in instars XII to XV.

5.6 FIELD EXPERIMENTS

5.6.1 Experiment 1

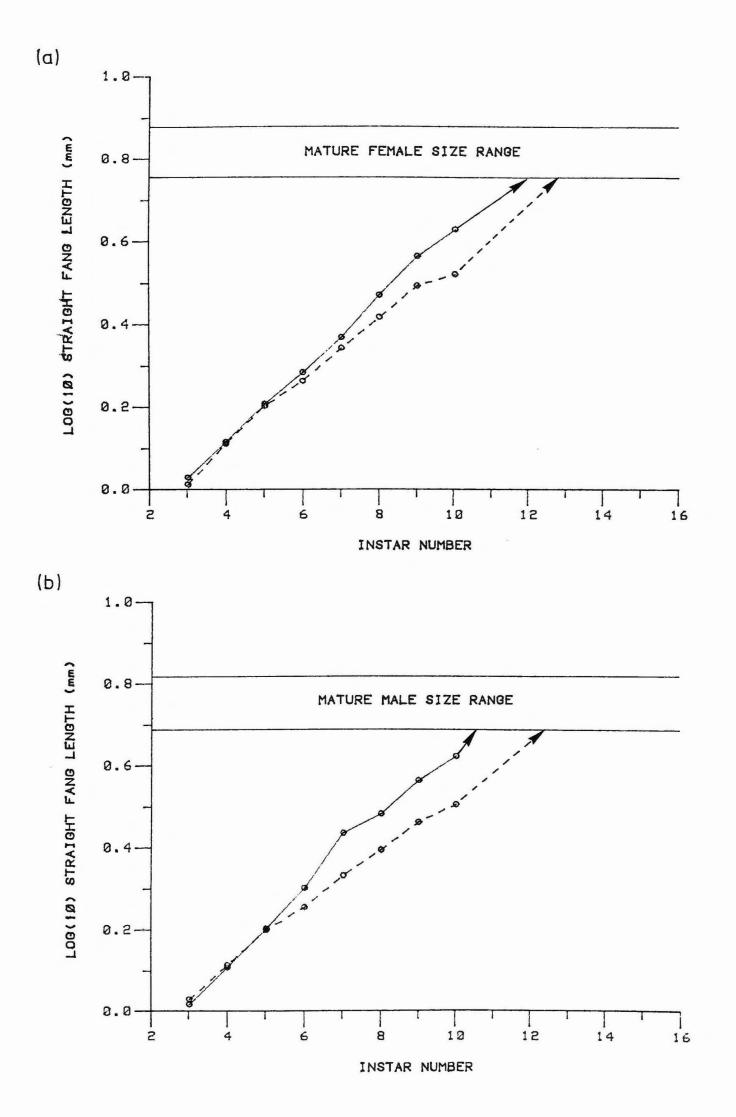
The initial release of juveniles in July 1982 was an unqualified failure; in spite of an increase in the activity of the field population shortly after the release, most of the artificial holes closed and only two of the spiderlings were seen 6 weeks later. None were seen again on following trips.

Figure 5.12.

Relationship between size, instar number and projected maturation of <u>Selenocosmia stirlingi</u> under different feeding conditions.

(a) Females: solid line, high feeding level; y = -0.2324 + 0.0874 x $r^2 = 0.999$. broken line, low feeding level; y = -0.1848 + 0.0741 x $r^2 = 0.990$.

(b) Males: solid line, high feeding level; y = -0.2379 + 0.0889 x $r^2 = 0.989$. broken line, low feeding level; y = -0.1559 + 0.0678 x $r^2 = 0.994$.



5.6.2 Experiment 2

The night following the second release attempt (June 1983), 100% of the spiderlings were observed in their artificial burrows. Six weeks later, 25% of the artificial burrows were blocked, and 14 of the spiderlings (87%) were recovered.

5.6.3 Experiment 3

Only 78% of the spiderlings released in the third experiment (October 1983) were seen the following night. Over subsequent trips, the proportion of these which were seen dropped from 11% to 3% and then 0%. At this stage (March 1984) the experiment was abandoned.

The matched group in the laboratory was only maintained long enough to assess the persistence of the individual markings (Figure 5.13a). Following one moult, the mark was still visible as a hairless patch (Figure 5.13b), but in subsequent instars, no evidence remained.

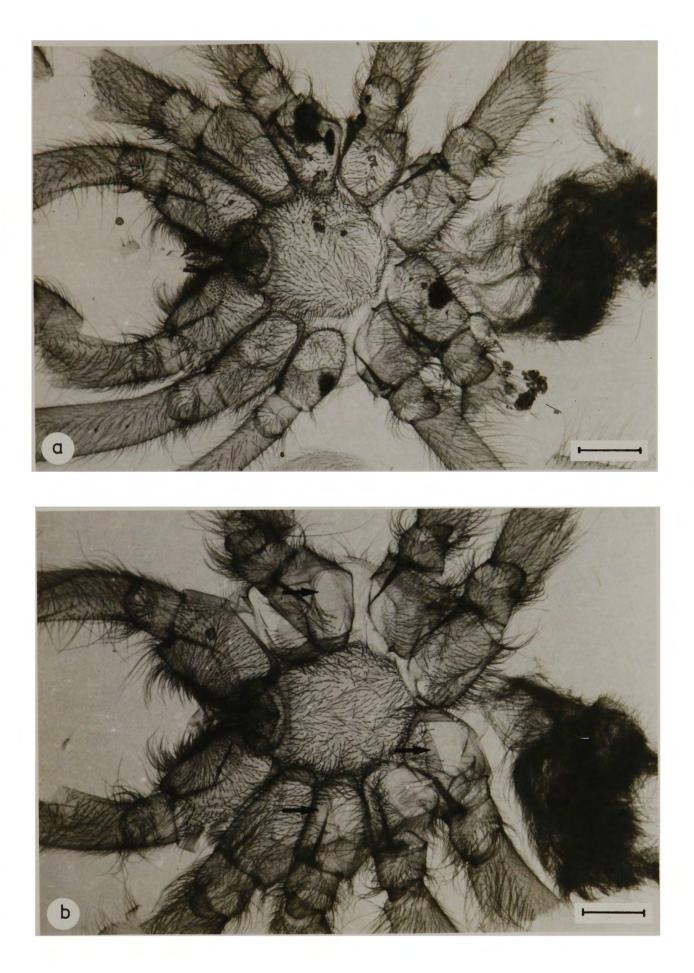
Figure 5.13.

Ventral surface of exuviae from branded juvenile <u>Selenocosmia</u> <u>stirlingi</u>.

(a) From the instar in which the brand was created.

(b) From the instar following that in which the brand was created (arrows indicate cuticle largely devoid of setae).

Scale bars: 1 mm.



CHAPTER SIX

DISCUSSION

6.1 INTRODUCTION

In this chapter, the results from the laboratory experiments are discussed and the findings related to the general biology and the field ecology of <u>S</u>. <u>stirlingi</u>. Only brief comments are included on the field experiments, as they yielded limited information.

6.2 BODY DIMENSIONS

6.2.1 Morphometrics

There were high correlations and strong linear relationships between the linear parameters used to estimate overall body size of the spiderlings, within the Coombah and Cairns populations. These observations were consistent with previous findings for other species (e.g. Stradling 1978, Vollrath 1983). Hence, any of the parameters could be used as an indicator of size without the confounding influence of allometry. In the event of missing values, each could be estimated from any of the others with a known degree of accuracy.

The highly significant, and consistent differences between the spiderlings from Coombah and Cairns confirmed that the populations were distinct, and suggested that either they simply represented samples drawn from populations at extreme ends of a cline, or that they belong to different species. While no attempt was made to resolve this taxonomic problem, or to assess the relative merits of different taxonomic procedures, a brief account of some of the relevant details of both is provided to identify some of the problems involved.

In Australia, eight species of theraphosids have been described from three genera: Selenocosmia crassipes (Koch) (1874), Selenocosmia strenua (Thorell) (1881), Selenocosmia stirlingi Hogg (1901), Selenocosmia vulpina Hogg (1901), Selenocosmia subvulpina Strand (1907), Selenocosmia stalkeri Hirst (1907), Selenotypus plumipes Pocock (1895), and Selenotholus foelschei Hogg (1902). On the basis of extant type material and original and subsequent descriptions, I could only identify, with any certainty, Selenocosmia stirlingi, Selencosmia crassipes, Selenotypus plumipes and possibly Selenocosmia subvulpina. Sexual dimorphism and individual variation in colour, hirsuteness and overall body condition, set against superficially conservative body forms and genitalia, have resulted in considerable confusion over both the identification of specimens and the value of previous descriptions. Vollrath (1983) has suggested that consistent significant differences in the relationships between body measurements, or the ratios of body parts (whose overall relationship passes through the origin), would be reliable taxonomic characters, as they are free from the confounding influence of size. Alternatively, Coyle (1985) found that variation in palpal characters was significantly less than variation of non-genital characters within field populations of Hypochilus. This implies that the factors causing variation had a diminished influence on the palps. In this case, adult male body proportions within the species would not be conservative if palpal characters were included. However, the degree of variation observed by Coyle (1985) may be relatively slight and therefore insignificant in relation to differences between species. There is no doubt that the Coombah and Cairns populations show distinctive relationships but as the regression lines of each pair of the various size parameters intersect, additional information would be necessary to assign specimens reliably to either group. The magnitude of the geographic

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separation of the two populations (ca. 2,000 km) together with suspected low dispersal rates and disjunct distributions suggest that such differences may be as easily attributed to variations within a species as to variation between species. Further study of inter- and intrapopulation variation would be necessary to resolve the taxonomic significance of the differences. As the doubt remains, the spiders from Cairns have been conservatively referred to as <u>Selenocosmia</u> sp.

6.2.2 Size-Weight Relationships

The soft extensible abdomen of spiders allows for considerable changes in weight in an instar, within which there is no significant change in the dimension of hardened cuticular parts such as the cephalothorax or the fangs (Miyashita 1968a). In these growth experiments, an indication of the weight range for a given size was revealed, under conditions of temperature, and of food and moisture availability which were probably far from the limits of tolerance. Both the initial weights and final weights could be estimated with considerable accuracy for a spider of known size. However, while size could be similarly estimated from a known final or initial weight, it would not give a precise indication of the instar, nor could any other weight from within an instar be used except perhaps as an indicator of overall condition for a known size (Anderson 1974).

Among the Coombah spiders (Figures 5.5a and 5.6a), the final weights are less strongly correlated with size $(r^2 = 0.962)$ than are the initial weights $(r^2 = 0.981)$. It seems likely that this has, in part, resulted from the method of estimation of final weight. The weight of the newly ecdysed spider was added to the weight of the exuvium to give a

conservative estimate of the final weight achieved in the previous instar (Section 4.4). Unquantified moisture loss during ecdysis (Stewart & Martin 1982) and evaporation from the exuvium may, in part, have caused the greater variation in final weights. Such effects were not observed in the Cairns population, probably due to a greater initial variation $(r^2 = 0.938)$ (Figures 5.5b and 5.6b).

The patterns of the differences in final weights for the offspring of MK36 and MK34 "estimated" by interpolation and "calculated" from final sizes, may be a function of weight fluctuations associated with ecdysis (see Section 5.2.3). Changes in weight directly associated with moulting have been examined in detail by Stewart and Martin (1982) in adults of the theraphosid Dugesiella hentzi. They observed the following changes in weight associated with drinking and moisture loss: a peak 25 to 41 days prior to ecdysis, a steady decline to ecdysis and a marked weight loss (10 to 15%) during ecdysis, which was recovered over the 10 days after ecdysis. In conditions 1 to 4, these non-linear changes in weight associated with ecdysis may have influenced the patterns of differences between the "estimated" and "calculated" final weights, as the time scale of these changes could be affected by factors such as temperature or food availability. At 25 degrees C, there was a tendency for "over-estimation" of weights. At 30 degrees C, the "estimated" weights were very close to the "calculated" weights at the higher feeding level, but at the lower feeding level, they appeared to be "underestimates". Although it is difficult to explain the patterns of these differences precisely, it would not be justified to use the interpolated ("estimated") final weights to analyse the effects of temperature and food availability, when these factors seem to affect the reliability of the "estimated" weights themselves.

6.2.3 Initial Weights

Examination of weight distribution of each litter at the commencement of the experiments revealed that, although they fell into three significantly different groups, the pattern was not associated with the provenance of the populations. In spite of the differences, there was also substantial overlap between all the litters, which enabled multivariate analyses to be performed on amalgamated samples (Sections 5.3.12 and 5.3.13).

The individuals identified as being significantly heavier than their siblings were believed to have eaten prior to the commencement of the experiment and were therefore excluded. Thus, the growth achieved during the experiments could be related to the conditions in which they were reared, without the need to accomodate significantly different individuals.

The delay in the commencement of the experiments involving the offspring of MK71 and some of MK69 provided an opportunity to attempt to hold those animals at an "ecological zero", that is, the temperature at which metabolic processes were depressed to the extent that feeding and development (moulting) ceased (Hagstrum 1970a). In this trial, the temperature was maintained at or below 20 degree C and food was not provided. Examination of the weights before and after the delay (191 days), revealed that there was a significant reduction of 1.6 mg (on average) or 0.0084 mg/day for 110 of 112 offspring of MK71 which survived the treatment. The mean weight of the offspring of MK71 was not significantly different from the mean weights obtained from the offspring of MK78 and MK34 which experienced no such delay. There was no significant weight change in the delayed offspring of MK69, although only 40 of 113 survived, the remainder dying less than 10 days prior to commencement of the experiments. Some of the survivors (9/40) also died shortly afterwards. It is possible that these spiders did not experience

significant weight loss and the conditions could be described as a true ecological "zero". It seems more likely that the high mortality (35%) was dependent on weight loss, thereby selectively truncating the population leaving only those which showed no significant weight loss alive, and the others dead before the second weighing.

Weight losses over this period would have resulted from basal metabolic processes and defaecation. Dehydration was unlikely to have been a significant factor due to the high humidities maintained in the jars (ca. 100% RH). No individuals moulted during the delay and none were consumed by their siblings, as was observed at higher temperatures in other litters. Although no attempt was made to feed these spiderlings, these results support the possibility that 20 degrees C approximates the ecological "zero" for these spiders. Low activities observed in the field at Coombah (see Section 3.4.2.2) suggest these spiders become more or less dormant when burrow temperature were below 20 degree C. Compared to values obtained for other species, Tarentula kochi (10 degrees C) (Hagstrum 1970a), Loxoceles sp. (15 degrees C), (Horner & Stewart 1967) and Chiracanthium inclusum (7 degrees C) (Peck & Whitcomb 1970), this value seems high. It may in part be due to the tropical origins of these spiders, where the temperature rarely drops below 20 degrees C (Stradling 1978).

6.3 Mortality

Apart from the mortality rate of the offspring of MK69 in the delay conditions, the survival of the Coombah spiders was generally high throughout the experiments and beyond. The high mortality of the Cairns spiders, generally prior to the first ecdysis, suggests that either these litters were "weaker" in some way, or that their transportation may have had deleterious effects which were not immediately apparent. It is also

possible that the medium on which they were reared (sterilised sand from Coombah), contained some component to which the Cairns spiders were particularly susceptible, or lacked a component important for their survival. Reductions in litter size due to substantial mortality, either before or after commencement of the experiments, may produce non-random sampling of the litters. In such cases the growth and development of the survivors may not reliably reflect the patterns of the underlying population.

6.4 Food Supply

Prey from a restricted size class were supplied at 7 and 14 days intervals to achieve the higher ("H") and lower ("L") feeding levels in the majority of the experiments. It might be expected that the ratio of the resultant rates of food supply (mg supplied/time) would be "H":"L" = 2.0. The actual ratios ranged from 1.23 to 1.96 (\overline{X} = 1.75) and can be explained in the following way. If two spiders from the different feeding levels completed the required amount of development in an even number of weeks, say in the fourth week, the ratio of food supplied (as a number of meals) would be "H":"L" = 4:2 = 2.0. However, if the development was completed in an odd week, say in the third week, the ratio would be "H":"L" = 3:2 = 1.5. Assuming that on average each of these outcomes was equally likely, the expected overall ratio would become "H":"L" = 1.75, which was the observed value.

To avoid this situation and provide food on a stricter factorial basis, it would have been possible to feed the spiderlings on identical time schedules with different numbers of prey items or different sized prey. The first strategy was used by Haynes and Sisojević (1966) to investigate the effect of prey density on the feeding rates of <u>Philodromus</u> <u>rufus</u>. They found that the effect of prey density was not a straightforward count of prey items, but included compounding influences of uncaptured prey on feeding patterns of the spiders and changes in the activity of the remaining prey (Hardman & Turnbull 1974). A further disadvantage of supplying multiple prey, when mealworms are used, is that they are inclined to consume not only each other, but also the spider when permitted to roam the container for extended periods (Deevey 1949). The use of different sized prey could have introduced additional, undesirable variables similar to those associated with the use of different prey species or different parts of prey items. Variations in calorific values, such as those noted by Breymeyer and Jóźwik (1975) for different prey species could also apply to Tenebrio larvae of different sizes. Haynes and Sisojević (1966) also observed preferential feeding on different body parts which may have been related to the net calorific or nutritional value of these parts. As the surface area: volume ratio decreases with increasing size, the proportion of indigestible cuticle in the body of such prey items may decrease, effectively enhancing the available food per unit body weight. The acceptability of different sized prey was shown to vary over a considerable size range for these spiders (Section 2.5). This prey selection may have had a small, but significant effect over narrower ranges, when growth and development were analysed. The strategy of food supply used in these experiments thus provided a direct mean estimate of the rate of food made available to the spiders during the experiment, in proportions which could be estimated with relative ease.

The rate of food supply could have been estimated from the number of prey items (Browning 1941, Deevey 1949, Miyashita 1968a,b, Peck & Whitcomb 1970, Tanaka & Itô 1982), and converted to a weight per day (dry or wet) using a standard conversion factor for the size classes used. In these experiments, the variations in mealworm size, and the noise in such conversion equations, would have yielded unreliable estimates of food

supply. By supplying food at standard meal rates, and weighing (except in condition 5) each prey item, an actual rate of supply was determined, rather than an estimate of that rate.

In conditions 1 to 4 (Table 4.1), the size class of mealworms provided as prey was somewhat loosely applied, resulting in unexpected differences in the rate of food supplied, to these spiderlings compared with those under other conditions. Confronted with the slow growth of the spiders at 25 degrees C, I may have inadvertantly supplied oversized mealworms in these conditions. This explanation would also account for the interactive effects of temperature and feeding level on the feeding rates of 25 degrees C. More rigid application of the mealworm size class limits prevented the recurrence of this problem in later experiments.

6.5 EXPERIMENTAL FINDINGS

6.5.1 Conceptual Framework of the Experiments

Questions as to how environmental factors affect growth and development can essentially be investigated in two ways. Field studies can attempt to quantify the factors within the system which are believed to be important, in conjunction with parameters of growth and development. While the advantage of such an approach is its inherent reality, there are problems associated the complexity of natural systems, including interactions between factors and the precision with which they can be quantified. Also, any attempt at such quantification (such as installing measuring apparatus or sampling the population), can alter the naturalness of the system and produce distorted results, in a manner analogous to Heisenberg's uncertainty principle in atomic physics (e.g. Beiser 1962). The reductionist approach offers an alternate or complementary method of investigation in which the system is broken into various components. Parts of the system may be varied and examined

systematically while the remainder is held constant. By their very nature, such experiments are unrealistic because of simplification of the system and the combinations of factors which can be devised. The ultimate goal of the reductionist approach can be to integrate the results, in order to reconstruct an overall picture of the total system as it appears in nature. Through an almost circular process, the final model could be tested under field conditions, in order to assess the degree to which it diverges from a natural reality. In this study both of these approaches were employed: field observations of the intact natural system, and laboratory and field experiments on some of its components.

Regardless of the approaches adopted, spider populations exist through time in natural systems which are essentially continuous. The lives of the spiders also have a type of continuity sustained by gene flow from generation to generation. In order to study such systems, it is necessary to decide precisely which parts of the continuum are to be investigated, and the degree of resolution required to address the questions which have been posed.

6.5.2 Conceptual Framework of the Analyses

The relationship or pattern of association between a pair of variables (i.e. the change in one which is accompanied by a change in the other) can take a variety of forms, and it may involve simple correlation, or dependence. In general, the relationship between two biologically significant variables is more or less curvilinear, but it often approximates a straight line over the range of ecological interest. As a result, linear models can be used to describe the relationship and hence, to compare two or more variables:

(1) By testing for significant differences in the dependent variable associated with different discrete values of the independent variables, for example, between two populations discriminated by discrete ranges of

the independent variable. Where the locations of the refective ranges of the independent variable are close, real differences in the dependent variable may be masked by "noise", which is seen as a large value of the variance. Where the ranges of the independent variable are widely separated, this "noise effect" may not prevent discrimination.

(2) The form of the relationship itself can be investigated by examining the changes in the dependent variable across the full range of the independent variables, with the greatest possible resolution.

In these experiments both approaches were employed. Analyses within the litters provide discrete tests for significant effects (e.g. feeding levels "H" and "L"), while analysis of pooled data was used to describe the overall relationships in more detail. The following discussion addresses these results.

6.5.3. Effects of Individual Factors

Investigation of individual factors involved the analysis of two to four discrete states of each factor, for which other conditions were held constant. Such analyses did not provide sufficient detail to describe the overall form of the relationship, but indicated the factors which had significant effects on growth and development.

6.5.3.1 The Delay

Specific analysis of the effects of the six months delay were made with the offspring of MK69. Unfortunately, there was also high mortality in this litter prior to the commencement of these experiments, so that two factors (i.e. delay and mortality), rather than the intended one (i.e. delay), were actually involved.

The delay (with its associated mortality) affected the rate of the size increase and the absolute size increase, significantly reducing both.

The responses to temperature (discussed in Section 6.5.3.3) were also inconsistent with the patterns observed in the other litters. The offspring of MK71 were also delayed, but experienced negligible mortality and had growth patterns which were consistent with the other litters. It therefore seems most likely that the anomalous patterns of growth and development displayed by the delayed offspring of MK69 were associated with the mortality rather than with the delay. The mortality resulted in sampling of the litter, non-random linked to survival. The anomalous growth patterns may have resulted from the selection of a group of spiderlings with different growth patterns or simply as a by-product of the sampling process. Similar sampling problems may have occurred in previous work where spiders with apparently abnormal or undesirable characteristics were eliminated from growth experiments or analyses. For example, Turnbull (1962) excluded from his experiments Linyphia triangularis which failed to construct a typical web within twenty-four hours of isolation. While there are sound practical reasons for examining limited samples of an entire population, it is necessary to place the resultant findings within these limitations. Owing to the anomolous growth patterns in the delayed offspring of MK69, they were not included in the multivariate analyses discussed in Section 6.5.4.

6.5.3.2 Food Supply

In all the comparisons involving two feeding levels, both the rate of size increase and rate of weight gain were significantly affected, with higher feeding levels enhancing both. Where four feeding levels were tested (comparison 9, Section 5.3.9), the rates were not significantly different at the two higher levels, but these differed significantly to the two lower levels. Miyashita (1968a) recorded lower rates of increase in carapace width in Lycosa tinsignata fed once every four days instead of

every day. This trend was extracted from his data, but as it was not specifically considered by Miyashita (1968a), no statistical analyses were provided to assess the significance of the trend. Turnbull (1962) revealed a linear increase in the rate of weight gain in <u>Linyphia</u> <u>triangularis</u> in relation to the rate at which food was consumed. As he had also shown that the rate of consumption was dependent on the rate of food supply (in a curvilinear relationship approaching an upper asymptote), the rate of weight gain was therefore also positively correlated with the rate of food supply.

In this study, the rates of size increase and weight gain were rendered into their components (of absolute increases in size and weight and the duration of the three instars), which revealed more detail about the nature of food supply effects. Without exception, the total weight gained over the three instars was greater at the higher of two feeding levels, supporting the obvious a priori comparison. Similarly, ANOVA revealed significant differences where four feeding levels were used, but the a posteriori test could not separate the means. This latter observation may have resulted from insufficient separation of the feeding levels or they may have bridged an optimum supply rate. In addition, the spiderlings in this comparison (9) (involving the offspring of MK79) experienced substantial mortality, with a 40% death rate. For the reasons described in the preceding section (6.3.3.1), mortality within the litter may well have masked the differences in the weight gained at the four feeding levels. Higher rates of feeding have been shown to increase the weight gained over nymphal instars in Latrodectus mactans (Deevey 1949), Agelenopsis potteri (Turnbull 1965) and Nephila clavipes (Wise 1975). Turnbull (1962) further resolved the food supply effect by showing that in Linyphia triangularis, the weight gain (mg wet weight) was related to the rate of food consumption (mg dry weight/day) in a similar manner as food consumption to

food supply, with an upper asymptote. Furthermore, as constant amounts of dry matter were consumed in each instar and there was a fixed number of instars, differences in final adult weights must have resulted from greater metabolic costs associated with lower rates of weight gain.

In general, significant increases in weight gain at the higher feeding levels were associated with significantly greater size increases, similar to those reported by Miyashita (1968a) and Vollrath (1983). At the four feeding levels in comparison 9, the size increase was affected, but the a posteriori test could not distinguish the means. Other notable exceptions to this association occurred in comparisons 2 and 4 (Sections 5.3.2 and 5.3.4), where there were no significant differences in the size increases at the high and low feeding levels. This was probably due to the overall elevation of the feeding rates in these groups, where the rates of supply at the lower feeding levels were only slightly less than the rates achieved at the high feeding levels in the other groups, and at the higher level were almost double again (Table 5.2). These results support Turnbull's (1962) model of the effect of food supply on growth, in that there appears to be an optimal rate of food supply (in this case about 2.147 mg/day), above which the benefits are minimal. The resolution of food supply within other conditions (e.g. temperature) was relatively crude, so further consideration of the food effect will be made in discussion of the multivariate analyses.

That the effects of feeding level on weight gain were not always reflected in significant effects on size increase, suggests two phenomena. Firstly, the strength of the association between weight gain and size increase is dependent on other factors, such as the rate of food supply through its influence on the rate of development (see Section 5.3.12). Secondly, there appears to be a degree of inertia in the system, so that only weight changes of a certain magnitude are translated into

size differences. Accumulation of subtle, but significant, differences in weight gain may require many instars to be reflected in size. Where food supply is patchy (in time or space), this inertia may provide a desirable buffer operating through the extensibility of the abdomen.

With one exception, the rate of development (the inverse of the time taken to complete the three instars) was greater at the higher feeding levels, where two were examined. Again, the significant effect the four levels used in comparison 9 (Section 4.3.9) could not be resolved with the a posteriori test. It is interesting that although none of the means of the separated components could be significantly ranked, when combined to form rates of size increase and weight gain a pattern, consistent with the remaining experiments, was revealed. Browning (1941), Deevey (1949), Turnbull (1962, 1965), Hagstrum (1970a) and Vollrath (1983) also documented increased rates of development associated with higher feeding rates. In some species (e.g. Lycosa tinsignata, Latrodectus mactans and female Nephila clavipes) the total number of instars to maturity was affected by the food supply (Deevey 1949, Miyashita 1968a, Vollrath 1983), while in others (e.g. Agelenopsis potteri, Linyphia triangularis and male Nephila clavipes), the number of moults was fixed (Turnbull 1962, 1965, Vollrath 1983). Comparison of adult sizes of Selenocosmia stirlingi (Table 2.1 and Appendix B), with projected growth curves for spiders at different feeding rates (Section 5.5 and Figure 5.11) suggested that the number of instars to maturity is not fixed. For female theraphosids, maturation may be followed by many more instars and is therefore not a terminal stage as it is with the males (e.g. studies by Baerg 1928, 1958, Stradling 1978, Minch 1979b, Stewart & Martin 1982).

In the isolated case where the rate of development was not significantly affected by the food supply (comparison 8, Section 4.2.8), it is difficult to propose a convincing explanation. Given the

non-absolute nature of statistical tests, there is always the possibility of a false positive: the rejection of the null hypothesis when it is really true. This may be such a case.

Examination of the growth and development of spiderlings in the following three instars (VI to VIII) revealed that weight differences produced in instar V at different feeding levels, could be eliminated by instar VIII through changes to the relative feeding levels (Section 5.4). The initial size differences were not significantly altered, but this was believed to have resulted from the inertia in the system described above. Had the spiders been grown through more instars, it is conceivable that size differences would also have been eliminated. The convergence of weights by instar VIII was achieved by a combination of weight gain and instar durations, which were related to not only the feeding levels, but also the preceding conditions. This latter influence may have been expressed through the relative size of the spiders, or their feeding behaviour, or a combination of the two; these experiments did not resolve these possibilities.

When no food was provided during the delay, there was no development (i.e. no moulting), but there was significant weight loss in one of the litters. Turnbull (1962) predicted that development would continue at a very slow rate in the absence of food, but that, owing to the dependence of weight maintenance on the presence of some food, moulting might result in negative growth. The results of this study support the observation of weight loss associated with no food, but not that of continued development. Indeed, death of many of the offspring of MK69 without moulting suggested that ecdysis was not a viable option under the circumstances.

In terms of the life history strategies described by Vollrath (1983), the spiders in these experiments appeared to have neither fixed

size increments nor fixed instar durations, but grew according to a balance of the two in a manner which is positively correlated with the rate of food supply within certain limits. As it was not possible to quantify the availability of prey in the field (Section 3.3.1.4 and 5.6.3), it is only possible to generalize about its possible effects. Dramatic increases in vegetation cover at the field site (Figure 3.4) were directly associated with rainfall, and could therefore be very patchy over time. Changes in the abundance of arthropods (i.e. potential prey species) might have been expected to follow the patterns of vegetation changes. Thus, it seems likely that the food supply in the field would have been low for much of the time, with relatively brief periods with abundant prey. The duration of development and the number of instars passed to maturity would be expected to vary greatly in the Coombah environment. In contrast, spiders living in the north of Australia in areas of reliable wet seasons (and the associated prey fauna), would be expected to attain maturity in fewer instars over a reduced period of time.

6.5.3.3 Temperature

The temperature at which the spiderlings were reared was found to have a significant effect on both the rate of size increase and the rate of weight gained, when two temperatures were compared. Jones (1941) also found that higher temperatures produced greater rates of size increase in <u>Agelena naevia</u>. Where the effects of three temperatures were compared (30, 32 and 35 degrees C in comparison 7, and 28, 31 and 33 degrees C in comparison 8), they were not directly related to the temperatures. In comparison 7, both the rates of size increase and weight gain were both significantly higher at 30 and 32 degrees C than at 35 degrees C, indicating the less favourable nature of the highest temperature. While

the overall effect of temperature was significant in the ANOVA of comparison 8, <u>a posteriori</u> testing of the ranked means (31 degrees C > 33 degrees C > 28 degrees C) showed no significant differences. Had the spiders been reared for a longer period, it is possible that the trend in the means would have supported the hypothesis that 31 to 32 degrees C approximated an optimal temperature, with growth rates reduced above or below that value.

In comparison 6, the reverse trend was observed, with higher rates at 28 degrees C than at 30 degrees C. This was most likely caused by the selective mortality which had occurred in this litter in the delay prior to this experiment and at 30 degrees C after its commencement (Section 6.2.3). For the multivariate analyses, the spiderlings reared at temperatures above 32 degrees C were excluded, owing to the apparent reversal in the relationship between growth and temperature in this part of the range, and the delayed offspring of MK69 were excluded because of their anomolous growth patterns.

Resolution of the growth rates into their components of weight gain, size increase and the duration of the instars (development rate) provided further information. Without exception, temperature had a significant effect on the rate of development as had been observed in <u>Agelena naevia</u> (Jones 1941), <u>Tarentula kochi</u> (Hagstrum 1970a) and <u>Chiracanthium inclusum</u> (Peck & Whitcomb 1980). While these authors found that higher temperatures were associated with faster development and indeed affected nothing else (other than mortality), in my experiments the pattern was not as simple. In comparison 7, while the mean rates of development were ranked 32 degrees C > 30 degrees C > 33 degrees C, this trend was not significant. In comparison 8, the rates at 31 and 33 degrees were greater than at 28 degrees C. The rates of development were also significantly greater at 30 degrees C than 25 degrees C in comparison 11, but comparison 6 (with 28 and 30 degrees C) produced the reverse trend. For the reasons

stated earlier (Section 6.5.3.1), it seems that this delayed group displayed unusual growth patterns owing to mortality that occurred. The optimum temperature for the rapid development of these spiders would seem to be approximately 32 degrees C.

The increase in size was not generally affected by temperature as was found by Jones (1941) and Workman (1978), except in comparison 6. The aberrant growth of this group has already been discussed above (Section 6.5.3.1) and is not considered to indicate the responses typical of these spiders.

The weight gained over the three instars was significantly affected by temperature in half of the comparisons. The differences in comparison 8 (at 28, 31 and 33 degrees C) were sufficiently subtle that although the mean weight gain declined with increasing temperature, the trend was not significant, as it was in comparison 6 (at 28 and 30 degrees C). Temperature differences of equal or greater magnitude produced no significant effects in comparisons 7 and 11. It is possible that unconventional patterns of growth and development occur in those spiders able to withstand the extended period of starvation (in comparison 6) or that the results were simply a sampling phenomenon (Section 6.5.3.1). In spite of the problems associated with the spiders in comparison 6, it must be concluded that temperature can have a significant effect on the weight gained over these instars. This contradicts the previous findings of Jones (1941) and Workman (1978).

The most consistently significant effect of temperature on the rates of size increase and weight gain was expressed in the rate of development, although changes in size or weight increase also occurred. In the latter event, it is possible that increased metabolic costs associated with higher temperatures (Anderson 1970, Anderson 1974, Hagstrum 1970b, Stewart & Martin 1982) reduced the weight gains and eventually the size increase

to some extent. As both rates of size increase and weight gain were significantly affected by the feeding level and temperature, it is perhaps surprising that there was only one case of significant interaction between the two (comparison 11). This may have been a consequence of the temperatures used in most comparisons, as comparison 11 was unique in that 25 degrees C was tested with a higher temperature under comparable feeding conditions. As suggested by Workman (1978), the effects of the rate of food supply may be of over-riding importance over a certain range of temperatures, between 28 and 35 degrees C in these experiments. Below 28 degrees C, the effects of the rate of food supply are influenced by the temperature.

The delay conditions suggested that at or below 20 degrees C, these spiders would lose little or no weight when deprived of food (Section 6.2.3). If it is assumed that food would not be accepted at such temperatures, then in the field, 4 to 5 months over winter would probably be non-feeding months. Low winter activity levels supported this hypothesis. The optimum time for development, in terms of burrow temperature, would be mid-summer, but exploitation of elevated surface temperature would extend this period into spring and autumn. Assuming mid-summer burrow-closure was related to moulting, mating and reproduction (Section 3.4.2), the period of greatest spider activity generally occurred over these seasons.

6.5.3.4 Photoperiod

Comparison of the growth and development of spiderlings reared at different photoperiods (Section 5.3.10) revealed no significant effects on the rates of size increase or weight gain. As there was no significant difference in the size increase, weight gain or instar duration at the different photoperiods, it was not possible that opposing effects in those

components had cancelled each other. This result was consistent with the observations of Jones (1941), but Peck and Whitcomb (1970) found variations in growth rates associated with photoperiod. As the trends varied between the instars, and no statistical analyses were provided by Peck and Whitcomb (1970), it is difficult to assess the significance of their observations. It seems fair to say that, all else being equal, the photoperiod does not affect growth or development in juvenile instars of <u>Selenocosmia</u> spp. Observations of loosely synchronized annual moulting in adults and "adolescents" (Minch 1979b) have been attributed to integrated assessment of changes in daylength or temperature (Gabel 1972), and indeed maturation in male <u>Tarentula kochi</u> (Hagstrum 1970a) was regulated by a photoperiod gate. Hence, photoperiod may have a role in regulating adult growth processes, if not those in juveniles.

6.5.4 Multivariate Analyses

As both feeding level and temperature were found to affect growth and development in more or less consistent patterns (excluding the delayed offspring of MK69), the results obtained from most of the spiderlings were pooled for multivariate analyses. Three main tasks were addressed, using various combinations of the available data: the estimation of the rates of size increase and weight gain (including their components of size increase, weight gain and time) for known combinations of food supply and temperature the prediction of the rate of food supply for known combinations of growth rates and temperature (for application in the field) and the estimation of size increase on the basis of external factors and the weight gain achieved. The main limitations which apply to the equations derived through stepwise linear regression (Sections 5.3.12 and 5.3.13) are the developmental stages for which they apply (instars III to VIII) the ranges of temperature (25 to 32 degrees C) and the precise nature of food supply (less than 3.0 mg/day wet weight mealworms, 15 to 25 mg range) for which they are valid.

For the estimation of both the rates of size increase and weight gain, the rate of food supply was the most important factor, accounting for 59.8% and 75.0% of the variances respectively. Temperature added 6.8% and 3.4%, so that totals of 66.6% and 78.4% of the variance in each of the rates was explained by the multiple regression equations respectively. Considering the infamous individual variation of spiders (e.g. Bonnet 1930, Peck & Whitcomb 1970, Hardman & Turnbull 1980), and the fact that the material analysed here represented the progeny from up to six females from Coombah and Cairns, the strength of the equations is quite remarkable.

The strength of the equations with which the components (size increases, weight gain and the duration of three instars) were estimated, was not quite as strong. In all cases, about 55% to 60% of the variance was explained by the equation, leaving 40% unexplained. The unexplained variance is composed of an array of factors, including the following: the amount of the food supply which was captured and/or consumed, the natural individual difference between the spiders in terms of their responses to the variables tested and those not specifically resolved, other factors not considered by the experimenter, non-linearity of the variables not apparent from the data set, and so on. All that aside, for known rates of food supply and temperature, meaningful estimates could be made of the duration of three instars and the weight gain and size increases over these stages. These models of growth and development were to be tested under field conditions by supplementing natural food levels at two known rates and running control groups in the laboratory (Section 4.7.2), but loss of the experimental animals through death or dispersal resulted in the failure of this experiment.

It was also intended to estimate the mean rate of food supply in the field (in the appropriate "mealworm equivalents"), from the rates of growth obtained from the field-released spiders under measured temperature conditions, compared with matched laboratory reared spiders as proposed by Vollrath (1983). The method was similar to Humphrey's (1975a) guanine measurements of field-raised spiders. The equations based on the growth and temperature information accounted for 60% to 70% of the variance, which was again remarkable, when the degree of "noise" between food supply and ingestion (Turnbull 1962) are considered. As previous analyses had suggested an upper asymptote to the effectiveness of increasing food supply (Section 6.5.3.2 and Turnbull 1962) and interaction with temperature (at least below 28 degree C, Section 6.5.3.3), two levels of food addition were provided in the third field experiment, in an attempt to attain an indication of the position of the natural values within (or outside) those tested in the laboratory. The disappearance of all of the field released experimental spiders prevented such natural comparisons, however it is believed that it may be possible, in future trials, to improve the survival of such spiders by more careful selection of the experimental animals (basically larger instars) and the location of the artificial burrows.

Finally, an attempt was made to examine the information which might be assimilated by the brain in order to determine (in so far as it does) the size increases achieved at ecdyses. Vollrath (1983) has suggested that there is a genetically determined body "stretch factor" which results in the appropriately proportional growth of body parts regardless of environmental conditions, but this does not explain the variations in size increase. In contrast, the magnitude of growth can be influenced by various factors, both external (e.g. the rate of food supply) and internal (e.g. rate of weight gain). The association between the weight gained

over three instars and the size increase at ecdysis was not particularly strong ($r^2 = 0.496$). However if the rate of food supply and temperature were included, 66.5% of the variance in size increase was explained. The brain may therefore determine a rate of weight gain or integrate the factors which regulate it, prior to initiating the moult. Hence, the spider appears to assess (or be regulated by) not only external factors, but also the manner in which the spider itself (e.g. in terms of weight gain) is responding to those conditions. It is not possible, from these results to determine whether the brain actually controls the size increase or whether it is simply a consequence of the body condition at the time of ecdysis. While the agents initiating the moult cycle have been elucidated in some insects (e.g. Manduca sexta, Gilbert & Goodman 1981) it is only possible to list the factors tested here as correlates rather than causative agents in these spiders. It would be interesting to examine the extent to which pre-ecdysial cell division and post-ecdysial stretching contribute to the overall size increase, and how each of these factors is related to specific titres of the neurohormones.

6.5.5 Field Experiments

6.5.5.1 Spider Releases

The initial experimental returns of spiderlings to the field suggested that it was necessary to provide an artificial burrow up to 500 mm deep. The failure of the first release may have resulted from a combination of artificial burrows of insufficient depth, and/or the coincidence with the beginning of a drought. Following the successful "recapture" of the spiderlings from the second release, the disappearance of all the spiderlings from the third release was unexpected. Baerg (1958) suggests that the juvenile stages of <u>Eurypelma californica</u>

disperse, and suffer high mortalities. In this study, it was intended to determine the patterns of dispersal, growth and mortality in the early instars, through observation of the formation, enlargement or disappearance of new small burrows around the maternal burrow. These methods have been successfully used in the study of other mygalomorphs (Main 1957, 1978, Salanitri pers. comm.). Unfortunately, neither spiderlings nor burrows of the early stages were found during the study. There are many possible explanations for this, of which the following are just a few: the burrows were not recognised, they were closed more often than adult burrows, the combination of small size and low frequency made them difficult to find, few or no spiderlings survived to disperse during the study, or perhaps dispersal occurred later in development. These or other factors may have contributed to the apparent lack of recruitment of juveniles to the population, but no truely satisfying explanation has been found.

The second release experiment confirmed that those spiderlings could be returned to the field and recaptured some time afterwards. The laboratory experiments indicated that equations based on the rates of growth and temperature could be used to estimate the mean rate of food supply in the field (in the appropriate units) (see Section 6.5.4). Further field experiments, possibly using "adolescent" spiders, might be more successful, and I believe this approach could provide interesting information about the growth strategies of these spiders and the validity of the growth models developed in the laboratory.

6.5.5.2 Spider Branding

Individual identification markings applied to spiders have generally consisted of paints or lacquers in combinations of colours and/or positions (Breymeyer & Jóźwik 1975, Hagstrum 1970b, Kiritani & Kakiya 1975,

Stradling 1978, Murakami 1983). While the markings themselves persisted over extended periods (e.g. in excess of 12 months), they were lost on the exuviae at ecdysis, leaving the newly emerged spider unmarked. In contrast, workers on crustaceans have successfully created brands which persist through ecdysis. Such brands include wedge-shaped nocthes or holes cut in the uropods (Arwidsson 1914, Svärdson 1948, George 1957, 1958) or burn marks in the carapace (Abrahamson 1965). In attempting to adapt the latter technique to spiders, it was considered necessary to avoid the carapace due to its close proximity to the central nervous system of theraphosids (Firstman 1954). The coxae of the walking legs provided alternate sites for the brands, however the marks did not persist through more than one ecdysis. This would have been sufficient for post-ecdysial recognition of the spiders for reapplication of the identification marks. Thus, the technique would be particularly suited to laboratory studies on large spiders housed in groups, or field studies involving intermittent recapture.

CHAPTER 7

CONCLUSIONS

Laboratory experiments revealed that rates of weight gain and size increase of <u>Selenocosmia stirlingi</u> were affected by the rate at which food was supplied and the ambient temperature, but not by the photoperiod. Within certain limits of the values tested, both of these rates could be estimated with considerable accuracy from regression equations which included the significant factors.

Resolution of these rates into their components of weight gain, size increase and duration of the instars revealed, more specifically, the nature of the effects of these environmental variables. The rate of food supply affected both growth (i.e increases in size and weight) and the rate of development. There appeared to be an upper limit to the positive effects of food supply, and the food effects were moderated by temperature below 28 degrees C. Temperature primarily had a direct influence on the rate of development up to about 30 degrees C. The mixed effects of temperature on weight gain suggested that over a greater temperature range and with spiders reared through more instars, the overall body size would also be affected by temperature.

In principle, the results from these experiments and the equations derived from them, could have been used to estimate the rate of food supply of spiderlings grown in the field. Unfortunately, attempts to carry out such investigations were unsuccessful.

Examination of the size increase over instars III to V revealed that not only weight gained, but also the environmental conditions (possibly through their effects on growth rates) explained much of the variance observed. Thus the spider's brain may integrate the rate of

growth and/or the perceived environmental conditions prior to initiating a moult.

The relative success of these laboratory experiments has been largely attributed to the rigid observation of specific conditions. Interpretations of the pooled results must be similarly restricted to the following combinations of spiderlings and environmental factors: Instar III to V or VI to VIII spiderlings from litters having experienced no substantial mortality, reared at temperatures ranging from 25 to 35 degrees C, fed at 3, 7, 14 or 17 day intervals with mealworms from 15 to 35 mg. Attempts to generalise beyond these specific conditions may well be invalid, and might produce higher unexplained variation similar to that described in previous work.

At the Coombah field site (New South Wales), soil temperatures fluctuated annually (from about 14 to 30 degrees C), and spider activity was greatest when these temperatures exceeded 20 degrees C, from spring to autumn. The more variable surface temperatures were probably exploited behaviourly by the spiders at both ends of the active season, in order to achieve body temperatures closer to the apparent optimum (ca. 32 degrees C), and exploit prey which may be more abundant there at those times. The temporal patchiness of potential prey (probably connected with the intermittent richness of the vegetation and thus rainfall) would probably have the greatest influence on growth of these spiders in the field. Considering adult sizes, mating behaviour and spermathecal development, there is likely to be considerable variation in the total number and duration of juvenile instars.

Investigations extending the ranges of spiderlings and environmental factors used, and further attempts to assess the field conditions along similar lines to this study, would provide an even fuller understanding of growth phenomena in these spiders.

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APPENDIX A

"Pseudo" Dark Field Illumination

The source providing epi-illumination of specimens viewed with a dissecting microscope can be partially obscured to produce "pseudo" dark field illumination (Roberts, pers. comm.). Such illumination is particularly suitable for examining otherwise transparent cuticular structures, such as the cuticular buds on the epigastric furrow. An object (such as a pair of forceps) is placed directly between the light source and the subject. The subject and its background are therefore not illuminated directly; however, diffracted and reflected light may reach the subject, so that it appears illuminated on a dark background. Edges of cuticular structures are highlighted by this form of illumination.

APPENDIX B

Size data for Adult Males

(a) Data on male <u>Selenocosmia</u> <u>stirlingi</u> from the

South Australian Museum.

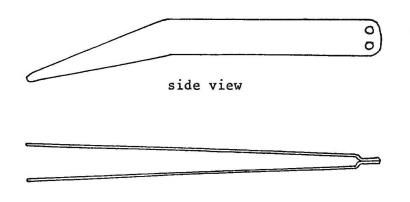
Locality	Date	Collector	Fang length (mm)	Cephalon length (mm)	thorax width (mm)
Crown Pt. Stn. S.A.	-	Gerrard	6.4	15.3	13.1
Broken Hill N.S.W.	15.iii.1892	F.A. Fiveash	4.9	12.2	11.1
Alice Springs N.T.	late 1956	Mrs. Rawcliffe	6.5	16.1	14.1
Barmera Hospital S.A.	April 1961	-	6.1	15.2	13.1
Hawker S.A.	April 1976	-	6.2	14.8	13.1
Oolder S.A.	-	A. Jones	6.2	14.6	12.8
Hawker S.A.	2.iv.1956	D.A.N. Turner	6.1	14.1	12.6
Broken Hill N.S.W.	17.iv.1964	Dr. P. Bryant	5.6	13.6	11.8
Arkaroola Hmstd S.A.	. Early 1972	Mr. T. Talp	5.8	13.5	12.3
Euro Bluff S.A.	1-4.IV.1983	T. Schwamer	5.8	13.4	11.8
Strathearn Hmstd. S.A.	2.iii.1978	T. Wilkin	5.5	13.3	11.3
Broken Hill N.S.W.	5.iii.1962	G.K. Gillet	5.6	13.3	11.5
Orroroo S.A.	March 1937	H. Gray	5.3	13.0	12.0

Locality	Date	Collector	Fang length (mm)	Cephalot length (mm)	horax width (mm)
9.8 km S of Canopus S.A. 33° 35′ S 140° 40′ E	26.ii.1976	S.P. Culic	5.6	12.6	11.1
McDonald Stn. N.T.	29.iv.1937	-	6.6	17.6	15.8
Mundallio Stn. S.A.	March 1958	A.R. Higginson	4.6	12.3	10.7
(b) Data on th	e single male	from Coombah (N.S.	.W.)		
5 km S of Coombah Hmstd.	Matured 16.iv.1983	M. Kotzman	5.1	12.8	11.2
			5	veight ca. 3	.3g
(c) Type spec	imen				
Crown Point Stn. S.A.	1898.6.19.2-3	Gerrard	6.4	15.3	13.1

APPENDIX C

Soft Forceps

Soft forceps, for handling small or fragile specimens, were constructed with 0.006 inch steel feeler gauge (Starret Co. Ltd.). Two strips were cut to length (about 10 cm) and joined at one end with spot welds. They were then formed to the desired shape on an abrasive grinding wheel (see below), and the points were separated with small creases formed near the base.



top view

1:1

APPENDIX D

Measuring Programme

A listing of the BASIC programme used in conjunction with the digitizer to measure the exuviae (Section 4.5.2) is provided below.

100 PAGE 110 PRINT "CHECKING SPACE IN DISK FILE - PLEASE WAITG_" 120 DPEN "FILENAME";1, "F", A\$ 140 FOR P=1 TO 3000 150 INPUT #1, P:D\$ 160 IF DS=" < filename >" THEN 180 170 NEXT P 180 R1=P 190 PRINT "G_G_ PLACE STYLUS DOWN AT LOWER LEFT OF MENU BOXES ONCE" 200 INPUT @8:X1, Y1, Z\$ 210 PRINT "6 " 220 REM LOOK FOR MENU COMMAND -----230 INPUT @8:X,Y,Z\$ 240 IF Y=> Y1 AND Y (= Y1+200 THEN 260 250 GO TO 230 260 FOR J=X1 TO X1+2000 STEP 200 270 IF X=> J AND X (= J+200 THEN 300 280 NEXT J 290 REM HERE WHEN BOX FOUND: NO. = (J/200)+1 300 N=(J-X1)/200+1 310 IF N=1 THEN 420 320 IF N=2 THEN 430 330 IF N=3 THEN 490 340 IF N=4 THEN 700 350 IF N=5 THEN 1130 360 IF N=6 THEN 1150 370 IF N=7 THEN 940 380 IF N=8 THEN 990 390 IF N=9 THEN 1020 400 IF N=10 THEN 1170 410 GO TO 230 420 GO TO 230 430 PRINT "ENTER 6-DIGIT ID NUMBER OF SPIDERG_" 440 INPUT S\$ 450 PRINT #1, R1: USING "10A":S\$ 460 PRINT USING "10A":S\$ 470 R1=R1+1 480 GO TO 230 490 P\$="H" 500 INPUT @8:X2, Y2, Z\$ 510 IF Y2=> Y1 AND Y2 (= Y1+200 THEN 530 520 GO TO 550 530 X=X2 540 GO TO 260 550 INPUT @8:X3, Y3, Z\$ 560 IF Y3=> Y1 AND Y3 (= Y1+200 THEN 580 570 GO TO 600 580 X=X3 590 GO TO 260 600 L=SQR((X3-X2)^2+(Y3-Y2)^2) 610 IF P\$="L" THEN 630 620 GD TO 650 630 L=L/200*C2 640 GO TO 660 650 L=L/200*C1 660 PRINT USING "2D. 2D":L 670 PRINT #1, R1: USING "2D. 2D":L 680 R1=R1+1 690 GO TO 230

700 P\$="H" 710 L1=0 720 INPUT @8:X4, Y4, Z\$ 730 IF Y4=> Y1 AND Y4 (= Y1+200 THEN 750 740 GO TO 770 750 X=X4 760 GO TO 260 770 FOR J=1 TO 1000 780 INPUT @8:X5, Y5, Z\$ 790 IF Y5=>Y1 AND Y5 (=Y1+200 THEN 900 800 L=SQR((X5-X4)^2+(Y5-Y4)^2) 810 IF P\$="L" THEN 830 820 GD TO 850 830 L=L/200*C2 840 GO TO 860 850 L=L/200*C1 860 L1=L1+L 870 X4=X5 880 Y4=Y5 890 NEXT J 900 PRINT USING "8D. 2D":L1; 910 PRINT #1, R1: USING "2D. 2D":L1 920 R1=R1+1 930 GO TO 230 940 0\$="00.00" 950 PRINT #1, R1: USING "5A":0\$ 960 PRINT USING "5A":0\$ 970 R1=R1+1 980 GO TO 230 990 R1=R1-1 1000 PRINT "CANCELLED" 1010 GO TO 230 1020 REM HIGH MAG CALIBRATION ROUTINE -----" 1030 PRINT "DIGITISE END-POINTS OF SCALE LINEG_" 1040 INPUT @8:X6, Y6, Z\$ 1050 INPUT @8:X7, Y7, Z\$ 1060 L=SQR((X7-X6)^2+(Y7-Y6)^2) 1070 PRINT USING "2D.2D":L/200 1080 M1=1 1090 L=L/200 1100 C1=M1/L 1110 PRINT "G_G_ O.K." 1120 GO TO 230 1130 P\$="L" 1140 GO TO 500 1150 P\$="L" 1160 GO TO 710 1170 REM LOW MAG CALIBRATION ROUTINE -----1180 PRINT "DIGITISE END POINTS OF SCALE LINEG_" 1190 INPUT @8:X8, Y8, Z\$ 1200 INPUT @8: X9, Y9, Z\$ 1210 L=SQR((X9-X8)^2+(Y9-Y8)^2) 1220 PRINT USING "20.2D":L/200 1230 M1=1 1240 L=L/200 1250 C2=M1/L 1260 PRINT "G_G_ O.K." 1270 GO TO 230

APPENDIX E

Accumulated Date File

The data file below is arranged in the following format. A block of four lines relates to an individual spider within a single experiment.* Details concerning the experimental conditions and the spiders identification number are contained in the first line. For example, 30HS01 represents 30 degrees C, High feeding level, Single spider per jar, first in the experimental series (Section 4.7) and 36.023 represents the twenty-third offspring of MK36 (Section 4.3). The remaining three lines contain data for instars III, IV and V or VI, VII and VIII in the following linear sequence from left to right: initial weight (g), final weight (g), instar duration (days), accumulated time (days), weight of food provided (g), number of meals, left straight fang length (SFL) (mm), Left curved fang length (CFL) (mm), right SFL (mm), right CFL (mm), cephalothorax length (mm), cephalothorax width (mm) and length of cuticular buds on the epigastric furrow (mm). Numbers consisting solely of 9's represent missing values.

* A spider used in more than one experiment thus has more than one block of data: these may be identified by the recurrence of the spider's identification number.

165.

30HS01 36.023	10	000	0.0400	•	3 05	1 00	1 00	1 00		0.46	0.00
0.0215 0.0389			0.0488						2.30		
0.0389 0.0739	27		0.0538						2.90		
0.0739 0.1353	50	.95	0.1449	8	1.65	1.94	1.67	1.91	3.72	3.97	9.99
30HS02 36.024	~~	000	0 0043	-							o oo
0.0196 0.0399			0.0841						2.24		
0.0339 0.0851	35		0.1115						2.87		
0.0851 0.1385	28	95	0.0896	4	1.62	1.90	1.62	1.91	3.57	3.75	9.99
30HS03 36.025					-			-			
0.0219 0.0369			0.0403						2.42		
0.0369 0.0636	20		0.0582						2.95		
0.0636 0.1215	42	87	0.1018	6	1.64	1.91	1.65	1.91	3.68	3.76	9.99
30HS04 36.026											
0.0172 0.0346			0.0473						9.99		
0.0346 0.0636	27		0.0478						2.80		
0.0636 0.1215	42	87	0.1136	6	1.50	1.75	1.50	1.73	3.37	3.45	9.99
30HS05 36.027	_			_							
0.0202 0.0375			0.0514						2.26		
0.0375 0.0783	27		0.0625						2.87		
0.0783 0.1212	36	81	0.0984	5	1.58	1.86	1.60	1.86	3.61	3.52	9.99
30HS06 36.028				-							
0.0160 0.0312			0.0558						2.15		
0.0312 0.0607			0.0598						2.76		
0.0607 0.1355	42	87	0.0839	5	1.56	1.82	1.53	1.80	9.99	9.99	9.99
30HS07 36.029				~	1 00	1 00		1 00		0.00	0 00
0.0186 0.0377	-		0.0517						2.24		
0.0377 0.0705	35		0.0935						2.85		
0.0705 0.1319	42	95	0.1357	6	1.65	1.93	1.6/	1.96	3.57	3.72	9.99
30HS08 36.030		000	0.0501	2	0 00	1 00	0 00	1 02	2 00	0 10	0 00
0.0145 0.0292			0.0591						2.09		
0.0292 0.0654	35		0.0963						2.79		
0.0654 0.0963	21	14	0.0334	2	1.49	1.74	1.4/	1.72	3.23	3.40	9.99
30HS09 36.123	10	000	0.0555	2	1 16	1 22	1 15	1 22	2.60	2 72	0 00
0.0279 0.0502			0.0988								
0.0502 0.1186			0.1633								
0.1106 0.1995	48	104	0.1033	/	1./0	2.07	1.//	2.00	4.00	4.22	9.99
30HS10 36.124	10	000	0.0540	3	1 06	1 25	1 04	1 20	2 22	2 12	0 00
0.0207 0.0412			0.0340								
0.0412 0.0825			0.0800								
0.0825 0.1973	11	124	0.2700	TO	T. 30	1.04	1.00	1.00	3.07	2.27	2.99
30HS11 36.125 0.0123 0.0445	10	000	0.0619	3	1 01	1 13	1 01	1 12	2 11	2 11	a aa
0.0123 0.0445			0.0887								
0.0849 0.1560			0.1199								
30HS12 36.126	42	90	0.1199	0	1.00	1.50	1.0/	1 ./1	J.02	2.22	2.99
0.0216 0.0427	10	000	0.0592	3	1 12	1.26	9,99	9 99	9 99	9 99	9 99
0.0218 0.0427			0.0888								
0.0836 0.1459	42		0.1085								
30HS13 36.127	42	55	0.1005	0	1.00	1.20	1.00	1.72	5.00	5.05	2.22
0.0203 0.0398	10	<u>a</u> aa	0.0618	3	1.05	1.23	1.09	1.28	2.38	2.45	9 99
			0.0939								
0.0398 0.0833 0.0833 0.0833 0.1315			0.1370						3.58		
30HS14 36.128	20	20	0.1010	,	1.07	2.23	1.05		5.50	2.11	2.22
0.0213 0.0411	10	000	0.0571	2	1.06	1.21	9,99	9.99	9.99	9 99	9 00
0.0213 0.0411			0.0894								
0.0411 0.0869	42		0.1138						3.54		
30HS15 36.129	42	30	0.1100	0	1./0	2.20	1.70	1.70	5.54	2.10	2.22
0.0136 0.0319	30	000	0.0893	5	0.94	1.09	0.89	1.05	2.05	2.12	g aa
0.0136 0.0319			0.0591								
0.0319 0.0701											9.99
0.0/01 0.112/	20	07	0.0702	7	1.40	2.10			74	2.00	2.22

						10/1						
30HS16 36.130												
0.0192 0.0268	18	999	0.	0601	3	1.00	1.18	1.03	1.19	9.99	2.42	9.99
0.0268 0.0838	35			0935			1.52					
0.0838 0.1348	42	95	0.	1277			1.95					
30HS17 36.131												
0.0219 0.0436	18	999	0.	0541	3	1.10	1.28	1.11	1.30	2.33	2.50	9.99
0.0436 0.0834	35	53	0.	0913	5	1.35	1.53	1.37	1.59	9.99	9.99	9.99
0.0834 0.1564	42	95	0.	1363	6	1.72	1.99	1.71	1.92	9.99	9.99	9.99
30HS18 36.132												
0.0206 0.0397				0497			9.99					
0.0397 0.0870	35			0981			1.56					
0.0870 0.1422	28	81	0.	0692	3	1.66	1.97	1.68	1.97	3.82	3.84	9.99
30HS19 36.133	~ ~		-									
0.0164 0.0284				0354			1.17					
0.0284 0.0585	28						1.48					
0.0585 0.1175 30HS20 36.134	34	87	0.	1024	C	1.49	1.75	1.49	1.74	3.45	3.3/	9.99
0.0221 0.0398	го	000	0	0481	2	1 06	1.24	1 00	1 26	2 27	2 51	0 00
0.0398 0.0944	41			0813			1.58					
0.0944 0.1600				1485			1.95					
30HS21 34.052	10	201	0.	1100	•	1.00	1.00	1.00		5.01	5.00	2.22
0.0230 0.0432	18	999	0.	0489	3	1.12	1.31	1.09	1.32	2.34	2.42	9.99
0.0432 0.0959	35	53	0.	0991	5	1.39	1.64	1.35	1.60	3.20	3.13	9.99
0.0959 0.1798	46	99	0.	1197	6	1.70	1.99	1.72	1.99	3.86	3.96	9.99
30HS22 34.053												
0.0234 0.0425				0606			1.29					
0.0425 0.0805	35			0863			1.61					
0.0805 0.1721	46	99	0.	1328	6	1.70	2.00	1.71	1.99	3.72	3.80	9.99
30HS23 34.054		000	~	0446	2	1 10	1 22	1 00	1 20	0 00	2 55	0.00
0.0237 0.0424				0446 0482			1.32					
0.0424 0.0885 0.0885 0.1472	35 42			1275			2.00					
30HS24 34.055	42	90	0.	1215	0	1.70	2.00	1.70	1.75	3.95	3.99	2.25
0.0178 0.0356	18	999	0.	0530	3	1.06	1.25	1.05	1.25	9.99	9.99	9,99
0.0356 0.0712				0480			1.45					-
0.0712 0.1315							1.80					
30HS25 34.056												
0.0227 0.0479	25						1.33					
0.0479 0.0806	28						1.59					
0.0806 0.1455	42	95	0.	1390	6	1.71	1.95	1.65	1.94	9.99	9.99	9.99
30HS26 34.057			_				2 00				~ ~~	
0.0226 0.0412							1.23					
0.0412 0.0918	35			1240			1.54					
0.0918 0.1630	42	95	0.	1240	0	1.09	1.94	1.00	1.95	3.33	9.99	9.99
30HS27 34.058 0.0219 0.0471	25	000	0	0513	3	1 07	1.29	1 08	1 30	2 33	2 42	a aa
$0.0219 \ 0.0471 \ 0.0934$							1.58					
$0.0934 \ 0.1503$							1.86					
30HS28 34.059	10	101										
0.0214 0.0464	18	999	0.	0712	3	1.09	1.30	1.11	1.32	2.30	2.43	9.99
0.0464 0.0929							1.53					
0.0929 0.1682	42	95	0.	1322	6	1.71	2.00	1.70	1.99	3.72	3.89	9.99
30HS29 34.060												
0.0219 0.0445							1.29					
0.0445 0.0850	34	59	0.	0848	5	1.36	1.60	1.35	1.61	2.96	3.14	9.99
0.0850 0.1507	45	104	0.	.1466	7	1.67	1.95	1.61	1.93	3.71	3.55	9.99
30HS30 34.061			~	0400	~	1 00	1 00	1 00	1 00	2 00	2	0.00
0.0230 0.0439												9.99
0.0439 0.0838				.1304			1.97					9.99
0.0838 0.1676	51	104	0.	. TOTO	1	T.0/	1.31	1.00	1.09	9.79	2.99	2.99

30HS31 34.192	10.000	0.0510	•		3 96	1				0.00
0.0222 0.0485		0.0519								
0.0485 0.0922		0.0552						9.99		
0.0922 0.1945	68 113	0.2298	10	1.61	1.89	1.64	1.93	3.62	3.74	9.99
30HS32 34.152	10.000		~							0.00
0.0241 0.0463		0.0422						2.34		
0.0463 0.1017		0.1136						9.99		
0.1017 0.1831	51 104	0.1426	/	1.76	2.09	1.75	2.09	3.83	4.06	9.99
30HS33 34.153 0.0217 0.0523	25 000		2		1 20	7 00	1 01	0.05	0 47	0 00
0.0523 0.0988		0.0563						2.35		
0.0988 0.1894		0.1012 0.2035				-		3.88		
30HS34 34.154	00 113	0.2055	0	1.10	2.02	1.75	2.00	2.00	3.92	9.99
0.0212 0.0388	10 000	0.0428	3	1 09	1 21	1 09	1 30	2.30	2 17	0 00
0.0388 0.0822		0.0428						3.02		
0.0822 0.1766		0.1655						3.62		
30HS35 34.155	JT 10-	. 0.1000		T.04	1.74	1.04	T.74	5.02	5.00	
0.0206 0.0407	25 999	0.0640	3	1.11	1.34	1,12	1.32	2.32	2.45	9,99
0.0407 0.0851		5 0.0883						3.00		
0.0851 0.1465		5 0.1327						3.66		
30HS36 34.156			-							
0.0208 0.0503	32 999	0.0863	5	1.05	1.27	1.07	1.29	2.26	2.40	9.99
0.0503 0.0897		7 0.0895						2.97		
0.0897 0.1543	51 118	3 0.1387	6	1.58	1.87	1.55	1.81	3.67	3.81	9.99
30HS37 34.157										
0.0217 0.0470	18 999	0.0645	3	9.99	9.99	1.10	1.32	9.99	9.99	9.99
0.0470 0.0832	27 4	5 0.0619	3	1.37	1.63	1.35	1.59	3.13	3.21	9.99
0.0832 0.1636	42 8	7 0.1440	6	1.73	1.98	9.99	9.99	9.99	9.99	9.99
30HS38 34.158										
0.0213 0.0485	25 999	0.0415						2.36		
0.0485 0.0967		0.0938						2.93		
0.0967 0.1853	45 104	1 0.1724	7	1.73	2.07	1.75	2.02	9.99	9.99	9.99
30HS39 34.159										
0.0211 0.0406		0.0573						9.99		
0.0406 0.0816		3 0.1029								
0.0816 0.1429	46 99	9 0.1336	6	1.54	1.82	1.56	1.84	3.81	3.73	9.99
30HS40 34.160	05 00			1 00	1 20	1 07	1 20	2 25	0 07	0.00
0.0212 0.0424		0.0423 0.0974								
0.0424 0.0814		5 0.1346								
0.0814 0.1470 30LS01 36.053	42 9:	0.1340	, 0	1.00	1.0/	1.01	1.09	3.11	3.00	9.99
0.0204 0.0363	25 00	9 0.0409	2	1 06	1 25	1 07	1 27	2 35	2 30	0 00
0.0363 0.0665		4 0.0527								
0.0665 0.1054		3 0.0802						3.41		
30LS02 36.054	11 11	0.0002	, .	1.05	2100	2000	1.00		0.00	2.22
0.0142 0.0232	25 99	9 0.0265	5 2	0.96	1.12	0.95	1.12	2.07	2.08	9.99
0.0232 0.0465		9 0.0626								
0.0465 0.0809		4 0.0753						2.94		
30IS03 36.055										
0.0235 0.0392	25 99	9 0.0370) 2	1.01	1.18	1.04	1.22	2.33	2.48	9.99
0.0392 0.0709		7 0.1016	5 3	1.32	1.54	1.36	1.58	2.97	3.16	9.99
0.0709 0.1155		8 0.0729	3	1.62	1.91	1.61	1.91	3.61	3.59	9.99
30LS04 36.056										
0.0167 0.0273		9 0.0307								
0.0273 0.0517		7 0.0522								
0.0517 0.0880	46 11	3 0.0777	7 3	1.46	1.73	1.45	1.71	3.33	3.28	9.99
30LS05 36.057										
0.0139 0.0236		9 0.0490								
0.0236 0.0489		4 0.0316								
0.0489 0.0728	39 11	3 0.0723	L 3	1.42	1.66	1.44	1.67	3.03	3.11	9.99

201006 26 050											
30LS06 36.058 0.0195 0.0281	18 0	000	0.0309	2	0 00	9.99	1 02	1 21	2 25	2 11	0 00
0.0281 0.0541			0.0361			1.45					
0.0541 0.0898		-	0.1020			1.45					
30LS07 36.059	40.	104	0.1020	4	1.40	1.12	1.4/	1.75	3.44	2.10	9.99
0.0275 0.0342	11 0	ممم	0.0167	٦	1 00	1.19	0 00	1 10	2 17	2 16	0 00
0.0342 0.0609			0.0107			1.46					
0.0609 0.1020			0.0889			1.83					
30LS08 36.060	50	55	0.0009	4	1.57	1.05	1.00	1.00	2.22	3.40	9.99
0.0143 0.0238	25	aaa	0.0302	2	0 92	1.08	0 92	1 00	1 00	2 05	a aa
0.0238 0.0469			0.0620			1.37					
0.0469 0.0926			0.0763			1.63					
30LS09 36.061	50	1	0.0705	5	1.00	1.05	T.47	1.00	3.14	3.11	2.22
0.0217 0.0368	25	999	0.0356	2	1.07	1.27	1.07	1.28	2.35	2.53	9,99
0.0368 0.0668			0.0518			1.59					
0.0668 0.1025			0.1166			1.84					
30LS10 36.135	50	774	0.1100	Ŧ	1.57	1.04	1.57	1.00	3.32	J.J.	5.55
0.0212 0.0375	25	999	0.0435	2	1.04	1.23	1.04	1.22	2 33	2.51	9,99
0.0375 0.0743			0.0644			1.56					
0.0743 0.1305			0.1637			1.92					
30LS11 36.136	02	100	0.100/	0	1.01	2.52	1.00	2	5.55	5.01	2.22
0.0221 0.0373	25	999	0.0365	2	1.05	1.25	1.06	1.25	2.33	2.53	9,99
0.0373 0.0619			0.0496			1.54					
0.0619 0.1015			0.0754			1.83					
30IS12 36.137	•••			-							
0.0192 0.0313	25	999	0.0260	2	1.03	1.23	1.02	1.21	2.25	2.33	9.99
0.0313 0.0559			0.0525			1.48					
0.0559 0.1005			0.1260			1.80					
30LS13 36.138											
0.0207 0.0376	25	999	0.0344	2	1.06	1.26	1.06	1.25	2.33	2.49	9.99
0.0376 0.0719	42	67	0.0720	3	1.31	1.56	1.33	1.59	3.01	3.08	9.99
0.0719 0.1534		131	0.1105	4	1.66	1.95	1.68	1.99	9.99	9.99	9.99
30LS14 36.139											
0.0210 0.0288			0.0307								
0.0288 0.0537	56	74	0.0415	3	1.23	1.45	1.25	1.45	2.73	2.89	9.99
0.0537 0.0831	39	113	0.0807	3	1.43	1.68	1.40	1.67	3.16	3.30	9.99
30IS15 36.140						A					
0.0201 0.0392			0.0551								
0.0392 0.0698			0.0497								
0.0698 0.1320	57	131	0.1070	4	1.57	1.84	1.57	1.85	3.59	3.69	9.99
30IS16 36.141				•		1 00	1 00				
0.0211 0.0385			0.0417								
0.0385 0.0740			0.0543								
0.0740 0.1454	57	131	0.1216	4	1.53	1.01	1.50	1.76	3.53	3.59	9.99
30LS17 36.142	05	000	0.0212	2	1 06	1 74	1 06	1 25	2 24	2 11	0 00
0.0203 0.0333			0.0212								
0.0333 0.0662			0.0986								
0.0662 0.1222	44	TOT	0.0980	5	1.00	1.00	1.02	1.09	2.35	2.99	9.99
30LS18 36.143 0.0213 0.0324	25	000	0.0299	2	1 08	1.27	1.06	1.25	2.36	2 52	9 99
0.0324 0.0519		60	0.0676	3	1.26	1.48	1.27	1.49	2.82	2.98	9.99
0.0519 0.1383			0.1123			1.82					
30LS19 36.144	1	101	011120								
0.0209 0.0364	25	999	0.0379	2	1.07	1.25	1.04	1.26	2.32	2.53	9,99
0.0364 0.0642			0.0498								
0.0384 0.0842			0.1068			1.83					
30LS20 36.145	57	191									
0.0116 0.0298	28	999	0.0347	2	1.07	1.25	1.04	1.23	2.28	2.51	9.99
0.0298 0.0526			0.0424								
0.0526 0.0880			0.0980								

30LS21 34.0	82										
0.0208 0.04	06 53	999	0.0578	4	1.06	1.26	1.06	1.26	2.33	2.47	9.99
0.0406 0.05	81 34	87	0.0364	2	1.29	1.50	1.29	1.53	2.89	2.97	9.99
0.0581 0.09	77 49	136	0.1410	4	1.51	1.77	1.51	1.79	3.44	3.42	9.99
30LS22 34.0	83										
0.0230 0.03	18 18	999	0.0262	2	1.09	1.33	1.09	1.31	2.37	9.99	9.99
0.0318 0.05			0.0474						2.81		
0.0536 0.09			0.0742						3.19		
30LS23 34.0											
0.0212 0.03		999	0.0253	2	1.07	1.31	1.07	1.30	9.99	9.99	9.99
0.0369 0.06			0.0458						2.96		
0.0639 0.13			0.1260						3.42		
30LS24 34.0				-							
0.0202 0.04		999	0.0655	3	1.09	1.32	1,10	1.32	2.23	2.41	9,99
0.0410 0.07			0.0596						2.96		
0.0733 0.13			0.1068						3.73		
30LS25 34.0		TOT	0.1000	5	1.03	1.72	5.55	2.22	5.75	3.40	5.55
0.0225 0.03		aaa	0.0296	2	1.06	1.29	3. 08	1.29	2.31	2.48	9,99
0.0372 0.03			0.0514						2.94		
0.0709 0.12			0.1137						3.50		
30LS26 34.0		TOT	0.110/	-	1.00	1.00	1.01	1.05	3.50	3.01	5.55
0.0233 0.03		000	0.0300	2	1 09	1 20	1 07	1 20	2.31	2 16	0 00
0.0306 0.00			0.0638						9.99		
			0.1074						3.44		
0.0628 0.1		TOT	0.10/4	4	1.59	1.0/	T.03	1.0/	2.44	2.00	9.99
30LS27 34.0		000	0.0400	2	1 07	1 20	1 06	1 20	2.23	2 22	0 00
0.0197 0.03			0.0490						2.23		
0.0369 0.0			0.0499						2.83		
0.0579 0.1		131	0.1229	4	1.49	1.75	1.40	1./4	3.35	2.22	9.99
30LS28 34.0		000	0.0581	2	1 07	1 20	1 00	1 21	2.30	2 20	0 00
0.0212 0.04			0.0428						2.96		
0.0431 0.0			0.1207						3.57		
0.0760 0.13 30LS29 34.		124	0.1207	**	1.00	1.04	1.00	1.00	5.57	5.00	9.99
		000	0.0459	3	1 08	1 20	1 06	1 29	2.36	2 23	9 99
0.0196 0.03			0.0334								
0.0371 0.0			0.1097								
0.0571 0.1 30LS30 34.		TOT	0.1097	-	1.55	1.01	T.22	1.01	2.41	5.50	5.55
0.0152 0.0		000	0.0196	2	1 09	1 31	1 10	1 31	2 17	2 35	9 99
			0.0273								
0.0220 0.0			0.02/5								
30LS31 34.		104	0.0900	-	1.00	1.01		T.04	2.55	5.27	2.25
0.0246 0.0		000	0.0338	2	1.12	1.36	1.13	1.37	2.30	2 44	9 99
0.0408 0.0			0.0574								
0.0742 0.1			0.1452								
30LS32 34.		100	0.1454	-	1	2.027	2072	1.00	5.55	2.25	2.25
0.0201 0.0		999	0.0561	3	1.11	1.31	1.10	1.32	2.23	2.45	9,99
0.0406 0.0			0.0584								
0.0685 0.1			0.1551								
30LS33 34.		100	0.1001		1.07	2.00	1.00	2.02	2122	2022	2.22
0.0208 0.0		999	0.0339	2	1.06	1.26	1.10	1.33	2.32	2.49	9,99
0.0306 0.0	-		0.0414								
0.0547 0.0			0.0914								9.99
30LS34 34.		104	0.0014	-					1.40	5155	
0.0228 0.0		000	0.0518	3	1.07	1.29	1.08	1.30	2.34	2.56	9 99
0.0228 0.0			0.0331								9.99
0.0422 0.0			0.1132								9.99
30IS35 34.		1.21		-	1.00	2.00	2.50	1.07	5.50	3.52	5.55
0.0220 0.0		000	0.0472	-	1.11	1.35	5 1.10	1.34	2.30	2 20	9 00
0.0220 0.0			0.0472								
0.0403 0.0			0.1372								
0.0000 0.1	T02 23	140	0.1312	-		1.00	4.00	1.00	5.55	9.00	2.99

30LS36 :																				
0.0242					0452			11							_	-				
0.0413	and the second second				0657			35												
0.0780		59	140	0.	1398	4	1.	66	1.9	95	1.	68	1.	97	3.	62	3.	84	9.	99
30LS37																				
0.0221					0605			10												
0.0415					0498			33												
0.0739		53	140	0.	1279	4	1.	59	1.8	87	1.	58	1.	86	3.	58	3.	62	9.	99
30LS38																				
0.0202					0556			07												
0.0410					0526			32										-		
0.0750		49	136	0.	1426	4	1.	59	1.	88	1.	60	1.	95	9.	99	9.	99	9.	99
30LS39	34.169																			
0.0196	0.0349	32	999	0.	0428			13												
0.0349	0.0638				0515			29								100 Jac				
0.0638	0.1190	53	140	0.	1440	4	1.	56	1.	79	1.	58	1.	82	9.	99	9.	99	9.	99
30LS40																				
0.0211	0.0316	32			0313			10												
0.0316		55			0454			.29												
0.0694	0.1180	53	140	0.	1500	4	1.	.57	1.	80	1.	55	1.	82	3.	38	3.	52	9.	99
25HS01	36.083																			
0.0151					0831															
0.0414					1012															
0.0805		81	155	0.	3925	12	1.	.45	1.	71	1.	44	1.	72	9.	99	9.	99	9.	99
25HS02																				
0.0200	0.0440				1177															
0.0440				-	9999															
9.9999		999	999	9.	9999	99	9.	.99	9.	99	9.	99	9.	99	9.	99	9.	99	9.	99
25HS03						_					_		_							
-	0.0403				0892			.00												
0.0403					1070	-		.25										-		
	0.1959	62	136	0.	3302	9	1.	.51	1.	80	1.	53	1.	80	9.	99	3.	78	9.	99
25HS04						_	-	05	-		-	20	-	~ 4	~	~~	~	~~	•	~~
	0.0450				0691															
0.0450					0955															
	0.2234	80	147	0.	3348	10	1	. 55	1.	18	۲.	55	1.	8T	3.	60	. د	11	9.	99
	36.087	45	000	0	1197	c	٦	05		21	Т	~1	т	25	2	22	2	20	0	00
	0.0424				1103															
	0.0903				4341															
	0.2134 36.088	87	1/4	0.	.4941	12	1	.00	1.	02	1.	20	4.0	00	J.	40	Э.	07	5.	23
	0.0484	22	000	0	.0841	5	٦	03	1.	21	1	02	1	19	2	36	2	35	q	99
	0.1320				2397															
	0.2129				.3376															
	36.089	00	104	0.		0	-				-	Ç,	and an a		.					22
	0.0649	39	999	0	.0812	5	1	.11	1.	27	1.	11	1.	.29	2.	.43	2.	60	9.	99
	0.1639				2687															
	0.3065				3684															
	36.090	_																		
	0.0424		999	0	.0812	5	1	.04	1.	21	1.	04	1.	.23	2.	.29	2	.39	9.	99
	0.0935				.0890															
	0.2223				.4342															
	36.091																			
	0.0359		999	0	.0888	5	0	.95	1.	15	0.	.96	1	.14	2	.12	9	.99	9.	.99
	0.0772				.0903															
	0.1566				.2636															.99
	36.092																			
	0.0480		999	0	.0823	5	1	.07	1.	.26	1.	.05	1	.24	2	.38	2	.43	9.	.99
	0.0992				.1693															
	0.1970				.3142															.99

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25HS11 36.146 0.0190 0.0457 32 999 0.0812 5 0.99 1.17 1.03 1.21 2.23 2.44 9.99 0.0457 0.0908 52 84 0.1424 7 1.26 1.46 1.28 1.47 2.91 3.05 9.99 0.0908 0.2040 78 162 0.3751 10 1.57 1.81 1.54 1.82 3.61 3.76 9.99 25HS12 36.147 0.0181 0.0371 32 999 0.0746 5 0.98 1.17 0.98 1.16 2.15 2.33 9.99 0.0371 0.0813 49 81 0.1177 6 1.21 1.39 1.18 1.37 2.80 2.80 9.99 0.0813 0.2373 93 174 0.4560 13 1.47 1.67 1.50 1.73 3.40 3.64 9.99 25HS13 36.148 0.0145 0.0324 32 999 0.0724 5 0.97 1.13 0.96 1.12 2.09 2.15 9.99 0.0324 0.0761 49 81 0.1114 6 1.18 1.37 1.16 1.36 2.71 2.53 9.99 0.0761 0.2142 84 165 0.4420 12 1.46 1.71 1.48 1.75 3.36 3.37 9.99 25HS14 36.149 0.0219 0.0524 32 999 0.0843 5 1.03 1.22 1.02 1.20 2.41 2.37 9.99 0.0524 0.0893 42 74 0.0770 5 1.32 1.52 1.31 1.51 2.98 3.17 9.99 0.0893 0.2062 91 165 0.4339 13 1.57 1.83 1.58 1.84 3.70 3.73 9.99 25HS15 36.150 0.0211 0.0525 32 999 0.0987 5 1.03 1.22 1.03 1.21 2.33 2.42 9.99 0.0525 0.1109 55 87 0.1297 7 1.28 1.48 1.30 1.51 3.01 3.14 9.99 0.1109 0.2312 96 183 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1.08 1.32 1.07 1.33 2.22 2.41 9.99 0.0521 0.1134 92 124 0.3191 13 1.29 1.51 1.30 1.53 2.93 3.15 9.99 0.1134 0.2790 127 251 0.7459 18 1.97 2.32 1.95 2.28 9.99 9.99 9.99 25HS27 34.118 0.0173 0.0407 53 999 0.1567 8 1.11 1.33 1.09 1.32 2.26 2.36 9.99 0.0407 0.0677 121 174 0.5054 16 1.29 1.51 1.29 1.51 2.80 2.97 9.99 0.0677 0.1067 56 230 0.3348 8 1.42 1.69 1.41 1.67 3.22 3.21 9.99 25HS28 34.119 0.0204 0.0428 45 999 0.1210 6 1.05 1.28 1.05 1.27 2.33 2.34 9.99 0.0428 0.0804 50 95 0.1627 8 1.24 1.48 1.24 1.47 2.92 2.87 9.99 0.0804 0.1372 88 183 0.4280 12 9.99 9.99 9.99 9.99 9.99 3.52 9.99 25HS29 34.120 0.0224 0.0555 32 999 0.1002 5 1.06 1.30 1.08 1.31 2.35 2.28 9.99 0.0555 0.1365 86 118 0.2689 11 1.33 1.53 1.33 1.56 3.09 9.99 9.99 0.1365 0.2362 56 174 0.3522 8 1.63 1.92 1.63 1.90 3.83 3.82 9.99 25HS30 34.121 0.0193 0.0430 39 999 0.0838 5 1.08 1.29 1.09 1.30 2.31 2.50 9.99 0.0430 0.0790 48 87 0.1206 7 1.30 1.50 1.31 1.53 2.96 3.13 9.99 0.0790 0.1605 81 168 0.4252 12 1.52 1.79 1.55 1.79 3.53 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1.90 9.99 3.86 9.99 25HS36 34.176 0.0212 0.0480 39 999 0.0808 5 1.10 1.34 1.10 1.33 2.24 2.45 9.99 0.0480 0.0903 79 118 0.2625 11 1.33 1.58 9.99 9.99 9.99 9.99 9.99 0.0903 0.1887 47 165 0.2918 7 1.57 1.89 1.59 1.87 3.50 3.67 9.99 25HS37 34.177 0.0207 0.0525 32 999 0.0936 5 1.08 1.29 1.08 1.29 2.38 2.41 9.99 0.0525 0.1019 49 81 0.1181 6 1.30 1.54 1.34 1.54 3.06 3.08 9.99 0.1019 0.2166 81 162 0.3817 11 1.62 1.90 1.69 1.94 9.99 3.96 9.99 25HS38 34.178 0.0194 0.0440 45 999 0.1057 6 1.07 1.30 1.08 1.31 2.32 2.31 9.99 0.0440 0.0824 132 177 0.5957 19 1.26 1.48 1.25 1.47 9.99 2.86 9.99 0.0824 0.1673 56 244 0.3124 8 1.45 1.70 1.44 1.71 3.31 3.52 9.99 25HS39 34.179 0.0214 0.0523 45 999 0.1157 6 1.10 1.33 1.10 1.30 2.38 2.46 9.99 0.0523 0.1237 59 104 0.2064 9 1.34 1.56 1.34 1.58 3.02 3.15 9.99 0.1237 0.2332 70 174 0.3790 9 1.63 1.91 1.65 1.96 9.99 3.90 9.99 25HS40 34.180 0.0198 0.0466 45 999 0.1117 6 1.10 1.33 1.08 1.33 9.99 2.39 9.99 0.0466 0.1042 115 160 0.4893 16 9.99 9.99 1.32 1.52 2.99 3.29 9.99 0.1042 0.1954 79 239 0.4156 10 1.61 1.90 1.59 1.88 3.76 3.95 9.99 25LS01 36.113 0.0228 0.0420 39 999 0.0598 3 1.12 1.26 1.11 1.27 2.39 2.55 9.99 0.0420 0.0966 85 123 0.2223 6 1.31 1.51 1.26 1.46 3.04 3.18 9.99 0.0966 0.1987 60 183 0.1727 4 1.62 1.89 1.64 1.91 3.70 3.89 9.99 25LS02 36.114 0.0204 0.0427 45 999 0.0488 3 1.01 1.21 1.02 1.24 2.32 2.44 9.99 0.0427 0.1021 110 155 0.2463 8 1.27 1.48 1.27 1.47 2.90 3.13 9.99 0.1021 0.1668 106 261 0.2322 6 1.63 1.92 1.61 1.91 3.73 3.82 9.99 25LS03 36.115 0.0206 0.0401 39 999 0.0685 3 1.03 1.23 1.01 1.22 2.35 2.43 9.99 0.0401 0.0803 80 119 0.0984 5 1.31 1.53 1.29 1.52 2.94 3.03 9.99 0.0803 0.1510 120 239 0.3368 8 1.60 1.87 1.60 1.85 3.66 3.66 9.99 251504 36.116 0.0192 0.0325 39 999 0.0535 3 1.03 1.22 0.99 1.15 2.32 2.32 9.99 0.0325 0.0795 79 124 0.1518 6 1.21 1.40 1.19 1.38 2.75 2.84 9.99 0.0795 0.1421 78 202 0.2132 5 1.46 1.69 1.43 1.66 3.39 3.47 9.99 25LS05 36.117 0.0193 0.0402 45 999 0.0392 3 1.04 1.21 1.00 1.18 2.33 2.44 9.99 9.9999 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999 9.9999 99 1.04 1.27 1.06 1.28 2.19 2.41 9.99 0.0360 0.0772 43 91 9.9999 99 1.27 1.49 1.26 1.50 2.80 2.88 9.99 0.0736 0.1160 60 151 9.9999 99 1.50 1.74 1.50 1.74 3.27 3.40 9.99 281015 69.016 0.0212 0.0368 36 999 9.9999 99 1.07 1.29 1.13 1.34 2.34 2.48 9.99 0.0355 0.0742 46 82 9.9999 99 1.30 1.52 1.27 1.49 2.76 2.95 9.99 0.0721 0.1174 67 149 9.9999 99 1.57 1.83 1.61 1.84 3.40 3.65 0.02 281016 69.017 0.0216 0.0460 47 999 9.9999 99 1.12 1.34 1.11 1.36 2.45 2.39 9.99 0.0430 0.0783 47 94 9.9999 99 1.34 1.59 1.35 1.61 2.90 3.06 9.99 0.0770 0.1431 82 176 9.9999 99 1.62 1.88 1.62 1.87 3.55 3.68 9.99 281017 69.018 0.0175 0.0351 48 999 9.9999 99 1.06 1.29 1.05 1.27 2.25 2.29 9.99 0.0337 0.0651 56 104 9.9999 99 1.24 1.48 1.22 1.46 2.75 2.79 9.99 0.0630 0.1252 73 177 9.9999 99 1.52 1.78 1.49 1.75 3.37 3.40 0.09 281018 69.019 0.0180 0.0364 48 999 9.9999 99 1.04 1.24 1.01 1.24 2.25 2.24 9.99 0.0352 0.0621 47 95 9.9999 99 1.25 1.47 1.22 1.46 2.77 2.79 9.99 0.0612 0.1126 68 113 9.9999 99 1.51 1.74 1.47 1.70 3.31 3.28 0.06 281019 69.020 0.0189 0.0471 61 999 9.9999 99 1.04 1.28 1.06 1.28 2.33 2.39 9.99 0.0456 0.0775 52 113 9.9999 99 1.32 1.54 1.31 1.50 3.00 3.09 9.99 0.0754 0.1210 66 179 9.9999 99 1.62 1.86 1.62 1.87 3.62 3.69 0.02 281020 69.021 0.0294 0.0588 47 999 9.9999 99 1.21 1.47 1.21 1.45 9.99 2.76 9.99 0.0551 0.1062 60 107 9.9999 99 1.49 1.74 1.47 1.73 3.25 3.43 9.99 0.0976 0.1792 96 203 9.9999 99 1.76 2.02 1.79 2.06 9.99 4.20 0.11 281021 69.022 0.0197 0.0433 38 999 9.9999 99 1.08 1.31 1.11 1.34 2.31 2.27 9.99 0.0414 0.0693 52 90 9.9999 99 1.29 1.51 1.33 1.54 2.95 2.96 9.99 0.0677 0.1228 91 181 9.9999 99 1.53 1.80 1.54 1.81 3.41 3.54 9.99 28LO22 69.023 0.0193 0.0448 46 999 9.9999 99 1.05 1.29 1.07 1.28 2.39 2.35 9.99 0.0429 0.0755 47 93 9.9999 99 1.30 1.50 1.32 1.55 2.89 3.05 9.99

0.07140.1265761699.9999991.501.761.491.773.453.540.0628L02369.024399999.9999991.051.231.071.272.312.379.990.03970.089150899.9999991.291.551.241.492.882.889.990.08540.1184621519.9999991.561.791.561.813.373.610.0128L02469.0250.02140.0442359999.9999991.301.101.312.342.539.990.04050.078250859.9999991.311.571.291.552.923.099.990.07690.1433951809.9999991.621.901.601.903.673.780.0528L02569.0260.01790.0399459999.9999991.041.251.021.239.992.309.990.03690.0753581039.9999991.281.521.291.522.922.819.990.07390.1274741779.9999991.591.841.601.833.553.670.07

28LO26 69.027 0.0176 0.0397 48 999 9.9999 99 1.05 1.26 1.05 1.27 2.20 2.29 9.99 0.0388 0.0687 44 92 9.9999 99 1.24 1.49 1.23 1.48 2.77 2.77 9.99 0.0639 0.0979 59 151 9.9999 99 1.48 1.73 1.47 1.75 3.19 3.40 9.99 281027 -69.028 0.0169 0.0397 39 999 9.9999 99 1.03 1.25 1.03 1.26 2.22 2.27 9.99 0.0379 0.0647 41 80 9.9999 99 1.24 1.47 1.25 1.49 2.79 2.95 9.99 0.0637 0.1034 55 135 9.9999 99 1.44 1.70 1.46 1.70 3.32 3.51 0.01 28LO28 69.029 0.0186 0.0355 48 999 9.9999 99 1.02 1.24 1.02 1.24 2.35 2.29 9.99 0.0348 0.0641 46 94 9.9999 99 1.26 1.49 1.27 1.50 2.87 2.83 9.99 0.0632 0.1063 58 152 9.9999 99 1.50 1.75 1.51 1.77 3.24 3.30 9.99 281029 69.030 0.0186 0.0407 45 999 9.9999 99 1.06 1.29 1.08 1.29 2.26 2.44 9.99 0.0389 0.0638 35 80 9.9999 99 1.28 1.55 1.30 1.54 2.89 2.93 9.99 0.0625 0.1158 59 139 9.9999 99 1.56 1.82 1.54 1.78 3.35 3.56 0.02 281030 69.031 0.0207 0.0409 35 999 9.9999 99 1.10 1.30 1.10 1.32 2.42 2.40 9.99 0.0376 0.0767 44 79 9.9999 99 1.29 1.52 1.31 1.54 2.87 2.95 9.99 0.0758 0.1180 69 148 9.9999 99 1.56 1.81 1.58 1.83 3.37 3.59 9.99 281031 69.032 0.0198 0.0354 48 999 9.9999 99 1.09 1.32 1.09 1.33 2.30 2.44 9.99 0.0347 0.0811 47 95 9.9999 99 1.31 1.53 1.31 1.55 2.90 9.99 9.99 0.0773 0.1425 81 176 9.9999 99 1.55 1.79 1.54 1.79 3.52 3.74 0.02 281032 69.033 0.0156 0.0358 40 999 9.9999 99 1.03 1.24 1.01 1.22 2.26 2.18 9.99 0.0352 0.0618 40 80 9.9999 99 1.22 1.47 1.23 1.46 2.76 2.73 9.99 0.0610 0.1069 54 134 9.9999 99 1.43 1.66 1.49 1.70 3.23 3.37 0.02 28L033 69.034 0.0204 0.0450 47 999 9.9999 99 1.13 1.34 1.12 1.34 2.39 2.42 9.99 0.0433 0.0835 59 106 9.9999 99 1.39 1.63 1.39 1.61 2.91 3.07 9.99 0.0806 0.1519 79 185 9.9999 99 1.61 1.88 1.63 1.87 3.46 3.61 9.99 28LO34 69.035 0.0188 0.0446 47 999 9.9999 99 1.08 1.30 1.08 1.31 2.24 2.21 9.99 0.0433 0.0885 45 92 9.9999 99 1.34 1.56 1.35 1.59 2.87 2.98 9.99 0.0794 0.1507 80 172 9.9999 99 1.58 1.84 1.59 1.86 3.42 3.57 0.03 281035 69.036 0.0178 0.0395 46 999 9.9999 99 1.06 1.27 1.08 1.28 2.30 2.23 9.99 0.0379 0.0828 44 90 9.9999 99 1.30 1.53 1.29 1.53 2.92 2.89 9.99 0.0765 0.1239 71 161 9.9999 99 1.58 1.84 1.58 1.84 3.33 3.59 9.99 281036 69.037 0.0156 0.0341 47 999 9.9999 99 1.02 1.21 1.02 1.21 2.14 2.21 9.99 0.0325 0.0600 39 86 9.9999 99 1.21 1.45 1.20 1.44 2.78 2.75 9.99 0.0558 0.0989 52 138 9.9999 99 1.49 1.73 1.51 1.77 3.30 3.37 9.99 281037 69.038 0.0187 0.0377 48 999 9.9999 99 1.08 1.29 1.05 1.26 2.24 2.46 9.99 0.0347 0.0679 46 94 9.9999 99 1.26 1.48 1.26 1.48 2.83 2.92 9.99 0.0670 0.1146 58 152 9.9999 99 1.46 1.70 1.49 1.72 3.30 3.57 9.99 28LO38 69.039 0.0215 0.0400 47 999 9.9999 99 1.12 1.33 1.11 1.33 2.46 2.37 9.99 0.0392 0.0827 44 91 9.9999 99 1.30 1.54 1.31 1.54 2.89 2.98 9.99 0.0798 0.1309 70 161 9.9999 99 1.58 1.83 1.59 1.85 3.43 3.59 9.99 281039 69.040 0.0267 0.0483 35 999 9.9999 99 1.18 1.40 1.19 1.41 2.56 2.66 9.99 0.0461 0.0832 69 104 9.9999 99 1.38 1.62 1.41 1.64 3.10 3.19 9.99 0.0785 0.1435 88 192 9.9999 99 1.64 1.93 1.62 1.92 3.72 3.82 9.99 281040 69.041 0.0213 0.0435 47 999 9.9999 99 1.13 1.33 1.14 1.35 2.42 2.47 9.99 0.0418 0.0761 47 94 9.9999 99 1.32 1.55 1.31 1.53 2.89 3.05 9.99 0.0742 0.1379 83 177 9.9999 99 1.51 1.75 1.53 1.76 3.39 3.65 0.02

28HD01 69.082 0.0214 0.0502 36 999 0.0841 5 1.11 1.35 1.11 1.34 2.35 2.45 9.99 0.0455 0.0957 39 75 0.1103 6 1.40 1.66 1.38 1.68 3.03 3.09 9.99 0.0945 0.1730 47 122 0.1418 7 1.66 1.95 1.66 1.97 3.68 3.87 0.10 28HD02 69.083 0.0201 0.0480 30 999 0.0844 5 1.11 1.31 1.09 1.30 2.40 2.44 9.99 0.0446 0.1010 35 65 0.0863 5 1.32 1.59 1.34 1.60 3.03 3.12 9.99 0.0954 0.1662 35 100 0.1232 6 1.65 1.92 1.61 1.90 3.65 3.91 0.02 28HD03 69.084 0.0179 0.0452 36 999 0.0719 5 1.08 1.30 1.07 1.28 2.44 2.47 9.99 0.0412 0.0826 33 69 0.0944 5 1.30 1.52 1.29 1.53 2.93 2.92 9.99 0.0786 0.1486 38 107 0.1194 6 1.59 1.85 1.57 1.85 3.68 3.61 0.07 28HD04 69.085 0.0181 0.0463 34 999 0.0803 5 1.03 1.26 1.02 1.25 2.25 2.23 9.99 0.0426 0.0836 36 70 0.0834 5 1.26 1.49 1.25 1.48 2.95 2.96 9.99 0.0804 0.1324 38 108 0.1169 6 1.57 1.86 1.54 1.81 3.48 3.72 0.01 28HD05 69.086 0.0175 0.0390 36 999 0.0931 5 1.06 1.27 1.06 1.27 2.28 2.35 9.99 0.0346 0.0758 33 69 0.0916 5 1.24 1.48 1.25 1.49 2.78 2.86 9.99 0.0731 0.1427 36 105 0.1262 6 1.54 1.83 1.59 1.87 3.45 3.68 0.06 28HD06 69.087 0.0208 0.0470 27 999 0.0588 4 1.07 1.29 1.10 1.33 2.33 2.40 9.99 0.0439 0.0892 33 60 0.0875 5 1.32 1.55 1.31 1.54 2.92 2.98 9.99 0.0879 0.1664 36 96 0.1424 7 1.62 1.91 1.64 1.92 3.65 3.77 0.09 28HD07 69.088 0.0193 0.0442 48 999 0.1238 7 1.09 1.30 1.06 1.29 2.43 2.43 9.99 0.0381 0.0824 38 86 0.0896 5 1.25 1.49 1.24 1.45 2.88 2.89 9.99 0.0787 0.1579 33 119 0.0997 5 1.54 1.79 1.54 1.79 3.66 3.55 0.06 28HD08 69.089 0.0178 0.0371 39 999 0.1098 6 1.07 1.28 1.08 1.26 2.37 2.43 9.99 0.0358 0.0859 32 71 0.0744 4 1.26 1.53 1.25 1.51 2.83 2.86 9.99 0.0832 0.1410 39 110 0.1247 6 1.59 1.88 1.59 1.88 3.43 3.61 0.06 28HD09 69.090 0.0203 0.0525 34 999 0.0796 5 1.06 1.27 1.06 1.28 2.24 2.37 9.99 0.0489 0.0993 37 71 0.0904 5 1.33 1.56 1.33 1.56 2.95 3.03 9.99 0.0962 0.1510 43 114 0.1176 6 1.61 1.91 1.60 1.90 3.61 3.72 0.02 28HD10 69.091 0.0281 0.0587 34 999 0.0727 5 1.14 1.37 1.16 1.43 2.47 2.61 9.99 0.0543 0.1023 56 90 0.1549 8 1.38 1.64 1.41 1.68 3.17 3.25 9.99 0.1018 0.1993 63 153 0.1874 9 1.71 2.01 1.75 2.06 3.92 3.99 0.10 28ID01 69.092 0.0177 0.0345 56 999 0.0747 4 1.07 1.29 1.06 1.30 2.34 2.40 9.99 0.0308 0.0657 57 113 0.0729 4 1.22 1.46 1.21 1.44 2.67 2.79 9.99 0.0633 0.1090 56 169 0.0856 4 1.45 1.71 1.46 1.74 3.30 3.42 0.05 28LD02 69.093 0.01530.0301739990.107861.031.251.021.242.252.379.990.02700.0543411140.036921.141.361.141.362.552.629.990.05190.0939451590.074341.401.651.351.603.123.200.06 28LD03 69.094 0.0172 0.0268 73 999 0.1043 6 1.08 1.30 1.06 1.30 2.27 2.38 9.99 0.0261 0.0585 35 108 0.0440 2 1.13 1.37 1.16 1.41 2.59 2.56 9.99 0.0544 0.1135 48 156 0.0884 4 1.44 1.71 1.43 1.70 3.20 3.30 0.05 28ID04 69.095 0.0208 0.0434 33 999 0.0504 3 1.06 1.27 1.05 1.27 2.28 2.37 9.99 0.0395 0.0691 52 85 0.0542 3 1.23 1.47 1.22 1.45 2.86 2.98 9.99 0.0669 0.1303 76 161 0.1206 6 1.50 1.76 1.54 1.82 3.43 3.66 0.02 28LD05 69.096 0.0194 0.0397 46 999 0.0751 4 1.11 1.33 1.09 1.31 2.40 2.49 9.99 0.0359 0.0647 65 111 0.0773 4 1.22 1.43 1.24 1.48 2.83 2.94 9.99 0.0609 0.0933 58 169 0.0846 4 1.51 1.77 1.50 1.77 9.99 9.99 0.01

28LD06 69.097											
0.0203 0.0444	52	aaa	0.0691	٨	1 09	1 20	1 07	1 21	2.45	2 60	0 00
0.0413 0.0940			0.0781						2.45		
0.0888 0.1484			0.0879					-	3.41		
28LD07 69.098	07	102	0.0072	-	1.04	T.04	T. JT	1.1/	J.41	J.02	0.07
0.0177 0.0319	45	999	0.0739	4	1 08	1 31	1 09	1 21	2.32	2 46	9 99
0.0280 0.0584			0.0585						2.70		
0.0565 0.0936			0.0793						3.19		
281D08 69.099	00	100	010/00	•	1.10	1.00	2.25	2.22	2.12	3.27	2.25
0.0236 0.0530	42	999	0.0506	3	1.13	1.38	1.13	1.37	2.50	2.49	9,99
0.0480 0.0805			0.0907						2.96		
0.0791 0.1566			0.1296						3.70		
28LD09 69.100				-				2.000			
0.0286 0.0462	42	999	0.0508	3	1.18	1.41	1.16	1.38	2.53	2.63	9.99
0.0432 0.0868			0.0954						3.02		
0.0847 0.1547			0.1232		1.67	1.94	1.64	1.96	3.78	3.72	0.03
28ID10 69.101											
0.0192 0.0338	44	999	0.0725	4	1.08	1.29	1.09	1.30	2.37	2.42	9.99
0.0325 0.0636			0.0731		1.22	1.44	1.21	1.46	9.99	9.99	9.99
0.0624 0.1323	74	187	0.1218	6	1.47	1.71	1.46	1.73	3.35	3.37	0.09
35H001 71.062											
0.0171 9.9999	999	999	9.9999	99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
9.9999 9.9999	999	999	9.9999	99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
9.9999 9.9999	999	999	9.9999	99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
35H002 71.063											
0.0186 0.0387	31	999	0.0913	5	1.04	1.27	1.04	1.27	2.35	2.39	9.99
0.0349 0.0817	26	57	0.0603						2.81		
0.0793 0.1350	41	98	0.1190	6	1.47	1.84	1.54	1.82	3.59	3.60	0.01
35H003 71.064											
0.0211 0.0425	30		0.0951						2.26		
0.0388 0.0843	38		0.0881						2.89		
0.0834 0.1481	45	113	0.1201	. 6	1.62	1.91	1.61	1.88	3.58	3.74	0.01
35H004 71.065											
0.0173 0.0398			0.0784	-					2.21		
0.0368 0.0749			0.0709	_					2.76		
0.0735 0.1370	46	103	0.1350	1	1.56	1.85	1.54	1.83	3.50	3.67	9.99
35H005 71.066			0 0500		1 00	1 20	1 07	1 21	0 07	0 00	0.00
0.0196 0.0390			0.0592								
0.0364 0.0743			0.0882								
0.0705 0.1323	68	109	0.1298	. /	1.00	1.00	1.00	1.90	3.40	3.00	0.05
35H006 71.067	25	000	0.0686		1 04	1 27	1 05	1 20	2 31	2 33	a aa
0.0197 0.0433	25 48		0.1250								
0.0400 0.0770 0.0757 0.1524			0.1250						3.51		
35H007 71.068	JT.	144	0.1400		1.00	1.00	1107	1.00	0.01	5.05	0.00
0.0211 0.0480	24	999	0.0715	5 4	1.08	1.31	1.06	1.30	2.34	2.42	9,99
0.0435 0.0872			0.1076								
0.0862 0.1526	_		0.1255						3.62		
35H008 71.069		220									
0.0235 0.0468		999	0.0828	3 5	1.10	1.35	1.10	1.35	2.42	2.49	9.99
0.0442 0.0891		73	0.1086	5 6	1.33	1.57	1.33	1.60	2.98	3.08	9.99
0.0873 0.1685		123	0.1443	37	1.65	1.93	1.64	1.93	3.66	3.92	0.01
354009 71.070											
0 0162 9,9999	999	999	9.9999	99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
9 9999 9 9999	999	999	9.9999	9 99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
9.9999 9.9999	999	999	9.9999	9 99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
358010 71.071											
0.0189 0.0390	24	999	0.063	7 4	1.05	5 1.28	1.06	1.29	2.28	2.29	9.99
0.0354 0.0762	32	56	0.0668	3 4	1.23	1.50) 1.22	1.48	2.74	2.80	9.99
0.0748 0.1168	34	90	0.101	3 5	5 1.52	1.81	1.51	1.80	3.28	3.50	0.01

35H011 71.072	00 000 0 0711			
0.0182 0.0406	28 999 0.0711		1.05 1.28 2.19 2.2	
0.0379 0.0913	44 72 0.1230		1.29 1.57 2.87 2.8	
0.0895 0.1465	47 119 0.1132	6 1.5/ 1.85	1.58 1.87 3.62 3.7	/1 0.04
35H012 71.073	~ ~ ~ ~ ~ ~ ~ ~ ~	5 3 65 3 66		
0.0214 0.0509	30 999 0.0862		1.04 1.26 2.38 2.3	
0.0475 0.0978	42 72 0.1181		1.26 1.52 2.98 3.	
0.0937 0.1638	43 115 0.1074	5 1.62 1.94	1.62 1.92 3.60 3.9	95 0.07
35H013 71.074		5 3 6 7 3 63		
0.0225 0.0468	36 999 0.0910		1.08 1.31 2.30 2.3	
0.0436 0.1036	20 56 0.1574		1.28 1.53 2.89 3.0	
0.1024 0.1589	88 144 0.1640	8 1.57 1.84	1.56 1.84 3.50 3.	/2 0.09
35H014 71.075				
0.0251 0.0511			1.11 1.35 2.46 2.3	
0.0463 0.0867	44 70 0.0984		1.33 1.58 2.97 3.2	
0.0849 0.1605	57 127 0.1615	8 1.63 1.94	1.62 1.93 3.69 3.8	86 0.07
35H015 71.076		4 1 00 1 04	1 01 1 00 0 07 0	
0.0200 0.0439			1.01 1.23 2.27 2.3	
0.0406 0.0792			1.23 1.49 2.82 2.4	
0.0775 0.1480		/ 1.5/ 1.83	1.53 1.79 3.52 3.	12 0.02
35H016 71.077		4 7 00 7 00	1 05 1 07 0 00 0	
0.0211 0.0424			1.05 1.27 2.29 2.3	
0.0381 0.0890			1.24 1.48 2.87 2.3	
0.0866 0.1543		/ 1.52 1.78	1.57 1.85 3.57 3.	/1 0.0/
35H017 71.078		E 1 06 1 07	1 00 1 04 0 06 0	26 0 00
0.0211 0.0454			1.02 1.24 2.36 2. 1.20 1.44 2.88 2.	
0.0422 0.0826			1.55 1.84 3.56 3.	
0.0806 0.1584		0 T.3/ T.00	1.05 1.04 5.06 5.	/8 0.01
35H018 71.079		1 1 00 1 22	1.07 1.32 2.32 2.	27 0 00
0.0210 0.0436			1.30 1.56 2.92 3.	
0.0407 0.0926			1.50 1.50 2.92 $3.$	
0.0889 0.1560		0 1.01 1.91	. 1.02 1.94 3.03 3.	04 0.07
35H019 71.080		1 1 09 1 31	1.07 1.31 2.32 2.	28 0 00
0.0206 0.0438			1.26 1.50 2.89 2.	
0.0390 0.0782 0.0767 0.1581		8 1 55 1.83	1.55 1.86 3.52 3.	69 0 02
35H020 71.081		0 1.00 1.00	1.00 1.00 3.02 3.	0,0.02
0.0178 0.0409		4 1.02 1.24	1.04 1.26 2.29 2.	35 9.99
0.0366 0.0712			1.28 1.54 2.80 2.	
0.0696 0.1342			1.56 1.88 3.53 3.	
351001 71.082				
0.0256 0.0389		3 1.10 1.35	1.09 1.33 2.38 2.	36 9.99
0.0381 0.0621			1.26 1.51 2.87 2.	
0.0597 0.0985			1.44 1.70 3.23 3.	67 0.05
35L002 71.083				
0.0178 0.0366		4 1.01 1.24	1.00 1.22 2.21 2.	18 9.99
0.0333 0.0642			1.19 1.42 2.71 2.	
0.0631 0.1184		4 1.48 1.70	1.43 1.69 3.38 3.	41 0.02
351003 71.084				
0.0208 0.0371	39 999 0.0623		1.05 1.29 2.28 2.	
0.0336 0.0562			1.25 1.48 9.99 9.	
0.0553 0.0982	68 165 0.1105	5 1.45 1.67	1.45 1.69 3.22 3.	43 0.06
351004 71.085				
0.0226 0.0369	25 999 0.0347		3 1.09 1.32 2.35 2.	
0.0346 0.0620	56 81 0.0740		1.31 1.52 2.84 2.	
0.0608 0.0924		4 1.45 1.72	2 1.46 1.75 3.27 3.	50 0.05
35LO05 71.086				
0.0211 0.0360	54 999 0.0729		1.05 1.27 2.24 2.	
0.0332 0.0688			5 1.21 1.45 2.73 2.	
0.0660 0.0620	26 135 0.0380	2 9.99 9.99	9.99 9.99 9.99 9.	99 9.99

351006 71.087 0.0213 0.0394 51 999 0.0661 4 1.06 1.29 1.06 1.29 2.37 2.34 9.99 0.0360 0.0770 56 107 0.0823 4 1.26 1.50 1.26 1.49 2.92 2.88 9.99 0.0746 0.1099 59 166 0.0886 4 1.56 1.82 1.56 1.82 3.57 3.78 0.08 351007 71.088 0.0202 0.0407 79 999 0.1068 6 1.09 1.34 1.10 1.34 2.27 2.41 9.99 0.0371 0.0721 48 127 0.0515 3 1.26 1.52 1.23 1.49 2.83 2.81 9.99 0.0712 0.1081 50 177 0.0886 4 1.48 1.76 1.46 1.74 3.30 3.58 0.02 351008 71.089 0.0213 0.0380 52 999 0.0621 4 1.05 1.30 1.07 1.32 2.27 2.32 9.99 0.0351 0.0666 56 108 0.0726 4 1.24 1.49 1.23 1.44 2.75 2.89 9.99 0.0632 0.1144 69 177 0.0780 4 1.54 1.83 1.52 1.78 3.39 3.56 9.99 351009 71.090 0.0177 0.0338 37 999 0.0462 3 1.03 1.25 1.02 1.23 2.21 2.19 9.99 0.0314 0.0505 44 81 0.0395 2 1.19 1.44 1.20 1.45 2.66 2.84 9.99 0.0496 0.0887 55 136 0.0976 5 1.44 1.70 1.42 1.70 3.13 3.34 0.01 35LO10 71.091 0.0214 0.0419 51 999 0.0648 4 1.04 1.30 1.02 1.26 2.33 2.31 9.99 0.0380 0.0783 47 98 0.0529 3 1.28 1.50 1.29 1.54 2.89 2.97 9.99 0.0761 0.1105 67 165 0.1048 5 1.48 1.75 1.47 1.78 3.33 3.53 0.01 35LO11 71.092 0.0188 0.0333 40 999 0.0532 3 1.01 1.23 1.02 1.23 2.18 2.22 9.99 0.0307 0.0572 56 96 0.0686 4 1.12 1.33 1.12 1.33 2.70 2.73 9.99 0.0549 0.0992 68 164 0.1048 5 1.39 1.64 1.41 1.66 3.28 3.37 0.02 351012 71.093 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 351013 71.094 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 35IO14 71.095 0.0160 0.0258 24 999 0.0285 2 0.94 1.17 0.93 1.15 1.99 2.00 9.99 0.0231 0.0388 41 65 0.0541 3 1.06 1.32 1.01 1.26 2.41 2.43 9.99 0.0382 0.0627 45 110 0.0592 3 1.30 1.52 1.26 1.50 2.82 3.04 0.02 35LO15 71.096 0.0198 0.0379 51 999 0.0678 4 1.02 1.23 1.03 1.24 2.23 2.29 9.99 0.0349 0.0657 55 106 0.0708 4 1.22 1.46 1.25 1.50 2.86 2.85 9.99 0.0644 0.1167 73 179 0.1128 5 1.48 1.75 1.52 1.79 3.42 3.52 0.07 35LO16 71.097 0.0204 0.0428 52 999 0.0748 4 1.08 1.29 1.07 1.31 2.31 2.28 9.99 0.0403 0.0687 56 108 0.0747 4 1.28 1.53 1.28 1.49 2.97 3.02 9.99 0.0675 0.1035 71 179 0.0847 4 1.50 1.75 1.50 1.78 3.45 3.42 0.08 351017 71.098 0.0202 0.0326 53 999 0.0663 4 1.03 1.26 1.06 1.28 2.29 2.34 9.99 0.0294 0.0585 55 108 0.0768 4 1.17 1.38 1.15 1.38 2.69 2.71 9.99 0.0558 0.0932 57 165 0.0872 4 1.41 1.65 1.41 1.67 3.21 3.40 0.06 35L018 71.099 0.0233 0.0422 51 999 0.0688 4 1.10 1.33 1.08 1.34 2.21 2.34 9.99 0.0375 0.0681 57 108 0.0728 4 1.26 1.51 1.21 1.45 2.86 2.93 9.99 0.0681 0.1200 68 176 0.0825 4 1.54 1.84 1.53 1.82 3.45 3.60 0.01 351019 71.100 0.0231 0.0369 37 999 0.0507 3 1.04 1.26 1.03 1.26 2.31 2.30 9.99 0.0329 0.0558 44 81 0.0564 3 1.20 1.43 1.21 1.45 2.77 2.86 9.99 0.0536 0.0868 56 137 0.0812 4 1.39 1.67 1.40 1.68 3.13 3.31 0.02 351020 71.101 0.0199 0.0320 65 999 0.0867 5 1.06 1.27 1.04 1.27 2.28 2.26 9.99 0.0288 0.0559 44 109 0.0612 3 1.17 1.39 1.17 1.38 2.71 2.60 9.99 0.0522 0.0932 55 164 0.0896 4 1.42 1.67 1.40 1.65 3.19 3.29 0.06

32HOO1 71.022											
0.0190 0.0376	22 9	99	0.0507	2	1 02	1 24	1 02	1 22	9.99	0 00	0 00
0.0360 0.0702			0.0675						2.80		
0.0642 0.1239			0.0892						3.42		
32HO02 71.023	54	05	0.0092	5	1.40	T. 10	1.02	1.19	3.44	5.54	0.01
0.0188 0.0389	28 9	aa	0.0743	Λ	1 00	1 22	1 00	1 22	2.42	2 21	0 00
0.0378 0.0731			0.0865						2.42		
0.0684 0.1470			0.1012						3.83		
32HO03 71.024	71	55	0.1012	5	1.02	1.91	1.00	1.74	2.02	5.33	0.09
0.0195 0.0426	27 0	000	0.0671	٨	1 02	1 26	1 02	1 24	2.34	2 27	0 00
0.0405 0.0909			0.0922						2.85		
0.0879 0.1558			0.1207						3.74		
32HO04 71.025	40 1		0.1207	0	1.59	1.00	1.00	1.90	2.14	2.12	0.00
0.0163 0.0374	20 0	000	0.0720	٨	1 01	1 22	1 00	1 21	2.22	2 32	a aa
0.0352 0.0689			0.0892						2.83		
0.0639 0.1400			0.1043						3.48		
32HO05 71.026	39	90	0.1045	5	T.40	T.12	TOT	1.//	2.40	5.55	0.05
0.0193 0.0424	20 0	000	0.0612	٨	1 07	1 27	1 07	1 22	2.29	2 38	<u>a</u> aa
0.0385 0.0849			0.1090						2.93		
0.0810 0.1536			0.1222						3.63		
32H006 71.027	40 1	510	V. 1222	Ų	1.00	1.00	T •0/	1.02	5.05	3.75	0.07
0.0275 0.0534	21 0	aa	0.0491	3	1.12	1.37	1.13	1.38	2.42	2.50	9,99
0.0506 0.1009	36		0.0854						3.11		
0.0960 0.1596			0.1458						3.79		
32HO07 71.028	10 1		012100	•	2002	2000	,			0.05	
0.0201 0.0403	21 9	999	0.0483	3	1.05	1.29	1.05	1.29	2.22	2.28	9.99
0.0390 0.0734			0.0924						2.86		
0.0719 0.1501	44		0.1162						3.54		
32HO08 71.029				-							
0.0193 0.0420	28 9	999	0.0686	4	1.06	1.25	1.04	1.25	2.27	2.28	9.99
0.0397 0.0763	39		0.1091						2.86		
0.0731 0.1448		105	0.1000	5	1.51	1.77	1.51	1.78	3.57	3.56	0.08
32HO09 71.030											
0.0268 0.0548	27 9	999	0.0603	4	1.16	1.42	1.18	1.41	2.49	2.65	9.99
0.0508 0.0987	46	73	0.1314	7	1.42	1.71	1.44	1.70	3.10	3.30	9.99
0.0972 0.2079	73	146	0.2069	10	1.73	2.03	1.72	2.04	4.06	3.99	0.02
32HO10 71.031											
0.0213 0.0481			0.0686								
0.0447 0.1009			0.0778								
0.0936 0.1657	46	103	0.1356	7	1.61	1.86	1.59	1.84	3.69	3.88	0.02
32HO11 71.032											
0.0178 0.0312	24 9		0.0672								
0.0280 0.0550	32		0.0685								
0.0531 0.1258	34	90	0.0981	5	9.99	9.99	1.45	1.73	3.27	3.37	0.07
32H012 71.033											
0.0241 0.0495	21 9	999	0.0402	3	1.04	1.28	1.07	1.29	2.32	2.32	9.99
0.0469 0.0814	35	56	0.0843	5	1.28	1.50	1.29	1.49	2.93	2.96	9.99
0.0782 0.1538	46	102	0.1373	7	1.58	1.84	1.62	1.86	3.70	3.82	0.02
32HO13 71.034											
0.0194 0.0418	27 9	999	0.0681	4	1.05	1.29	1.05	1.29	2.21	2.25	9.99
0.0383 0.0740	33	60	0.0850	5	1.27	1.53	1.27	1.52	2.83	2.86	9.99
0.0723 0.1312	34	94	0.0960	5	1.61	1.85	T.28	1.82	3.69	3.15	0.01
32H014 71.035									0.40	0	0 0 -
0.0279 0.0560	26	999	0.0609	4	1.14	1.36	1.12	1.34	2.49	2.62	9.99
0.0533 0.1024			0.0753								
0.1007 0.1703	47	104	0.1365	7	1.66	1.86	1.69	1.92	4.01	9.99	0.10
32H015 71.036						1	1	1 60	0.00	0.00	0.55
0.0184 0.0423	27	999	0.0625	4	1.05	1.29	1.06	1.32	2.36	2.23	9.99
0.0383 0.0876			0.0909		1.30	1.00	T.30	1.00	2.94	2.96	9.99
0.0824 0.1577	49	113	0.1472	1	T.01	т.93	T.00	1.89	3.14	3.14	0.01

32HO16 71.037 0.0192 0.0448 32 999 0.0802 5 1.03 1.25 1.05 1.28 2.29 2.43 9.99 0.0403 0.0751 37 69 0.0885 5 1.19 1.39 1.21 1.43 2.84 2.92 9.99 0.0697 0.1275 37 106 0.1008 5 1.54 1.84 1.50 1.80 3.41 3.63 0.07 32HO17 71.038 0.01860.0419259990.073041.031.251.051.272.262.299.990.03930.073830550.076941.201.381.231.412.762.919.990.07030.128742970.116061.561.831.551.823.493.660.01 32HO18 71.039 0.0185 0.0407 25 999 0.0711 4 1.01 1.22 1.02 1.21 2.25 2.32 9.99 0.0372 0.0666 33 58 0.0866 5 1.21 1.45 1.20 1.44 2.83 2.82 9.99 0.0649 0.1336 47 105 0.1229 6 1.54 1.80 1.51 1.77 3.54 3.63 0.02 32HO19 71.040 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 32HO20 71.041 0.0283 0.0548 21 999 0.0490 3 1.16 1.41 1.17 1.40 2.41 2.57 9.99 0.0526 0.0935 41 62 0.1021 6 1.39 1.65 1.42 1.70 3.15 3.00 9.99 0.0923 0.1710 49 111 0.1398 7 1.69 1.99 1.70 2.01 3.87 3.86 0.08 321001 71.042 0.0258 0.0431 42 999 0.0595 3 1.17 1.39 1.14 1.37 2.54 2.60 9.99 0.0421 0.0858 58 100 0.0778 4 1.28 1.55 1.30 1.55 2.96 3.04 9.99 0.0832 0.1154 68 168 0.0823 4 1.58 1.86 1.59 1.87 3.67 3.72 0.01 321002 71.043 0.0278 0.0505 32 999 0.0511 3 1.13 1.36 1.13 1.37 2.56 2.61 9.99 0.0439 0.0770 57 89 0.0814 4 1.27 1.50 1.28 1.51 2.99 3.05 9.99 0.0758 0.1198 66 155 0.0786 4 1.52 1.78 1.50 1.76 3.54 3.70 9.99 321003 71.044

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 321005 71.046 0.02000.0322449990.068541.041.261.061.282.342.389.990.02940.057640840.041321.211.401.221.422.552.749.990.05600.0771441280.079741.501.751.491.743.313.430.06 321006 71.047

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 321007 71.048 0.0246 0.0431 40 999 0.0491 3 1.08 1.30 1.09 1.33 2.44 2.46 9.99 0.0396 0.0724 58 98 0.0812 4 1.28 1.50 1.31 1.54 2.88 3.00 9.99 0.0713 0.1206 59 157 0.1043 5 1.55 1.82 1.55 1.81 3.51 3.62 0.10 32LO08 71.049 0.01940.0344409990.047731.041.271.051.282.222.349.990.03320.056947870.057631.191.451.201.442.802.829.990.05330.0934521390.083741.441.721.441.703.293.269.99 321009 71.050 0.0205 0.0389 33 999 0.0445 3 1.06 1.30 1.08 1.32 2.24 2.32 9.99 0.0348 0.0627 49 82 0.0552 3 1.24 1.48 1.25 1.47 2.71 2.83 9.99 0.0609 0.1175 59 139 0.0764 4 1.51 1.78 1.50 1.77 3.44 3.46 0.08 32101071.0510.02200.0443379990.052231.121.341.121.342.382.549.990.04100.077860970.07350.1147821790.095651.571.861.591.903.543.710.01

321011 71.052	47 6	200	0.0540	~							
0.0233 0.0416			0.0563						9.99		
0.0391 0.0684			0.0957						2.89		
0.0646 0.1060	68.	163	0.0901	4	1.52	1.78	1.52	1.79	3.56	3.55	0.03
32LO12 71.053	22.4		0 0457	•	1 07						
0.0201 0.0318			0.0457						2.25		
0.0270 0.0484 0.0470 0.0745			0.0582						2.58		
	54.	141	0.0851	4	1.40	1.64	1.41	1.65	3.16	3.20	0.01
32IO13 71.054 0.0240 0.0429	22.0	000	0 0500	2		3 95	1 00	1 20	0.05	0 17	0.00
0.0395 0.0664			0.0582						2.35		
0.0612 0.1058			0.0974						2.89		
321014 71.055	01.	140	0.0974	5	T. OT	1./4	1.51	1.75	J.41	3.00	0.00
0.0208 0.0403	38 0	aaa	0.0475	2	1 06	1 29	1 07	1 30	9.99	a aa	a aa
0.0361 0.0717			0.0592						2.83		
0.0703 0.1162			0.0919						3.57		
32L015 71.056		202	010515			2.00		11/0	0.0.	5157	0102
0.0191 0.0336	40	999	0.0539	3	1.05	1.30	1.04	1.29	2.19	2.31	9.99
0.0299 0.0605	42		0.0568						2.69		
0.0580 0.0939			0.0728						3.30		
321016 71.057											
0.0187 0.0364	52	999	0.0669	4	1.00	1.21	0.99	1.21	2.19	2.20	9.99
0.0325 0.0605	44	96	0.0574	3	1.21	1.43	1.20	1.42	2.76	2.75	9.99
0.0591 0.1006	50	146	0.0862	4	1.41	1.66	1.38	1.65	3.28	3.42	0.06
321017 71.058											
0.0203 0.0331			0.0449						2.35		
0.0295 0.0643			0.0901						2.73		
0.0633 0.0956	60	169	0.0809	4	1.49	1.75	1.48	1.71	3.44	3.46	0.05
321018 71.059											
0.0188 0.0327			0.0385						2.25		
0.0296 0.0577	56		0.1054	-					2.68		
0.0569 0.0936	46	128	0.0832	4	1.37	1.62	9.99	9.99	3.24	3.22	9.99
321019 71.060			0.0760			7 40	1 10	1 40	0 40	0 00	0.00
0.0230 0.0396			0.0768								
0.0375 0.0717	55	109	0.0716	4	1.20	1.01	1.20	1.50	2.83	2.90	9.99
0.0704 0.1123	58	161	0.0791	4	1.53	1.01	1.00	1.03	3.51	3.5/	0.01
32LO20 71.061 9.9999 9.9999	000	000	0 0000	00	0 00	0 00	0 00	0 00	a aa	0 00	0 00
9.9999 9.9999	999	999	9.9999	22	9.99	9.99	9.99	9.99	9.99	9.99	9.99
9.9999 9.9999	999	999	0 0000	99	9.99 a aa	9.99	9.99	9.99	9.99 9 99	9.99 9 99	9.99 9 99
	999	999	3.3333	99	2.55	5.55	2.55	2.22	9.99	5.55	2.99
30HC01 71.002 0.0263 0.0553	26	000	0.0761	4	1 17	1 43	1 18	1.44	2 49	2 57	9 99
0.0263 0.0553		555	0.1105	6	1.39	1.66	1.39	1.66	3.15	3.24	9,99
0.0860 0.1609		110	0.1242	6	1.55	1.83	1.55	1.84	3.63	3.77	0.10
30HC02 71.003	40	110	0.17.15	0	2000					••••	
0.0187 0.0376	31	999	0.0772	5	1.06	1.29	1.04	1.26	2.30	2.27	9.99
0.0364 0.0697		67	0.0926	5	1.28	1.52	1.26	1.51	2.85	2.86	9.99
0.0682 0.1426			0.1232		1.53	1.85	1.53	1.82	3.49	3.52	0.07
30HC03 71.004											
0.0211 0.0518	27	999	0.0705	4	1.09	1.31	1.10	1.33	9.99	9.99	9.99
0.0467 0.0861		59	0.0959	5	1.32	1.58	1.29	1.52	2.92	3.09	9.99
0.0844 0.1546			0.1222						3.78		
30HC04 71.005											
0.0183 0.0392	33	999	0.0744	5	1.01	1.21	1.04	1.25	2.26	2.32	9.99
0.0367 0.0859	41	74	0.1083	6	1.23	1.49	1.25	1.50	2.80	2.90	9.99
0.0839 0.1415			0.1690		1.53	1.82	1.55	1.83	3.53	3.72	0.02
30HC05 71.006							_				
0.0204 0.0458	30	999	0.0823	5	1.05	1.29	1.05	1.28	2.25	2.32	9.99
0.0430 0.0833			0.0668		1.30	1.55	1.30	1.53	2.87	2.97	9.99
0.0772 0.1547	43	107	0.1419	7	1.63	1.94	1.63	1.90	3.70	3.68	0.08

30HC06	71.007																		
0.0182		29	999	0.0	696	4	1.0	06	1.3	0	1.05	1.	26	2.1	7	2.	31	9.9	99
0.0438	0.0786	31	60	0.0	874						1.33								
0.0737		48	108	0.1	454						1.60								
30HC07	71.008																		
0.0203	0.0482	30	999	0.0	789	5	1.0	05	1.2	8	1.05	1.	25	2.2	28	2.	35	9.9	99
0.0433	0.0854	34			791						1.29								
0.0823	0.1497	50	114	0.1	392						1.63					-			
30HC08										-			-				•••		
0.0214		30	999	0.0	867	5	1.0	06	1.2	8	1.05	1.	26	2.3	39	2.	39	9.9	99
0.0442			72								1.31								
0.0891			119								1.61								
	71.010											_			_				
	0.0575	28	999	0.0	703	4	1.	13	1.3	7	1.11	1.	27	2.4	8	2.	58	9.9	99
	0.1108		69								1.40								
	0.1865		116								1.70								
	71.011									-									
	0.0434	27	999	0.0	609	4	1.	05	1.2	7	1.08	1.	31	2.3	33	2.	40	9.9	99
	0.0792		60								1.30								
	0.1483		108								1.59								
	71.012																		
	0.0314	43	999	0.0)530	3	1.	03	1.2	6	1.02	1.	24	2.2	29	2.	32	9.9	99
	0.0530	58	101	0.0	0862	5	1.	18	1.4	1	1.20	1.	42	2.7	74	2.	59	9.9	99
-	0.0980	59	160	0.0	0846	4	1.	42	1.6	8	1.40	1.	66	3.1	LO	3.	34	0.0	06
	71.013																		
	0.0431	44	999	0.0	0680	4	1.	03	1.2	6	1.03	1.	24	2.2	26	2.	17	9.9	99
0.0390	0.0727	43	87	0.0	0394	2	1.	17	1.3	8	1.16	1.	40	2.7	72	2.	79	9.9	99
	0.1026	51	138	0.0	0589	3	1.	39	1.6	53	1.37	1.	63	3.1	17	3.	42	0.0	02
	71.014																		
0.0244	0.0456	42	999	0.0	0498	3	1.	15	1.3	39	1.15	1.	39	2.5	56	2.	42	9.9	99
0.0426	0.0836	45	87	0.0	0549						1.30								
0.0805	0.1093	56	143	0.0	0972	5	1.	53	1.8	31	1.53	1.	80	3.4	45	3.	61	0.0	02
30LC04	71.015																		
	0.0421		999								1.16								
0.0410	0.0716	60	118	0.0	0806						1.36								
0.0700	0.1131	78	196	0.	1089	5	1.	53	1.8	32	1.50	1.	78	3.4	47	3.	57	0.0	09
	71.016																		
-	0.0439				0468						1.07								
	0.0747				0687						1.26								
	0.1049	66	155	0.	0754	4	1.	50	1.7	/8	1.48	1.	78	3.	38	3.	58	0.	07
	71.017					-	•	~~						-		~	10	~	~~
	0.0311				0445						1.00								
	0.0533					-												-	
	0.0903	49	135	0.	0805	4	1.	41	1.0	57	1.45	1.	13	2.	99	3.	10	0.	01
	71.018		000	•	0000	٨	٦	01		74	1 02	1	22	2	22	2	24	0	00
	0.0304				0608						1.13								
	0.0446				0530						1.29								
	0.0830	62	152	0.	0851	4	1.	20	1	55	1.23	1.	54	5.	05	5.	07	0.	UT.
	71.019			•	0422	2	1	01	1 -	20	1 02	7	22	2	21	2	10	0	00
	0.0316	41	999	0.	0422	2	1.	10	1.4	11	1 15	1	11	2.	65	2.	10	9.	99
	0.0672					C A	1.	10	1.4	±±	1.46	·	70	2.	25	2.	20	9.	99
	0.1013	52	157	0.	0851	4	1.	41	1.0	00	1.40		10	5.	30	э.	29	9.	99
	71.020		000	0	0601	٨	٦	14	1 -	27	1.15	г	36	2	61	2	53	a	90
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	0.0688				0826	-					1.54								
	0.1128	56	109	0.	0903	4	1.	55	1.0	50	1.04	-		5.	1	5.		0.	ΟT.
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	0.0375				1003						1.19								
	0.0583				0665	_	_	-			1.41								
0.05/3	0.1011	51	100	0.	0000	5		10				-					51	••	4

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0.0179 0.0356 76 999 0.1049 6 1.11 1.33 1.10 1.31 2.34 2.44 9.99 0.0342 0.0667 51 127 0.0669 3 1.22 1.45 1.23 1.45 2.77 2.73 9.99 0.0654 0.1085 74 201 0.1333 6 1.47 1.70 1.48 1.71 3.35 3.40 0.09 30LC03 69.114 0.0176 0.0343 59 999 0.0941 5 1.07 1.30 1.09 1.32 2.32 2.32 9.99 0.0329 0.0611 57 116 0.0779 4 1.24 1.46 1.26 1.48 2.72 2.72 9.99 0.0600 0.1057 63 179 0.0611 3 1.47 1.73 1.47 1.75 3.34 3.38 0.09 30LC04 69.115 0.0167 0.0298 58 999 0.0861 5 1.05 1.28 1.03 1.26 2.26 2.25 9.99 0.0274 0.0664 58 116 0.0818 4 1.15 1.41 1.18 1.42 9.99 9.99 9.99 0.0651 0.1065 53 169 0.0679 3 1.40 1.65 1.40 1.64 3.14 3.34 0.03 30LC05 69.116 9.9999 9.9999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 30LC06 69.117 9.9999 9.9999 999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 30LC07 69.118 0.0192 0.0353 76 999 0.0979 6 1.09 1.30 1.08 1.29 2.43 2.49 9.99 0.0331 0.0504 54 130 0.0790 4 1.16 1.37 1.17 1.40 9.99 2.79 9.99 0.0496 0.0961 52 182 0.0695 3 1.34 1.56 1.36 1.61 3.20 3.13 0.02 30LC08 69.119 9.9999 9.9999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 30LC09 69.120 9.9999 9.9999 999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 30LC10 69.121 0.0185 0.0333 109 999 0.1503 8 1.07 1.32 1.09 1.33 2.41 2.37 9.99 0.0308 0.0544 48 157 0.0806 4 1.18 1.46 1.18 1.44 2.71 2.67 9.99 0.0520 0.1050 68 225 0.0911 4 1.42 1.68 1.41 1.68 3.15 3.24 9.99 32HH01 71.022 0.1187 0.1909 89 999 0.0946 4 1.82 2.18 1.83 2.14 4.12 4.26 0.02 0.1856 0.3140 47 66 0.1685 6 2.10 2.45 2.07 2.41 4.76 4.81 0.02 0.3067 0.4590 74 140 0.3443 11 2.45 2.92 2.44 2.89 5.45 5.58 9.99 32HH02 71.023 0.1438 0.2292 23 999 0.0930 3 2.03 2.34 2.01 2.31 4.58 4.57 0.15 0.2178 0.3615 51 74 0.2545 8 2.41 2.84 2.30 2.55 5.05 5.26 0.25 0.3532 0.5655 70 144 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0.26 32III4 71.055 0.1089 0.2087 58 999 0.1154 4 1.85 2.17 1.84 2.14 4.09 4.23 0.02 0.2047 0.2795 78 136 0.1843 6 2.12 2.54 2.10 2.50 4.73 4.79 0.02 0.2742 0.4218 138 274 0.3239 10 2.41 2.84 2.37 2.83 5.35 5.52 0.05 32IL18 71.059 0.0923 0.1182 31 999 0.0644 2 1.54 1.84 1.56 1.84 3.63 3.75 9.99 0.1147 0.2025 54 84 0.1229 4 1.80 2.12 1.79 2.10 3.92 4.13 0.01 0.1986 0.2663 71 155 0.1586 5 2.14 2.50 2.08 2.46 9.99 9.99 9.99 32IIJ9 71.060 0.1103 0.1869 52 999 0.1185 4 1.82 2.10 1.80 2.10 4.03 4.19 0.01 0.1793 0.2403 59 111 0.1145 4 2.15 2.53 2.17 2.54 4.84 4.94 0.03 0.2345 0.3573 100 211 0.2304 7 2.47 2.91 2.45 2.89 5.34 5.50 0.02 28H001 79.022 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 28HO02 79.023 0.0163 0.0261 26 999 0.0876 4 0.98 1.16 0.98 1.14 2.28 2.09 9.99 0.0250 0.0480 35 61 0.0996 5 1.12 1.33 1.12 1.33 2.52 2.50 9.99 0.0467 0.0973 39 100 0.1016 5 1.38 1.61 1.32 1.56 3.21 3.05 0.02 28H003 79.024 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 9.999 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 28HO04 79.025 0.0215 0.0508 47 999 0.1322 7 1.20 1.43 1.18 1.41 2.67 2.53 9.99 0.0449 0.0998 44 91 0.0996 5 1.39 1.66 1.37 1.64 3.11 3.03 9.99 0.0934 0.1584 56 147 0.1491 7 1.66 1.95 1.70 1.99 3.93 3.64 0.01 28H005 79.026 9.9999 9.9999 999 9.999 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 9.999 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 28H006 79.027 0.0174 0.0368 52 999 0.1350 7 1.16 1.36 1.17 1.35 2.54 2.33 9.99 0.0338 0.0740 40 92 0.1234 6 1.31 1.52 1.30 1.50 2.82 2.79 9.99 0.0710 0.1229 56 148 0.1449 7 1.49 1.77 1.47 1.77 3.51 3.30 0.06 28H007 79.028 9.9999 9.9999 999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 28H008 79.029 0.0218 0.0559 48 999 0.1395 7 1.18 1.43 1.18 1.21 2.71 2.55 9.99 0.0530 0.1054 39 87 0.1037 5 1.40 1.66 1.38 1.64 3.19 2.95 9.99 0.1023 0.1787 74 161 0.2113 10 1.67 1.95 1.70 2.00 3.88 3.77 0.01 28H009 79.030 9.9999 9.9999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 28H010 79.031 0.0225 0.0620 46 999 0.1192 6 1.19 1.43 1.18 1.42 2.72 2.52 9.99 0.0592 0.1167 46 92 0.1416 7 1.51 1.83 1.51 1.81 3.38 3.15 9.99 0.1049 0.2238 91 183 0.2696 12 1.73 2.09 1.75 2.06 3.99 3.78 0.14 28H011 79.032 0.0211 0.0456 52 999 0.1333 7 1.17 1.40 1.19 1.40 2.65 2.47 9.99 0.0430 0.0827 38 90 0.1189 6 1.39 1.59 1.37 1.60 3.02 3.01 9.99 0.0815 0.1601 64 154 0.1798 8 1.63 1.88 1.64 1.91 3.67 3.60 0.01 28H012 79.033 0.0196 0.0583 52 999 0.1382 7 1.17 1.39 1.15 1.37 2.56 2.46 9.99 0.0490 0.1033 53 105 0.1560 8 1.34 1.63 1.37 1.66 3.13 2.99 9.99 0.1014 0.2105 77 182 0.2387 11 1.63 1.94 1.62 1.92 4.01 9.99 9.99 28H013 79.034 0.02160.0518619990.170091.221.471.241.452.612.629.990.05030.1147641250.171991.431.711.461.723.103.069.990.11340.1974651900.206391.681.971.691.983.863.770.14 28H014 79.035 0.0196 0.0454 51 999 0.1402 7 1.17 1.40 1.16 1.38 2.50 2.53 9.99 0.0445 0.1030 46 97 0.1416 7 1.38 1.65 1.36 1.62 3.08 2.94 9.99 0.1010 0.1884 64 161 0.1895 9 1.70 1.98 1.66 1.94 3.78 3.75 0.02 28H015 79.036 0.0210 0.0472 51 999 0.1490 7 9.99 9.99 1.22 1.44 2.62 2.56 9.99 0.0442 0.0942 49 100 0.1360 7 1.36 1.63 1.38 1.62 3.13 2.97 9.99 0.0926 0.2116 81 181 0.2766 12 1.67 1.98 1.65 1.94 3.79 3.64 0.02 281001 79.067 0.0148 0.0247 32 999 0.0619 3 1.00 1.16 9.99 9.99 9.99 2.11 9.99 9.9999 9.9999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 281002 79.068 0.0178 0.0363 100 999 0.1297 7 1.10 1.31 1.11 1.34 2.41 2.41 9.99 0.0356 0.0710 52 152 0.0883 4 1.33 1.57 1.29 1.54 2.85 2.74 9.99 0.0679 0.1274 79 231 0.1279 6 1.53 1.79 1.49 1.75 3.45 3.36 0.02 281003 79.069 0.0209 0.0430 70 999 0.0892 5 1.19 1.42 1.20 1.40 2.58 2.57 9.99 0.0395 0.0791 84 154 0.1225 6 1.36 1.60 1.34 1.58 3.01 2.87 9.99 0.0776 0.1332 66 220 0.1078 5 1.46 1.75 1.48 1.77 3.41 3.15 0.03 281004 79.070 0.0156 0.0243 40 999 0.0569 3 0.99 1.16 1.00 1.18 2.19 2.07 9.99 0.0225 0.0371 34 74 0.0541 3 1.11 1.32 1.11 1.32 2.48 2.43 9.99 0.0363 0.0751 49 123 0.0683 3 1.37 1.59 1.34 1.57 2.91 2.81 0.03 281005 79.071 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 28L006 79.072 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 9.999 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 281007 79.073 9.9999 9.9999 999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 281008 79.074 0.0172 0.0372 75 999 0.1168 6 1.13 1.34 1.13 1.34 2.43 2.38 9.99 0.0351 0.0831 70 145 0.1080 5 1.29 1.51 1.30 1.52 2.94 2.83 9.99 281009 79.075 9.9999 9.9999 999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 281010 79.076 9.9999 9.9999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 28LO11 79.097 0.0139 0.0222 23 999 0.0424 2 0.95 1.14 0.97 1.15 2.14 2.08 9.99 0.0199 0.0278 42 65 0.0547 3 1.06 1.20 1.07 1.25 2.50 2.30 9.99 281012 79.100 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 281013 79.103 0.0132 0.0199 32 999 0.0583 3 0.95 1.11 0.96 1.14 2.15 2.10 9.99 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 28LO14 79.106 9.9999 9.9999 999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 281015 79.109 0.0120 0.0191 29 999 0.0348 2 0.95 1.12 0.95 1.13 2.07 2.05 9.99 0.0171 0.0263 50 79 0.0739 4 1.06 1.26 1.02 1.24 2.33 2.30 9.99 0.0246 0.0484 42 121 0.0647 3 1.17 1.39 1.15 1.38 2.55 2.54 0.03 31HO01 79.037 0.0176 0.0429 41 999 0.1242 6 1.12 1.34 1.12 1.33 2.49 2.40 9.99 0.0379 0.0805 32 73 0.0740 4 1.33 1.55 1.31 1.55 2.96 2.94 9.99 0.0786 0.1612 49 122 0.1428 7 1.60 1.89 1.59 1.87 3.70 3.52 0.04 31H002 79.038 0.0206 0.0530 43 999 0.1270 6 1.16 1.37 1.16 1.38 2.62 2.43 9.99 0.0520 0.1109 31 74 0.0769 4 1.43 1.68 1.46 1.70 3.16 3.12 9.99 0.1074 0.1511 35 109 0.1003 5 1.67 1.95 1.70 1.96 3.78 3.84 9.99 31H003 79.039 0.0208 0.0594 42 999 0.1211 6 1.18 1.37 1.17 1.39 2.66 2.52 9.99 0.0581 0.1230 41 83 0.1132 6 1.44 1.69 1.43 1.68 3.35 3.27 9.99 0.1214 0.2258 67 150 0.1943 9 1.73 1.99 1.72 1.98 4.20 3.97 0.02 31H004 79.040 9.9999 9.9999 999 999 9.999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 9.9999 9.9999 999 999 9.9999 99 9.99 9.99 9.99 9.99 9.99 9.99 9.99 31H005 79.041 0.0151 0.0290 38 999 0.0901 5 1.11 1.32 1.10 1.30 2.38 2.34 9.99 0.0276 0.0623 36 74 0.0964 5 1.25 1.50 1.21 1.47 2.66 2.62 9.99 0.0602 0.1138 31 105 0.1169 5 1.46 1.73 1.45 1.74 3.35 3.22 0.04 31H006 79.042 0.0200 0.0544 36 999 0.0894 5 1.16 1.38 1.16 1.39 2.48 2.47 9.99 0.0503 0.1066 32 68 0.1009 5 1.41 1.67 1.42 1.68 3.10 3.00 9.99 0.1044 0.1974 68 138 0.1874 9 1.66 1.95 1.69 1.99 3.85 3.77 0.03

31H007 79.043				•							
0.0167 0.0299			0.0362						2.11		
0.0293 0.1002			0.1740						3.16		
0.0987 0.1615	44	112	0.1198	6	1.6/	1.95	1.66	1.96	9.99	3.73	0.01
31H008 79.044				_				-			
0.0224 0.0454			0.1448						2.67		
0.0432 0.0929			0.1126						3.14		
0.0881 0.1626	52	138	0.1644	8	1.62	1.92	1.67	1.98	3.96	3.83	0.13
31H009 79.045											
0.0254 0.0627			0.0701						2.74		
0.0606 0.1092			0.0835						3.52		
0.1072 0.1782	50	105	0.1434	7	1.73	2.02	1.74	2.03	4.09	3.96	0.13
31HO10 79.046											
0.0188 9.9999											
9.9999 9.9999	-								-		
9.9999 9.9999	999	999	9.9999	99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
31HO11 79.047											
0.0164 0.0267	21		0.0630						2.27		
0.0236 0.0495			0.0725						2.55		
0.0482 0.0873	30	78	0.0873	4	1.35	1.60	1.37	1.63	3.20	2.97	9.99
31H012 79.048											
0.0185 0.0301			0.0809						2.61		
0.0291 0.0670	27		0.0800						9.99		
0.0646 0.1254	39	98	0.1001	5	1.51	1.77	1.51	1.78	3.31	3.17	0.08
31H013 79.049											
0.0129 0.0230			0.0759						2.15		
0.0218 0.0553	25		0.0609						2.48		
0.0545 0.1196	27	79	0.0845	4	1.41	1.64	1.41	1.64	3.22	3.13	0.03
31H014 79.050								_			
0.0213 0.0444			0.0531						2.63		
0.0424 0.0881			0.0959						3.11		
0.0864 0.1421	57	115	0.1453	8	1.56	1.83	1.61	1.90	3.73	3.61	0.08
31H015 79.051								_		-	
0.0219 0.0417			0.0892								
0.0395 0.0938											
0.0922 0.1322	31	100	0.0875	4	1.62	1.88	1.61	1.89	3.91	3.54	0.13
311001 79.077							-	-			
0.0176 9.9999											
9.9999 9.9999											
9.9999 9.9999	999	999	9.9999	99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
311002 79.078					-			-			
0.0204 0.0400			0.0581								
0.0390 0.0800											
0.0790 0.1332		170	0.1101	5	1.62	1.91	1.62	1.93	3.70	3.70	0.02
311003 79.079								1 00	~ ~ ~		
0.0198 0.0401											
0.0375 0.0854											
0.0841 0.1576	95	199	0.1524	7	1.54	1.82	1.55	1.83	3.70	3.48	0.13
311004 79.080											
0.0126 9.9999											
9.9999 9.9999											
9.9999 9.9999		999	9.9999	99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
311005 79.081				-							
0.0176 0.0370											
0.0354 0.0822											
0.0803 0.1067		170	0.0913	4	1.55	1.81	1.55	1.82	3.53	3.38	0.06
311006 79.082				-							
0.0140 0.0244											
0.0240 0.0528			0.0570								
0.0511 0.0865	58	127	0.0782	4	1.37	1.62	1.38	1.63	3.08	3.02	0.06

311007											a sala	
0.0199				0.0577						2.69		
0.0388				0.0406						2.96		
0.0597		61	131	0.1086	5	1.58	1.87	1.56	1.84	3.59	3.34	0.07
311008												
0.0174	9.9999											
9.9999	9.9999	999	999	9.9999	99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
9.9999	9.9999	999	999	9.9999	99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
311009	79.085											
0.0224	0.0445	42	999	0.0594	3	1.18	1.40	1.17	1.37	9.99	9.99	9.99
0.0428	0.0580	33	75	0.0621	3	1.33	1.57	1.32	1.58	3.14	3.08	9.99
0.0552	0.1174	67	142	0.1048	5	1.51	1.80	1.48	1.77	3.46	3.35	0.02
311010	79.086											
0.0120	0.0220	30	999	0.0393	2	1.00	1.17	1.00	1.18	2.23	2.17	9.99
0.0200	0.0188	33	63	0.0540	3	1.11	1.34	1.11	1.34	9.99	9.99	9.99
	0.0413	35	98	0.0392	2	1.14	1.35	1.15	1.37	2.53	2.46	9.99
	79.098											
	9.9999	999	999	9.9999	99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
	9.9999			9.9999								
	9.9999			9.9999								
•	79.101											
	0.0189	17	999	0.0135	1	0.96	1.14	0.97	1.12	2.16	2.15	9,99
	0.0387			0.0612						9.99		
	0.0560	40		0.0622						2.83		
	79.104	40	00	0.0022	-	2.022		/	1.07	2.00	2.00	0.02
	0.0229	27	999	0.0355	2	0 99	1.18	0.96	1.13	2.18	2 13	9 99
	0.0397			0.0430						2.54		
	0.0713			0.0658						3.05		
	79.107	-10	TOT	0.0000	5	1.52	1.07	1.01	1.00	5.05	2.50	0.00
	9.9999	000	<u>a</u> aa	9.9999	99	9 99	9 99	a aa	9 99	a aa	a aa	9 99
	9.9999											
	9.9999											
	79.110		555	9.9999	"		5.55	5.55	2.22	9.99	9.99	9.99
	0.0224		000	0.0358	2	0 98	1 16	0 97	1 16	2.31	2 13	0 00
	0.0224											
				0.0658								
	0.0685		90	0.0000	5	1.20	1.00	1.30	1.52	2.04	2.01	0.02
	79.052		000	0.1019	5	1 15	1 36	אר ר	1 22	2 12	2 12	0 00
	0.0369			0.1019								
	0.0808			0.1171								
			100	0.11/1	5	T.00	1.02	1.00	1.03	9.99	9.99	0.02
	79.053 0.0616		000	0.1015	5	1 16	1 27	1 16	1 27	2 65	2 51	0 00
				0.0966								
	0.0989			0.1324								
	0.1521		T T T	0.1324	0	1.00	1.90	T.00	1.99	3.90	3.00	0.05
-	79.054		000	0.0985	5	1-10	1 12	1 17	1 40	2 60	2 51	0 00
	0.0455			0.1223								
	0.0818			0.0838								
	0.1208		101	0.0030	4	1.04	1.00	1.00	1.0/	2.59	3.21	0.07
	79.055		000	0.0817	1	0 95	1 12	0 95	1 12	2 20	2 09	0 00
	0.0217			0.0623								
	0.0476			0.1275						3.19		
	0.0789		92	0.12/5	0	1.00	1.55	1.04	1.00	2.19	2.00	0.05
	79.056		000	0.0509	2	0 07	1 12	0.05	1 12	2 00	2 07	0 00
	0.0185			0.0509								
	0.0423			0.0644								
	79.057		69	0.0699	4	1.24	1.40	1.21	1.43	2.11	2.00	0.05
			000	0 0000	00	0.00	0.00	0 00	0 00	0.00	0.00	0.00
	9.9999											
	9.9999											
2.2222	2.2229	222	222	9.9999	99	9.99	9.99	9.99	9.99	9.99	9.99	9.99

33H007 79		40	000	0 1	1100	c	1		1 22	7	00	1 0			0.01	0 00
0.0177 0.			999 71		L129											9.99 9.99
0.0362 0			116													9.99
33HO08 79		40	TTO	0.1	1214	0	1.	57	1.00	1.	57	1.0	э.	3.59	3.43	0.10
0.0171 0		40	ممم	0.1	1139	6	1	00	1 22	٦	רר	1 2	4 -	2 51	2.33	0 00
0.0305 0)650										2.33	
0.0640 0			112												3.31	
33HO09 79		45	112	0.1	L-4 / L	'	T • .	40	1.70	1.	40	1.7	<u>,</u>	5.52	2.21	9.99
0.0209 0		38	999	0 -	1052	5	1	17	1 40	٦	10	7 1		2 61	2.47	<u>a</u> aa
0.0399 0					0842										2.98	
0.0847 0			104												3.69	
33HO10 7				•••		•		~~	1.00		00				0.05	0.05
0.0196 0		37	999	0.0	0970	5	1.	19	1.38	1.	19	1.39	9 2	2.56	2.49	9,99
0.0410 0					0883										2.94	
0.0791 0		57	123	0.3	1784										3.47	
33H011 7	9.062															
0.0219 0	.0399	32	999	0.0	0850	4	1.	18	1.40	1.	20	1.4	2 2	2.60	2.56	9.99
0.0391 0	.0813	34	66	0.0	0926	5	9.	99	9.99	1.	36	1.6	1 :	3.18	2.91	9.99
0.0774 0	.1435	49	115	0.	1507	7	9.	99	9.99	1.	60	1.8	5 3	3.76	3.59	0.02
33H012 7																
0.0132 0					0457										2.10	
0.0182 0																9.99
0.0560 0		14	64	0.	0394	2	1.	33	1.58	1.	30	1.5	5 3	3.11	2.75	0.02
33H013 7				_			_									
0.0177 9																
9.9999 9																
9.9999 9		999	999	9.	9999	99	9.	99	9.99	9.	.99	9.9	9 9	9.99	9.99	9.99
33H014 7		40	000	0	1100	c	٦	10	1 22	7	10	1 2	<i>.</i> .	0 40	2 20	9.99
0.0170 0					1198 0912											9.99
0.0409 0					1672											0.09
33HO15 7		50	120	0.	10/2	0	1.	07	1.91	ہ ط	04	1.7	ς.	2.00	3.02	0.09
0.0178 0		58	999	0.	1638	8	1.	12	1.33	1	13	1.3	२ '	2 48	2 39	9.99
0.0483 0																
0.0891 0																
331001 7		0,	100		2000	-		•.				1.0		••••	0.01	5.55
0.0135 9		999	999	9.	9999	99	9.	99	9.99	9.	.99	9.9	9 9	9.99	9.99	9.99
9.9999 9																
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331002 7																
0.0149 9																
9.9999 9																
9.9999 9	.9999	999	999	9.	9999	99	9.	99	9.99	9.	99	9.9	9 !	9.99	9.99	9.99
331003 7																
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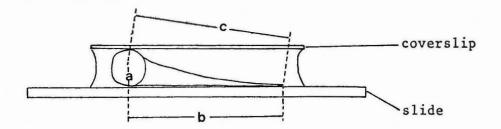
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31HW07		10	000	0 1010	C	1 00	1 50	1 07	1 50	0 70	0 71	0 00
0.0243				0.1219		1.28						
0.0624		59		0.1934		1.56						
0.1540		81	180	0.2432	11	1.86	2.14	1.87	2.15	4.20	4.03	0.04
31HW08				2								
	0.0539			0.0915		1.13						
0.0512		43		0.1144		1.39						
0.1024		57	132	0.1761	8	1.75	2.05	1.75	2.06	3.74	3.74	0.04
	78.050											
0.0196	0.0488	33	999	0.1023	5	1.20	1.43	1.20	1.42	2.58	2.59	9.99
0.0475	0.1172	44	77	0.1126	6	1.48	1.76	1.47	1.75	3.21	3.15	9.99
0.1159	0.1863	57	134	0.1969	9	1.76	2.06	1.77	2.07	3.94	3.79	0.03
31LW01	78.052											
	0.0323	105	999	0.1454	8	1.19	1.39	1.20	1.43	2.60	2.61	9.99
	0.0709			0.0624		1.21						
	0.0899			0.0758		1.46						
	78.053	50	200		•			1.00	1112		0.00	0.05
	0.0442	63	999	0.0981	5	1.21	1.44	1.20	1 44	2.73	2.69	9 99
	0.0796			0.0860		1.37						
	0.1328			0.1344		1.61						
	78.054	15	199	0.1344	0	1.01	1.92	1.02	1.95	3.70	J.40	0.11
	78.054 9.9999	000	000	9.9999	00	0 00	0 00	0 00	0 00	0 00	0 00	0 00
	9.9999			9.9999								
	9.9999	999	999	9.9999	99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
	78.055											
	0.0238			0.0536		1.19						
	0.0468			0.0548		1.19						
	0.0833	49	131	0.0855	4	1.36	1.60	1.38	1.62	3.10	3.09	0.01
	78.056											
	9.9999			9.9999								
	9.9999			9.9999								
	9.9999	999	999	9.9999	99	9.99	9.99	9.99	9.99	9.99	9.99	9.99
711W06	78.057											
	0.0388			0.0720								
0.0380	0.0853	68	122	0.1089	5	1.33	1.58	1.32	1.56	3.00	2.94	9.99
0.0804	0.1348	77	199	0.1303	6	1.63	1.92	1.58	1.88	3.58	3.48	0.02
	78.058											
	0.0550											
0.0500	0.1067	64	111	0.0837	4	1.51	1.80	1.52	1.80	3.25	3.14	9.99
0.1041	0.1753	115	226	0.1887	9	1.73	2.04	1.74	2.05	3.78	3.81	0.02
	78.059											
	0.0605	66	999	0.1016	5	1.24	1.46	1.24	1.46	2.75	2.70	9.99
	0.1092			0.1259								
	0.1740			0.1632								
	78.060									_ ,		
0.0102	0.0380	55	999	0.0799	4	1.20	1.39	1.17	1.39	2.63	2.50	9.99
0.0262	0.0765	72	127	0.1292	6	1.37	1.62	1.35	1.61	2.99	2.90	9.99
0.0303	0.1309	106	222	0.1480	7	1.61	1.86	1.59	1.88	3.48	3.50	0.02
0.0722	0.1209	100	200	0.1400	,	2.01	2.00	,			2.50	0.02

APPENDIX F

Systematic Measurement Errors

The tapered fangs lay on the microscope slides in a non-planar orientation (see below). The extent to which the measured length underestimated the true length therefore depended upon the width of the base of the fang. Using Stradling's (1978) equation relating these two variables, estimates of the error have been calculated for two hypothetical fang lengths.



a = radius of the fang base b = measured length c = true length % error of measurement = $\frac{c-b}{c} = \frac{\sqrt{b^2+a^2}}{\sqrt{b^2+a^2}} \frac{b}{b}$ 100

Example 1

For a fang 1.0 mm long. Width estimated as 0.32 mm Error 1.26%

Example 2

For a fang 5.0 mm long. Width estimated as 1.72 mm Error 1.45%

APPENDIX G

Linear Regression Programme

The follow programme was adapted by Dr. G. Ettershank to perform simple linear regression and correlation, and to provide the sums of squares required for the comparison of the slopes.

SUBROUTINE LINREG (XARRAY, YARRAY, NN) DIMENSION XARRAY (2000), YARRAY (2000) REAL MSGR, MSR, MSDREG, MSW С LINREG COMPUTES SIMPLE REGRESSION LINES FOR DATA С С PRESENTED IN TWO ARRAYS, XARRAY AND YARRAY. THERE ARE MN С POINTS. С LP=6 С ZERO X-ACCUMULATORS С C SUMX=0.0 SUMXSQ=0.0 SUMN=NN SUMY=0.0 SUMYSQ=0.0 С С COMPUTE SUMS OF X, Y AND X-SQ, Y-SQ AND CROSS PRODUCTS. С 10 DO 90 J=1,NN X=XARRAY(J) Y=YARRAY(J) SUMX=SUMX+X SUMY=SUMY+Y SUMXSQ=SUMXSQ+X*X SUMYSQ=SUMYSQ+Y*Y SUMXY=SUMXY+X*Y 90 CONTINUE С С CALCULATE X SUMS OF SQUARES C XBAR-SUMX/SUMN CTX=SUMX*SUMX/SUMN SSQX = SUMXSQ - CTXC C CALCULATE Y SUMS OF SQUARES С YBAR=SUMY/SUMN CTY = (SUMY * SUMY) / SUMNSSY = SUMYSQ - CTYSSXY=SUMXY-(SUMX*SUMY)/SUMN EXPSS =(SSXY*SSXY)/SSQX UNXPSS=SSY-EXPSS С С COMPUTE DEGREES OF FREEDOM С IDFTOT=NN-1 DFIOT=IDFIOT IDFREG=1 DFREG=1.0 IDFDRG =NN-2 DFDREG=IDFDRG

```
C
      COMPUTE MEAN SQUARES AND THIER SIGNIFICANCE
C
C
      MSR = EXPSS
      MSDREG=UNXPSS/DFDREG
      FR = MSR/MSDREG
C
      COMPUTE SIGNIFICANCE OF F"S
C
C
      SIGR = PROBF (FR, IDFREG, IDFDRG)
С
C
      COMPUTE REGRESSION COEFFICIENT AND Y INTERCEPTS
C
      B = SSXY/SSQX
      YBAR = SUMY/SUMN
      A = YBAR - (B * XBAR)
C
С
      COMPUTE STANDARD ERROR OF B AND DEGREES OF FREEDOM
C
      STDERB = SQRT (MSDREG / SSQX)
      IDFB = NN - 2
C
      CALCULATE PRODUCT-MOMENT CORRELATION COEFFICIENT
C
C
      PMCC=SSXY/(SQRT(SSQX*SSY))
C
C
      PRINT HEADINGS AND OUTPUT.
C
      WRITE(LP,257)A,B
  257 FORMAT(1X, 15X, "REGRESSION EQUATION IS Y = ", F10.5,
     *" + ",F10.5," X")
      WRITE (LP, 258) STDERB, IDFB
  258 FORMAT (//, 15X, "STANDARD ERROR OF SLOPE IS ",
     *F10.5,/,1X,15X,"WITH ",14," DEGREES OF FREEDOM",/)
      WRITE (LP, 259) XBAR, YBAR
  259 FORMAT(1X, 15X, "XBAR = ", F10.4, /, 16X, "YBAR = ", F10.4, ///)
      WRITE (LP, 260) PMCC
  260 FORMAT(1X, 15X, "PRODUCT-MOMENT CORREL.COEF. IS ", F10.5)
      WRITE(LP,261)SSQX,SSY,SSXY
  261 FORMAT(1X,/,15X,"SUM OF SQUARES FOR X = ",F10.4,
      */,15X,"SUM OF SQUARES FOR Y = ",F10.4,/,15X,
      *"SUM OF CROSS PRODUCTS = ",F10.4)
      WRITE(LP, 250)
      WRITE(LP,255)
      WRITE (LP, 256) IDFREG, EXPSS, MSR, FR, SIGR, IDFDRG, UNXPSS,
      *MSDREG, IDFTOT, SSY
  250 FORMAT (///25X, " ANALYSIS OF VARIANCE ",//)
  255 FORMAT(1X,/,3X,"SOURCE",8X,"DF",8X,"SS",8X,"MS",
      *8X, "F", 11X, "PROB")
  256 FORMAT(1X,/," REGRESSION", 2X, 16, 6X, F8.4, 2X, F8.4, 2X,
      *F10.3,2X,F8.5,/,1X,"UNEXPLAINED",1X,I6,6X,F8.4,2X,
      *F8.4,//,1X,"TOTAL",7X,16,6X,F8.4,//)
      END
```

```
FUNCTION PROBF(F,N1,N2)
  PROBF=1.0
  IF(F*N1*N2)1,1,2
2 IF(F.LT.1.0)GOTO 5
  A=N1
  B=N2
  FF=F
  GO TO 10
5 A=N2
  B=N1
  FF=1./F
10 AA=.2222222222/A
  BB=.2222222222/B
   Z=ABS((((1.-BB)*FF**.333333333-1.+AA)/SQRT(BB*FF**.666666666667+AA))
   IF(B.IT.4.0) Z=Z*(1.+0.08*Z**4/B**3)
   PROBF=.5/(1.+Z*(.196854+Z*(.115194+Z*(.000344+Z* .019527))))**4
   IF(F.LT.1.) PROBF=1.-PROBF
 1 RETURN
   END
```

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