A Comparative Study of Life Histories in the Grasshoppers, Chorthippus brunneus and Myrmeleotettix maculatus in a Sand Dunes Habitat

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For my parents.

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by David Atkinson.

SUMMARY

The aims of the study were (i) to describe the variation in life histories in two co-existing grasshopper species at three different sites in a sand dunes area, and (ii) to assess the relative importance of a wide range of potential causes of the variation by examining ecological correlates of the life history traits and covariation between traits.

The sites differed in topography, rates of evaporative water loss, vegetational structure, amounts of grass and its species-composition, and in their amounts of bare sand.

Grasshopper densities, the periods between second-instar moult and adult moult, and the rates at which the grasshoppers were lost from the populations also differed between the sites, years, and species.

Consistent significant differences in adult size between sites were found in each sex of each species in each year, but none of eleven indices of adult competition (for space, grass, grass with thin-edged leaves, and sandy areas) showed a positive correlation with adult size; nor did the degree of evaporative water loss at each site.

However, those populations containing earlier-emerging adults tended to have larger adults. Also, within all populations of M.maculatus examined, and in one population of C.brunneus, earlier-emerging individuals were larger than later ones. The possible reasons for the relationship were then

explored by constructing a simple graphical model which predicted the nature of covariation in moulting date and body size of grasshoppers subject to different constraints on growth. By comparing the predictions of various forms of the model with the data, a number of reasonable hypotheses, *a priori*, were thereby eliminated.

Heavier adult females laid heavier pods containing more eggs. These two linear relationships were able to explain the significant difference in pod weight between two sites, and differences in pod weight and egg number in the two species.

M.maculatus laid heavier eggs than *C.brunneus*, and the eggs of the former species showed significant differences between sites and years. These intraspecific differences in *M.maculatus* could be explained by the fact that females with longer hind femurs (an index of size at adult moult) laid heavier eggs. Mean egg weights also correlated positively with estimates of the amount of local competition for grasses with thin-edged leaves, and to a lesser extent with the degree of evaporative water loss at the sites.

I have suggested that adults - by virtue of their larger size and greater motility - are more immune than hatchlings to the pressures exerted at the sites by competition for thin-edged grasses and by risks of desiccation. This suggestion would explain why egg size, but not adult size, correlates with these pressures.

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CHAPTER 1: **A general introduction**

SUMMARY

1. Major developments in the study of adaptive life histories are reviewed, with especial emphasis on concepts and theories referred to in the present study.

2. Differences in the effects of historical (phylogenetic) constraints can override adaptive variation, as can differences in the effects of constraints imposed on an animal by its immediate environment.

3. The comparative method of studying life histories allows us to assess the relative importance of a number of competing hypotheses which can potentially explain some observed variation in life histories, and will be used in the present study.

4. The life histories of British grasshoppers, and particularly _C.brunneus_ and _M.maculatus_, are outlined.

1.1. INTRODUCTION

This chapter has two main sections. The first is a general introduction to the study of life histories (Section 1.2), and the second introduces this particular investigation into the causes of variation in the life histories of the grasshoppers _Chorthippus brunneus_ (Thunb.) and _Myrmeleotettix maculatus_ (Thunb.) at Ainsdale Sand Dunes National Nature Reserve, Merseyside (Section 1.3).

1.2. VARIATION IN LIFE HISTORIES

1.2.1. _Recent interest in life-history evolution_

The study of life histories has recently progressed from descriptions of natural history to an area of science containing a body of theory which predicts what sorts of life histories should evolve in specified ecological circumstances (Stearns, 1976).

The current high level of interest in life-history evolution is both recent and increasing rapidly. According to one estimate (Stearns, 1980) the rise in the numbers of papers on life-history evolution between 1975 and 1979 was exponential, increasing at two to three times the rate of science as a whole, whereas prior to 1975 the publication rate was lower and more variable. The subject has been extensively reviewed (Giesel, 1976; Stearns, 1976, 1977, 1980; Calow, 1978, 1979; Horn, 1978; Horn and Rubenstein, 1984; Begon and Mortimer, 1981; Begon *et al.*, in press) and therefore a detailed review here would only add to the multiplicity. Instead, I shall give a brief account of what I perceive to be the major developments in the study of life histories, stressing those aspects which are particularly relevant to this study of grasshopper life-history variation. In so doing, I introduce and define some of the basic concepts that will be referred to later in the thesis. The next section therefore acts both as a critical review and as a glossary.

1.2.2. Some major developments in the study of life histories

1.2.2.1. Early demographic models

Current studies of life histories have brought together ideas originally conceived in separate areas of ecology, evolution, and physiology.

Lotka (1913) produced a demographic model which related the life table and fecundity schedule of a population in stable age distribution to its growth rate, r. This model expressed formally the clear link between the basic life history and demographic change, and has been central to most subsequent theoretical work. In particular, the model related the average number of young born to a female aged x (b_x) and the probability of surviving to age x (l_x) for every age (**x**=0 to maximum age attained, **x**=max.) to the rate of population increase.

Demographic theory was linked to the adaptive value of life histories by Cole (1954) who considered the relative contributions to population growth of organisms with different birth rates, ages at first reproduction, and number of reproductive events per lifetime. He concluded that an organism which gives birth to **n**+1 offspring before dying will contribute as much to population growth as an immortal organism producing **n** offspring at regular intervals. Organisms which breed once and then die are termed **semelparous**, whereas repeated breeders are termed **iteroparous**. Stearns (1976) equated semelparous with annual, and iteroparous with perennial life histories, but some organisms, such as the grasshoppers in this study, may be both annual and iteroparous. Fritz et al. (1982) also make this point. The results of Cole (op. cit.) have since been shown to be based on a hidden assumption - that all juveniles survived to adulthood and that perennial adults lived forever - which when relaxed produces a more general result (Charnov and Schaffer, 1973). According to this more general proof, the important determinant of how many times an organism should breed is the ratio of the juvenile mortality rate to that of the adult between each reproductive attempt. If parental survival between reproductive attempts is high compared with juvenile survival, the organism should breed repeatedly and not recklessly, whereas if adult and juvenile survivorship show the opposite trend, semelparity is favoured. This theory only applies to populations with overlapping generations, however, and not, therefore, to the grasshoppers in this study.

1.2.2.2. Reproductive value

Another demographic concept central to theories of life-history evolution (or theories of adaptive life histories; Horn and Rubenstein, 1984) is that of **reproductive value (RV)** (Fisher, 1930) which is the average number of young that a female can expect to have over the remainder of her life, discounted back to the present. This definition incorporates the product of the probability of surviving to each age and the expected number of offspring to be produced at each age, summed over every age ($\sum_{t}^{max.} l_x b_x$), and also the fact that in a growing population of organisms with overlapping generations an offspring which is produced early in life will form a larger proportion of the total population at that time (i.e. has a higher value) than an offspring produced later - the converse is true for declining populations. Reproductive value can therefore be expressed as:

$$\sum_{t}^{max.} l_x \, b_x \, e^{-r(x-t)}$$

For the above population, which is growing at the *per capita* rate of r, young born $x-t$ time intervals in the future should be discounted by $e^{-r(x-t)}$ because they will face $e^{r(x-t)}$ times as many competitors as those at time t.

This equation can, however, be simplified for animals such as grasshoppers which have discrete (non-overlapping) generations because the value (as defined above) of an early-born offspring will be equivalent to that of a later one. The simplified form of reproductive value

$$\sum_{t}^{max.} l_x \, b_x$$

can therefore be equated with lifetime reproductive success from time t.

1.2.2.3. Trade-offs

It is clear from an examination of the above equation that a maximal lifetime reproductive success can be achieved by producing an enormous number of offspring immediately after birth and continuing this pattern of reproduction forever. Such an unbridled life history does not exist in nature because there are constraints which limit the capabilities of organisms (Maynard Smith, 1978; Law, 1979a). For example, food may be limiting, or the organism may have a restricted range of developmental, physiological or behavioural responses to selection pressures. Part of the art of building useful optimization models of life histories is being able to incorporate into them realistic constraints. If time and materials are limiting, their diversion by an organism from one activity (e.g. growth) to another (e.g. reproduction) may have detrimental effects on the efficacy of the first activity. A negative correlation between activities, such as growth and reproduction, which utilize a common limiting resource is called a **trade-off**.

1.2.2.4. Trade-offs with reproduction

The trade-off between present reproduction and future reproductive value was explored by Williams (1966a,b) who coined the terms reproductive effort, the cost of reproduction, and residual reproductive value.

He thought of **reproductive effort** "in terms of physiological stress and risk of life" resulting from reproduction, and, when discussing the relative amounts of effort expended by small and large fish, said, "There is no way of obtaining a numerical measure of reproductive effort, but it is possible to rank different kinds of breeding habits according to which involves the greater and which the lesser effort and sacrifice" (Williams, 1966a). Hirshfield and Tinkle (1975) defined reproductive effort more narrowly but more precisely as "the proportion of total energy procured over a specified and biologically meaningful time interval, that an organism devotes to reproduction". However, this narrowly-defined measure has been shown to be inadequate, in certain circumstances, as an expression of the risks associated with reproduction (Calow, 1979; Tuomi *et al.*, 1983). Bell (1980) says "The measurement of reproductive effort is technically difficult and laborious, and the results meaningless unless they can be related to effects on fitness". In order to avoid the problems associated with the term reproductive effort, therefore, I do not refer to it again in this thesis. Instead, I talk about the allocation of limited resources to reproduction and the costs of reproduction.

The **cost of reproduction** describes the reduction in future reproductive value as a consequence of current reproduction (Williams, 1966b; Calow, 1979; Law, 1979b; Bell, 1980). Nonetheless, Stearns (1976) only partially defined it when he described it as "the marginal increase in adult mortality between time t and time t+1 caused by the decision to commit a certain proportion of available resources to reproduction at time t". This definition ignored the potential trade-off between current reproduction and future reproduction.

Residual reproductive value (RRV) is simply the future reproductive value or the RV after excluding the expected number of offspring to be born in the present reproductive attempt (b_t). For a population which is not growing or which has non-overlapping generations, RV can be expressed as its present and future components thus:

$$RV = b_t + \sum_{t+1}^{max.} l_x b_x$$

This distinction makes clear the potential trade-off between current reproduction and reproduction and survival in the future, and has provided the basis of much theoretical work (Schaffer, 1974a,b; Pianka and Parker, 1975; Bell, 1980; Goodman, 1982). These workers suggest that an optimal life history, that is one which makes a maximal genetic contribution to the future of the population, can be achieved by behaviour that maximizes reproductive value at each age. Indeed, Goodman (1982) has provided a proof that maximizing reproductive value at each age ensures a life history that is unbeatable by slightly different life histories.

1.2.2.5. r- and K-selection

Another major contribution to recent ideas on the organization of life histories came from Pianka (1970) who applied the notion of r- and K-selection (MacArthur and Wilson, 1967) to the evolution of life histories. The terms r- and K-selection were derived from the logistic equation which describes density-dependent population growth. **r-selection** represents the selection pressures on organisms when the population is growing exponentially (the *per capita* growth rate is r) and is free from the effects of crowding. The population is kept at low densities by density-independent disasters. At the other extreme, **K-selection** applies to those selection pressures operating on organisms when the population size is normally at or near to the carrying capacity, K, for the environment. Pianka (op. cit.) proposed that r-selection would favour rapid development (and consequently a small size), and early "big-bang" reproduction (leading to a shorter lifespan) with many (and consequently smaller) offspring produced. Conversely, in crowded conditions, K-selection would favour an ability to compete which, Pianka suggested, would increase with body size. Therefore, K-selection would favour large adults (and consequently with a long developmental period and delayed reproduction) and large offspring (and consequently fewer of them). The survival of offspring would be enhanced in a crowded environment by a period of extended parental care. This would result in the parents taking fewer risks when reproducing until parental care had been completed, and therefore K-selected organisms would be likely to have a longer adult as well as juvenile stage of the life-history. However, this does not lead logically to the conclusion of Pianka (op. cit.) that K-selected organisms should be iteroparous. They could, for example, put a lot of parental investment into the rearing of a single brood during a long adult life. Pianka's prediction that r-selection should favour a single "big-bang" reproductive event (semelparity) and K-selection should favour iteroparity is not wholly convincing for another reason. M. Begon (pers. comm.) argues that semelparity may not enable an organism to breed earlier than an iteroparous one since it could take longer to produce a large number of offspring than it would to produce one offspring after another in rapid succession. Indeed, the first few offspring produced by an iteroparous organism are likely to be released earlier than the whole brood produced by an semelparous organism which starts reproducing at the same time.

The combination of traits expected under conditions of r- and K-selection have been described in the appropriate environmental conditions for populations of dandelions, Taraxacum officionale, (Gadgil and Solbrig, 1972), and the annual meadow grass, Poa annua, (Law et al., 1977).

There are, however, a number of limitations of the r-K scheme caused by assumptions built into the theory which are unstated. The theory does not apply, for instance, to organisms which experience different environmental conditions in the adult and juvenile stages. Many amphibians and holometabolous insects are obvious examples of organisms which may not experience degrees of competition which are consistently higher (or lower) in both the adult and juvenile stages than the competition experienced by other organisms with which their life histories are being compared. It is conceivable, for instance, that one population or species experiences a higher density-dependent mortality in the juvenile stage than another population or species but a lower density-dependent mortality and reduced reproduction in the adult stage. This argument may, however, apply to all organisms, and not just those with complex life histories. For example, a population of grasshoppers in which the adults experience higher levels of competition than those of another population may exhibit lower levels of juvenile competition if either the habitat changes during the season or the way the grasshoppers perceive it changes. The range of food sizes available may increase as the grasshopper increases in size, for example (as discussed in Chapter 6).

Another assumption of the theory is that density-dependent factors exert stronger selection pressures favouring a large body size than do density-independent factors. This assumption was violated by a pair of populations of the rough winkle, Littorina rudis (Hart and Begon, 1982), one of which experienced less severe competition yet had larger shells and bodies. This result is probably due to the largely density-independent selective effect on body size of predation and crushing by boulders being stronger than the effects of competition. In addition, in the population in which competition was most severe, there was probably selection for not outgrowing the sizes of the crevices in which the winkles lived and which were in short supply. The general conclusion is that other selection pressures on body size, besides that for competitive ability, should also be taken into account when the causes of life-history variation are being considered. In this study of grasshopper life histories, I relate not only indices of competition to the size of adults and of eggs but also measures of desiccation stress (Chapters 4 and 6).

1.2.2.6. Life-history tactics

The theory of r- and K-selection predicts differences in groups of traits, or tactics, rather than differences in only a single trait. A **tactic** is a set of co-adapted traits designed by natural selection, to solve particular ecological problems (Stearns, 1976).

A tactic is not qualitatively different from a trait because what constitutes a trait can be variously defined in the first place; a tactic is therefore just a more complex adaptation.

Differences between some ill-defined traits may not in themselves appear to be adaptive. Lewontin (1979) noted that "The yellow color of the Malpighian tubules of an insect cannot itself be the subject of natural selection since that color can never be seen by any organism. Rather it is the pleiotropic consequence of red eye pigment metabolism, which may be adaptive." Notwithstanding the element of illogicality in Lewontin's argument, a valid general point can be made: students of adaptive phenotypic variation should take care how they define the phenotypic unit or "trait", the variation in which they intend to investigate.

An example more relevant to this study is provided by Berven (1982). After a detailed study of life-history variation and covariation in populations of wood frogs, Rana sylvatica, he hypthesized that adult size varied between populations because large adults unavoidably produced large eggs, and that selection pressures on egg size therefore caused the variation in adult size. In this example, egg size would be subject to **direct selection**, and adult size to **indirect selection** (in the same way that the yellow colour of the Malpighian tubules would have been in the previous example).

In order to investigate as fully as possible the adaptive significance of a trait, therefore, we should relate the variation in a trait to the rest of the phenotype. The complete phenotype is really the ultimate tactic. Students of adaptive life histories implicitly try to discover how many, and what sorts of simplifying assumptions (e.g. how many traits) need to be considered to make empirical studies more practicable, but still retaining the predictive power of the models.

In this study of grasshopper life histories, I have reduced the potential criticism of using ill-defined or incomplete phenotypic units by examining not only the variation in single traits but also the covariation among a number of them.

1.2.2.7. Bet-hedging theories

The differences in environmental effects on mortality and reproductive success described so far have been predictable; they have been predictably higher or lower, or predictably mainly density-dependent or mainly density-independent. These models are therefore deterministic.

An alternative set of models can be produced which considers the effects of unpredictable or stochastic changes in the environment on survival and reproduction (i.e. environmental uncertainty). These models have been called **variance models** by Lacey et al. (1983) since they take into account the advantages to the organism of not only increasing the mean pay-off from a particular life-history strategy but also reducing the variance in pay-offs. A strategy which yields a small variance in pay-offs is less likely to become extinct than one which has the same mean but a larger variance in pay-offs since, occasionally, the pay-off to organisms adopting the latter strategy may be so low that they become extinct despite an otherwise high mean pay-off. A **bet-hedging** strategy reduces the probability of extinction by reducing the expected variance in pay-off. This may, however, entail a cost if a less risky strategy has a lower mean pay-off. The advantages of adopting a bet-hedging rather than a risky strategy will therefore depend on the nature of the trade-off between the mean and the variance (Ekbohm et al., 1980; Real, 1980).

One particular bet-hedging argument, proposed by Capinera (1979), is that a female insect should produce a range of egg sizes in environments with different effects on hatchling survival (and, ultimately, the insect's reproduction) and when these different environmental effects favour different-sized hatchlings. In Chapter 6, I consider this argument in relation to the variance in egg sizes observed within clutches produced by grasshoppers in the field.

The effects of unpredictable environments on life histories have been considered by Cohen (1966), Murphy (1968), Schaffer (1974a,b), Wilbur *et al.* (1974), Capinera (1979), Crump (1981), Rubenstein (1982), Lacey *et al.* (1983), and Kaplan and Cooper (1984).

1.2.2.8. Allometry, and genetic causes of apparently maladaptive variation.

So far, this introduction has described only adaptive responses to environmental conditions, but because this study is concerned with the causes of *variation* in life histories rather than with the *evolution* of life-histories *per se*, other effects on the phenotype (which may override the adaptive responses) should also be considered.

Much recent work has examined the effects of body size and phylogeny on life-history traits (Blueweiss *et al.*, 1978; Gould, 1977; Hines, 1982; Kaplan and Salthe, 1979; Leutenegger, 1979; Stearns, 1983c, 1984). All these authors have found them to be important determinants of differences in life histories between species and among larger taxonomic groups.

Body size is often related to the magnitude of a trait raised to a power because of constraints on the design of organisms. In such cases, a graph of log (trait "size") against log (body size) is a straight line. A relationship of this form is called **allometric**, and the phenomenon is called **allometry.**

The slope and intercept of allometric relationships between a life-history trait and body size can sometimes differ between phylogenetic lines (e.g. between the Haplorhini and Strepsorhini primate groups; Leutenegger, 1979); this difference is due to differences in historical or phylogenetic effects, and, if these differences are no longer adaptive, they can be regarded as constraints since they may cause the phenotypic variation between them to appear maladaptive (Fig. 1.1). This is not to say that all phylogenetic differences are constraints. Indeed, most may be adaptive. It is also important to recognize that my talk of apparent maladaptation does not imply that each organism is not as well-adapted as it can be, given the constraints under which it lives. Instead, the term refers to the idea that some organisms have a different range of possible phenotypes from other organisms (i.e. the **phenotype sets** (Maynard Smith, 1978) are different), and any apparent maladaptation applies to the phenotypic difference between some organisms with different phenotype sets.

Differences in **historical (phylogenetic) constraints** are therefore the effects on phenotypes of genetic variation which originated at some time in the past, which has now become fixed in the phylogenetic lines, and which is no longer adaptive. Genetic differences between groups of organisms may arise originally if the differences are at first adaptive. Once a lineage has begun to evolve in a given direction, this may in itself close evolutionary options that were formerly available. If environmental conditions then change and the phenotypic differences do not remain adaptive, these differences may constrain the range of adaptive responses that are available to the organisms. In its simplest form, a difference in historical constraint is a difference between organisms in the nature of genetically-based phenotypic variation on which selection can act, and which prevents the production of phenotypic variation between organisms which appears adaptive.

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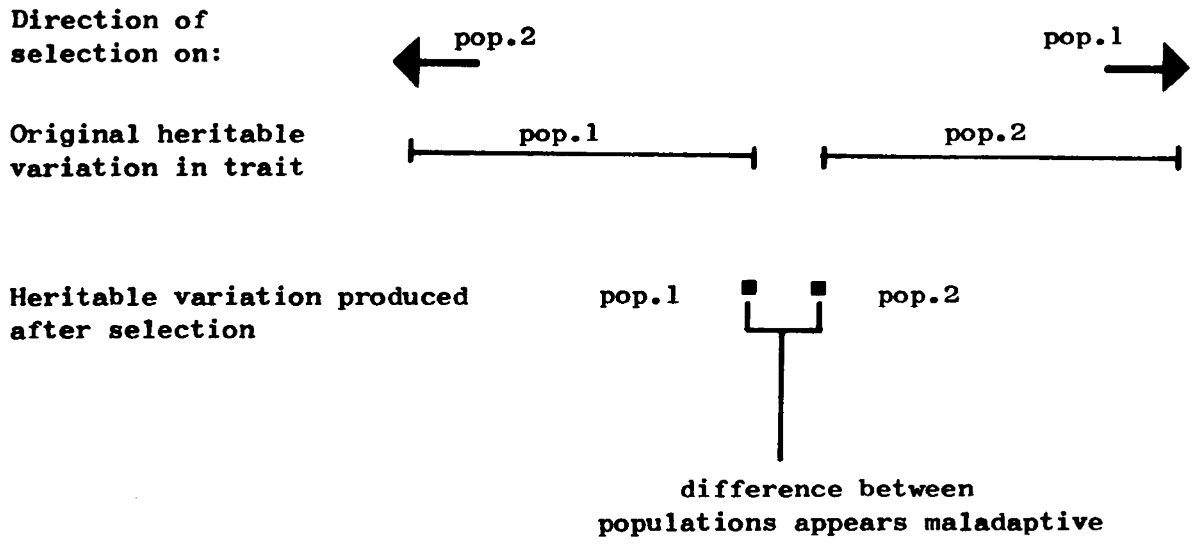
[illegible] 1.1. Apparent maladaptive variation caused by insufficient original variation



Although differences in historical constraints are likely to be more important as determinants of phenotypic variation between distantly-related organisms, they can potentially occur between populations which experienced different selection pressures only one generation ago. This can be true providing that (i) they had lost different genes from their gene pools, (ii) gene flow or new mutations have not replaced them, and (iii) the selection pressures are different now from what they were in the previous generation.

In this comparative study of grasshopper life histories I have at least reduced the likelihood of historical constraints affecting phenotypic variation, since I have compared closely-related species - both species belong to the same sub-family, the Gomphocerinae (Uvarov, 1966) - and, for the major part of the comparison, have examined intraspecific variation among populations which probably became separated only earlier this century (Chapter 2).

Adaptive responses to the environment may be overridden when gene frequencies have not reached equilibrium. Stearns and Sage (1980) provide an example of this in a natural population of mosquitofish, *Gambusia affinis*. They describe apparent maladaptation in this species resulting from physiological constraints - the osmoregulatory system of fish from freshwater was less well adapted to freshwater than to brackish water, probably because the fish were either recent colonizers from brackish water, or were being swamped by gene flow from brackish sites (or both).

Therefore, genetic effects which, potentially, can obscure adaptive phenotypic variation have recently been shown to be important in determining how life histories will vary.

1.2.2.9. Constraints imposed by the immediate environment

Recent work has also emphasized the effects of the immediate environment on life histories (Berven and Gill, 1983; Caswell, 1983; Gill *et al.*, 1983; Stearns, 1983a,b).

Because theories of life-history evolution predict optimal *phenotypes* (Maynard Smith, 1978), the adaptive life histories that they predict may result from **adaptive phenotypic plasticity** (the adaptive alteration of a phenotype by environmental influences) as well as from a change in gene frequencies (Bradshaw, 1965; Caswell, 1983).

Differences in the immediate environment may not only elicit adaptive phenotypic responses. They may also override and constrain adaptive phenotypic variation. For example, insects reared at high densities generally have a longer developmental period and emerge as adults at a smaller size than those reared at low densities (Peters and Barbosa, 1977). This slower growth and development occurs, presumably, because the crowded animals have less food *per capita*. The amount of resources available to an organism may therefore limit the expression of a number of life-history traits, and may be an important determinant of life-history variation, especially between genetically similar organisms (i.e. where environmental differences are *relatively* more important causes of variation).

In the next section I briefly mention the importance of considering adaptive *differences* in life-histories rather than optimization *per se*. I then discuss the ways in which the causes of life-history variation can be studied, and, in particular, introduce the comparative method used in this study.

1.2.3. Optimal life histories or better adapted life histories ?

Theories of life-history evolution are expressed in comparative terms. That is, they predict that an organism will, for instance, lay more or fewer eggs than another organism rather than six or four eggs (Begon and Mortimer, 1981). Comparative theories are more useful to the empiricist trying to understand the diversity of life histories than are theories stated in absolute terms for at least two reasons.

First, we can rarely say that a life history is optimal but we can say that one is better adapted to a particular environment than another life history. This is because we can rarely be confident that we have identified all the alternative life histories available to an organism or group of organisms (the phenotype set). The range of potential alternative life histories that a theoretician considers may not only be incomplete but may also include alternatives which are biologically unrealistic. For this reason, when I have discussed the life histories observed in this study, I have constantly referred to the differences or variation in life histories present in the natural populations rather than speculated whether or not a life history was optimal.

A second, more pragmatic, reason why the theories are more useful when expressed in comparative terms is that the full range of measurements needed to test the theories would be extremely difficult to measure as absolute values (Begon and Mortimer, 1981). Every behavioural and physiological activity which impinged upon the benefits of producing, say, a certain clutch size would have to be measured to test whether a clutch size was optimal, and this might, for instance, require the measurement of an organism's full energy budget. By performing comparisons, however, these behavioural and physiological activities only become important as determinants of differences in life histories if they themselves differ.

1.2.4. Ways of studying life histories.

Stearns (1977) describes the two general approaches taken by empiricists studying life-history evolution - the direct approach and the comparative approach.

1.2.4.1. The direct approach

The direct approach is to subject a group of organisms to a particular selective regime and to observe the change in life-history traits after several generations under the new selective regime. The new life history should be compared with the original one under the same environmental conditions; this would ensure that any difference in life history was not caused by differences in the immediate effects of the environment (phenotypic plasticity). It is rarely possible to control the environmental conditions tightly enough in the field to test demographic theories of life-history evolution rigorously. Consequently, laboratory studies have been performed instead, though they are few in number (Barclay and Gregory, 1981,1982; Luckinbill, 1978, 1979).

The direct approach can be defined more broadly to incorporate also the testing of other causes of life-history variation in natural populations which can override adaptive responses (Sections 1.2.2.8 and 1.2.2.9). The direct approach to the study of life-history variation (c.f. adaptive life-histories), therefore, would involve the manipulation not only of selection pressures, but could also involve manipulation of the amount of variation on which selection could act. This might perhaps be performed by subjecting a population to a high level of a mutagen or by applying techniques of genetic engineering to increase the amount of genetic variation available, and then subjecting the "treated" and the control populations to the same selection regime. Other causes which override adaptive variation (e.g. the stresses of the immediate environment on a plastic phenotype) could also, in principle, be manipulated.

1.2.4.2. The comparative approach

The comparative approach, described by Stearns (1977), compares the life histories of organisms in different environments, assuming that the conditions under which they are living represent the conditions under which they evolved, and tests possible explanations against field observations.

A broader comparison would look not only at the relationship between the life history and the postulated selection pressures, but also at the relationship between the life history and other causes of the variation such as phylogenetic differences (Section 1.2.2.8) and the amount of resources available to the different organisms (Section 1.2.2.9).

In order to design an efficient experimental programme which tests the most likely hypotheses (of those which can predict the nature of variation in life histories) it is useful, first of all, to assess the relative importance of the different causes of phenotypic differences. The comparative approach allows us to do this: it can enable us to ignore (provisionally) a number of the competing hypotheses when the evidence is contrary to their predictions, and thus allows us to design a small number of experiments to test the remaining hypotheses.

The comparative approach is used in this study, and has also been used recently to compare intraspecific life-history variation in a wide range of organisms including a grass (Law *et al*., 1977), an amphibian (Berven *et al*., 1979; Berven, 1982; Berven and Gill, 1983), a fish (Stearns, 1983b), molluscs (Way *et al*., 1980; Hart and Begon, 1982), a crustacean (Miller and Cameron, 1983), a heteropteran insect (Fairburn, 1984), a butterfly (Blau, 1981) and grasshoppers (Dearn, 1977; Monk, 1981, 1985).

1.3. LIFE-HISTORY VARIATION IN THE GRASSHOPPERS, *C.BRUNNEUS* AND *M.MACULATUS* AT AINSDALE SAND DUNES NNR.

1.3.1. *Life-history variation in British grasshoppers*

Before this project was started, it was clear from the latest review of the subject by Stearns (1977) that there was very little reliable data against which the theories of life-history evolution could be judged. One important reason for this is that there are very few animals which can be simply and cheaply studied in the laboratory and which can also be sampled accurately and effectively throughout their life cycles in the field. British grasshoppers, however, combine these properties (Brown, 1983; Kelly-Stebbings and Hewitt, 1972; Monk, 1981; Ragge, 1965; Richards and Waloff, 1954). They are, therefore, ideal material for a study of life-history strategies. The following outline of the typical life history of a British grasshopper is a summary of the fuller accounts given by Brown (1983) and Ragge (1965).

Up to fourteen eggs are laid at a time in the soil or on the ground at the base of grass tufts. They are enclosed in a protective case called an egg pod, which has a spongy matrix made from a solidified frothy secretion produced by the female with soil or fragments of vegetation attached to it. The eggs develop as far as the resting stage (diapause) at which differentiation either ceases or is very slow. After spending the winter in this stage, diapause is broken in the spring by warmer temperatures. Hatching occurs from April onwards and is highly temperature-dependent. The young grasshoppers emerge from the egg as vermiform larvae, wriggle out of the pod, and then immediately shed their cuticle on reaching the open air to become first-instar nymphs. After another four moults, between which the nymphs feed on vegetation and grow, they emerge as adults (this occurs usually from June onwards). Sexual maturity is not reached until several days after the final moult. Several egg pods are normally produced during the summer months, and all adults die before the winter. They are therefore iteroparous, annual insects with discrete (non-overlapping) generations.

1.3.2. Life-history variation in *C.brunneus* and *M.maculatus*

C.brunneus and *M.maculatus* both occur throughout Europe and temperate Asia; *C.brunneus* also occurs in north Africa (Ragge, 1965). In Britain both species inhabit dry grassy places including sand dunes, and places such as quarries where the vegetation is broken up with exposed soil and rocks. *C.brunneus* is also typically found in roadside verges, dryish fields and large woodland clearings, whereas *M.maculatus* would be commoner on dry heaths and moorland (Ragge, 1965). Areas of bare soil are required for both species since they both lay their egg pods in bare soil 12-30 mm beneath the surface (Richards and Waloff, 1954; Waloff, 1950).

C.brunneus adults are about twice as heavy as those of M.maculatus; they lay larger egg pods containing more eggs which hatch later in the spring, and they have a lifetime fecundity about twice that of M.maculatus (Richards and Waloff, 1954). In the populations studied by Richards and Waloff (op. cit.), there were usually more male than female adults of C.brunneus, but no such difference was observed in M.maculatus.

Intraspecific phenotypic variation in C.brunneus has recently been examined by Monk (1981, 1985) and Grayson (1984), and found to differ significantly between sites less than 1 km apart (Monk, 1985) and to differ significantly in response to rabbit grazing (Grayson, op. cit.). Intraspecific variation in the life-history characters of M.maculatus has not been studied in detail, although Harvey and Hewitt (1979) documented in this species a slower development rate in those animals possessing two or more B chromosomes.

1.3.3. Grasshopper populations at Ainsdale Sand Dunes NNR

Three species of grasshopper occur at Ainsdale Sand Dunes NNR, Merseyside - C.brunneus, M.maculatus, and Omocestus viridulus(L.) (Payne, 1978). The distribution of O.viridulus is limited to the areas with lush grassy vegetation which is mainly on the eastern (most inland) parts of the Nature Reserve, whereas the other two species are more widespread and co-occur at a number of sites including the three examined in this study. Physical and biological characteristics of the these three sites are described in Chapter 2.

The outline of the thesis is as follows: Chapter 2 describes the three study sites, and Chapter 3 documents the variation in density, mortality, and developmental period in the grasshoppers in each of the populations at these sites. Chapter 4 describes the variation in adult size within and among the populations of both species and, using the results from Chapters 2 and 3, correlates adult size with a number of potential causes of variation in this trait. Because the existing body of life-history theory, used on its own, could not have predicted the differences in adult size of the different populations, I develop in Chapter 5 a general graphical model for predicting the optimal size and time at moult in environments which impose different constraints on growth. Chapter 6 describes the variation in, and the correlates of egg size. Finally, in Chapter 7, the thesis is concluded by bringing together some of the findings of the work.

CHAPTER 2: **The study sites**

SUMMARY

1. The physical and vegetational characteristics of the three study sites and two field enclosures at site 1 are described.

2. The sites (and enclosures) differed in topography, vegetational structure, rates of evaporative water loss, the relative amounts and species-composition of grasses, and in their amounts of bare sand.

2.1. INTRODUCTION

The initial aim of the empirical part of this study is to describe the variation in the grasshoppers' life histories in relation to the nature of their habitats. These descriptions can then provide comparative data which can be used to investigate the most likely causes of the variation and assess how adequate are existing theories of adaptive life histories for explaining and predicting it.

The geographical distribution of grasshoppers correlates with both climate and vegetation (Uvarov, 1977) which themselves will be highly correlated. Temperature and humidity, for instance, are the two most important limiting factors for the distribution of European (Dreux, 1972) and North American species (Gage and Mukerji, 1977), and the structure and species composition of vegetation has long been recognized as a major determinant of grasshopper distribution (Vestal, 1913; Clark, 1948; Dempster, 1955; Lensink, 1963; Otte, 1977; Uvarov, 1977; Von Sanger, 1977; Joern, 1982). In this study, the sites will be subject to the same major climatic influences because they are geographically proximate, but the grasshoppers may experience different microclimates due to the effect of habitat structure (Lensink, 1963; Ruscoe, 1970; Von Sanger, 1977).

The choice of microhabitat by grasshoppers is likely to be determined not only by its associated microclimate (temperature, humidity, amount of solar radiation, and evaporation rates) but also by the presence of particular foods or nutrients, structural qualities, oviposition sites, and suitable hiding places (Joern, 1982). In this chapter I describe these habitat characters for the three study sites and two field enclosures.

2.2 CRITERIA FOR CHOOSING SITES

The choice of study sites was dictated by the following requirements:

(a) they should contain both grasshopper species, so that an interspecific comparison could be made in addition to intraspecific ones

(b) they should exhibit differences in their habitat characteristics

(c) they should contain discrete populations or be representative of the contiguous habitat containing the two species (This should minimize <u>net</u> emigration or immigration at any particular stage in the life history, and ensure the correlations between habitat and life history are not invalid as tests of life history theories)

(d) they should be close together and separated by a fairly recent barrier in order to minimize any differences in historical constraints among populations (Chapter 1)

(e) they should be as free as possible from public disturbance.

All criteria were satisfied although (c) and (e) were satisfied only partially, since site 2 was adjacent to a public footpath (criterion (e)), and C.brunneus was observed in one of the years at two of the sites to move into taller, denser vegetation during its life history (which resulted in a net emigration of animals - criterion (c) - see Section 2.3).

2.3. THE LOCATION AND SIZE OF THE SITES

The three study sites at Ainsdale Sand Dunes NNR, Merseyside were between 0.86 and 1.23km apart and separated by areas of dune grassland and dense woodland, mainly of Corsican Pine (Pinus nigra) (Fig. 2.1). The trees were planted from about 1914 (Greenwood, 1970) and appeared to restrict grasshopper migration, since animals were never seen moving through the woodland, only through open ground.

The sites differed markedly in their vegetational structure and composition and in their topographies (Figs. 2.2a,b,c).

Site 1 was the most seaward of the sites, was situated in the open dunes, and initially had an area of $925m^2$. In 1982 the site was extended to incorporate more of the surrounding dense vegetation, because in 1981 some C.brunneus (and possibly M.maculatus; see Chapter 3) appeared to move a few metres out of the study areas during their development, and returned as adults to lay eggs. There appeared to be little net migration from the extended site which was $1150m^2$ in area. The boundaries chosen for the site were determined by the nature of the vegetation and topography of the area.

The northwestern boundary was just over the dune ridge where

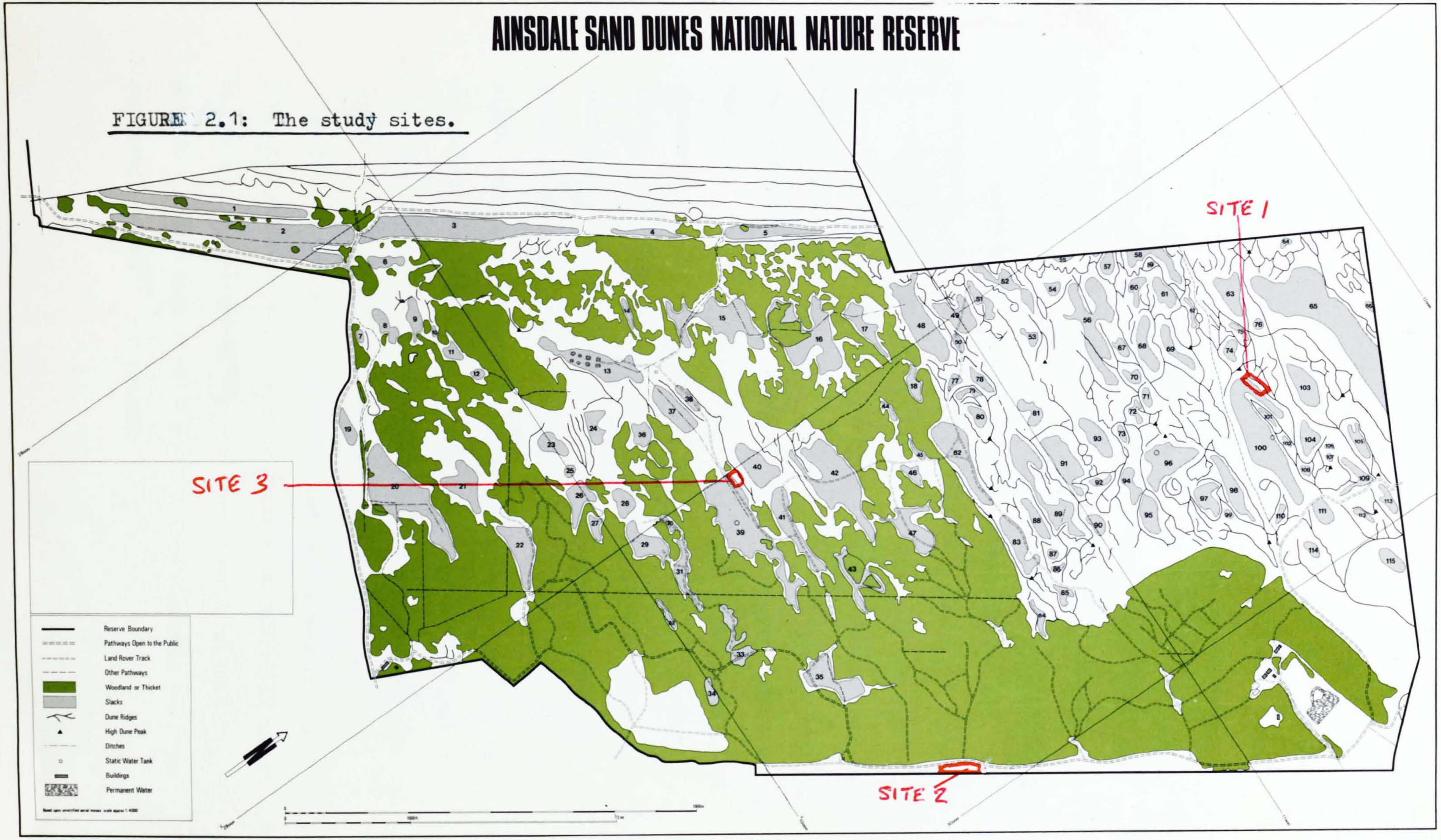


FIGURE 2.1: The study sites.

the slope of the ground changed from the mainly southeasterly slope of the study site to mainly northwesterly, and where grasshopper density was lower. The southeastern boundary was demarcated by a change to a damp slack vegetation with dense *Salix repens*, and with moss rather than grass as its main understorey vegetation. The site was extended (in 1982) to include the edge of this slack where a transitional vegetation between dune slope and damp slack occurred, which included long grass with the *Salix*, and into which some of the *C.brunneus* moved. A change to a taller grassy vegetation along the southwestern edge of the site was used to define a site boundary in 1981 but this vegetation was also colonized by some late-instar *C.brunneus*, so the boundary was pushed back to include some more of this vegetation in 1982. The northeastern boundary was an open one - it represented a line across which there was no noticeable change in vegetation, topography, or net movement of grasshoppers.

In April 1981, two enclosures were built, each 10m by 8m with 1m-high walls of 1000-gauge polythene sheeting sunk into the ground. The location of the enclosures was determined by the slope, aspect, and vegetation of the enclosed ground. In the enclosures, all these habitat characteristics were typical of the surrounding site: the only major difference was that the aspect of enclosure 1 was more south-facing than the predominantly southeast-facing site and enclosure 2 (Section 2.6). The enclosures were used to examine the effect of aspect on adult size (Chapter 4), and enclosure 1 was also used to provide a closed population from which marked animals could be collected, returned, and recaught (Chapter 6).

FIGURE 2.2a: Site n. (enclosure 1 is nearest the camera).

Site 2 was the furthest inland and was situated on the eastern boundary of the Nature Reserve. Its area of 960m^2 was defined by the position of a track on its northwestern edge, beyond which was dense coniferous woodland; by a dense grassy verge adjacent to a railway line on its southeastern edge; and by a change to tall dense vegetation on its northeastern and southwestern edges. The aspect along the northeastern edge also changed from southeast- to northeast-facing, though the change in slope was slight. In 1982, some C.brunneus, but not M.maculatus, appeared to move out into some of the denser vegetation of the northwestern and southeastern edges.

Site 3 comprised a dune slope with part of an adjacent dry slack partially enclosed by trees. The site was 610m^2 in area and could be clearly defined on three sides by (i) the crest of the dune, and its associated sharp change to tall lush vegetation on its steep north-facing side (on the northern edge of the site), (ii) the edge of some coniferous woodland (on the western edge), and (iii) a change to tall lush vegetation (on the southern edge). Grasshoppers seemed to be largely contained by these boundaries. The eastern boundary was drawn through an area of Salix repens where grasshopper density was low and through which there appeared to be no net migration between adjacent grassland areas.

The nature of the vegetation at each site - its structure and species composition - topographic features, the amounts of bare sand, and rates of evaporation, were all examined in this study.

FIGURE 2.2b: Site 2.

FIGURE 2.2c: Site 3.

2.4. GENERAL METHODS

The site descriptions were initiated with a list of plant species.

The following vegetational and topographic characteristics were also described, using data derived from observations on between 61 (enclosure 2 at site 1) and 942 (site 3) randomly-chosen quadrats each of 1m^2: "vegetation type" (sensu Lensink, 1963; see Section 2.5.1), percentage vegetational canopy, percentage of bare sand, slope, and aspect. These observations were made between April and October in 1982.

The random distribution of sample quadrats was achieved by first mapping out the sites and placing pegs every five or ten metres (depending on the topography) in the form of a grid to which a system of co-ordinates could be applied to describe the location of particular metre-square quadrats. Then, using random numbers produced by a computer random number generator, random co-ordinates were produced. These were then used to choose the squares to be sampled. The data were obtained whilst carrying out sequential censuses on the grasshopper populations using a 1m^2 box-quadrat (Chapter 3).

Vegetational differences observed between sites were corroborated by a quantitative study of the vegetational structure at each site in June 1983 (Section 2.5.1). Details of the methods used for measuring each habitat characteristic are described in the appropriate section.

2.5. VEGETATIONAL CHARACTERISTICS AND THE AMOUNT OF BARE SAND

2.5.1. The use of quadrat data and the point-intercept method

The structure of the grassy herb vegetation within each metre-square quadrat was assigned to one of six "vegetation types" based on the categories used by Lensink (1963) who studied the microdistribution of grasshoppers in the dunes of Voorne in the Netherlands. Figure 2.3 illustrates the differences between the six categories that were used.

In addition to the grasses and sedges, the percentage cover of vegetation that tended to shade these monocots was estimated to the nearest 5%. Overall, the two most abundant species contributing to the canopy were dewberry (Rubus caesius) and creeping willow (Salix repens), although the latter was absent from site 2.

The observations describing the differences in vegetational structure were supplemented by a more quantitative approach - the point-intercept method, described by Mueller-Dombois and Ellenberg (1974). A note was made of the species which were touched by a 2mm diameter pin in the five 10cm height ranges from 0 (ground level) to 50cm as the pin was lowered vertically. This was repeated at a hundred randomly-chosen points at each site, and at fifty points in each enclosure.

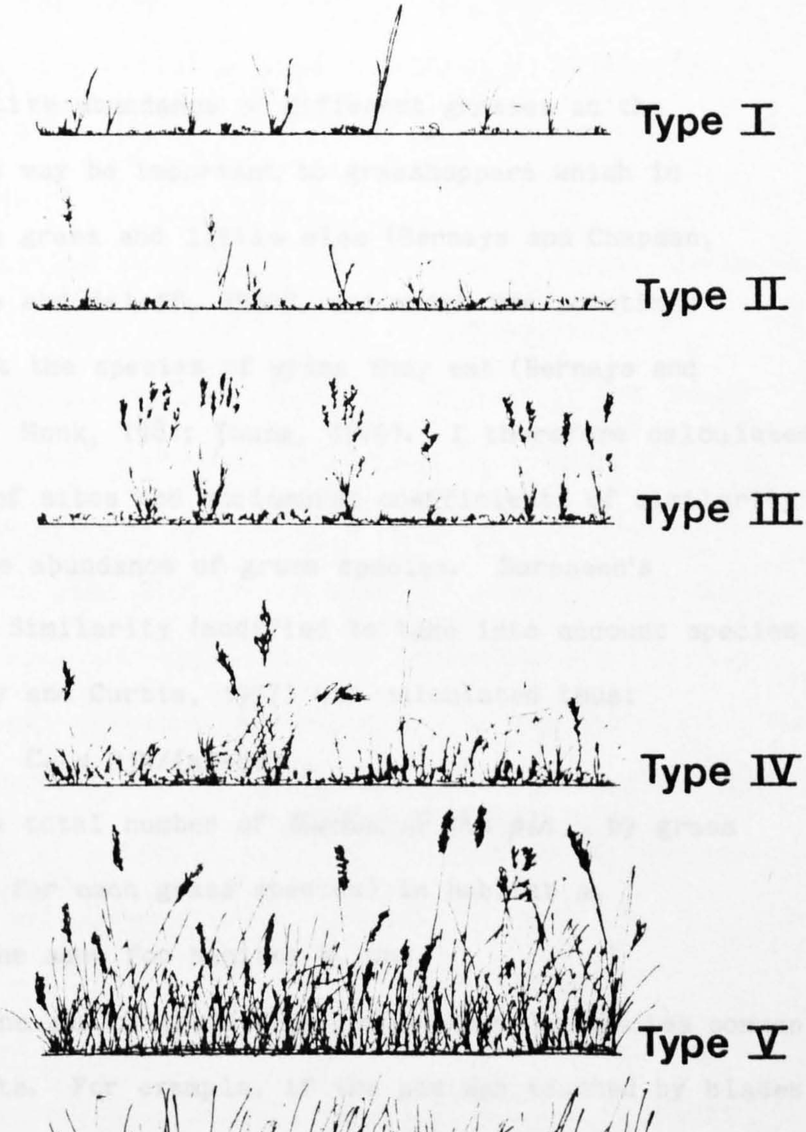
The vegetational height profile for each site was described by calculating the number of times the pin touched vegetation at each height divided by the number of times the pin touched vegetation at all heights. They were plotted as layer diagrams (Mueller-Dombois and Ellenberg, 1974).

The degree of dominance of the major grass species was assessed by calculating the Berger-Parker dominance index, **d**, thus

$$d = N_{max}/N_T$$

where N_{max} = the number of times the pin was touched by blades of the most abundant species,

FIGURE 2.3: The six "vegetation types" to which vegetation in each metre-square quadrat was assigned (after Lensink, 1963)



and N_T = the total number of times the pin was touched by blades of all grasses (except the inedible marram grass, Ammophila arenaria).

May (1975) concluded that this index, although simple, seems "to characterize the distribution as well as any, and better than most".

The relative abundance of different grasses at the different sites may be important to grasshoppers which in Britain feed on grass and little else (Bernays and Chapman, 1970b; Richards and Waloff, 1954), and which are sometimes selective about the species of grass they eat (Bernays and Chapman, 1970a; Monk, 1981; Young, 1979). I therefore calculated for each pair of sites and enclosures coefficients of similarity of the relative abundance of grass species. Sorensen's Coefficient of Similarity (modified to take into account species abundance; Bray and Curtis, 1957) was calculated thus:

$$C_N = 2jN/(aN+bN)$$

where **aN** = the total number of touches of the pin by grass blades (summed for each grass species) in habitat **a**,

bN = the same for habitat **b**, and

jN = the sum of the lesser values for the species common to both habitats. For example, if the pin was touched by blades of Festuca rubra ten times at site 1, and three times at site 2, and if it was touched by Agrostis tenuis on six and fifteen occasions, respectively, the value of **jN** would be (6 + 3 + the lower values for other species found at both sites).

In order to avoid a spurious dissimilarity between the sites and enclosures due to differences in sample size (100 pins at the sites and 50 in the enclosures) the number of touches of the pin by each grass species at the sites was halved.

This index is more appropriate for comparing the grasshopper habitats than is a simple measure of similarity of grass species (such as the unmodified Sorensen's Coefficient), since, by taking into account the relative abundance of the grasses, it does not place too much significance on rare species, the sampling of which will depend heavily on chance (Southwood, 1978). This coefficient is widely used in plant ecology (Goldsmith and Harrison, 1976).

This particular study represents part of a larger one which includes other aspects of the ecology of grasshoppers at Ainsdale. Grass samples were collected as part of the larger study in 1981, 1982, and 1983, and stored at -18deg.C for a future analysis of food quality by M. Begon and D. Atkinson.

Two methods were used to estimate the proportion of bare sand at each site. In the first, the percentage area of bare sand in each sample quadrat was estimated to the nearest 5%. The second estimate was derived, using the point-intercept method, from the number of points at which no vegetation was touched by the pin as it was lowered to the ground.

2.5.2. Species composition

The plants recorded at each site and in each enclosure are listed in Table 2.1. Some of them were so uncommon that they were not recorded when the point-intercept method was used. Site 2 had the most grass species (10) and enclosure 2 at site 1 had the least (3).

Site 1 (including enclosure 1) had a little Phleum arenarium and Vulpia fasciculata - both dune annuals - and enclosure 2 had none at all. The species abundances were similar

TABLE 2.1: **The occurrence of plant species at the three sites, and in the enclosures at site 1**

* now known as *Agrostis capillaris* L.

Taxa	Site(enclosure): 1	1(1)	1(2)	2	3
Monocotyledons:					
Gramineae:					
Festuca spp.	x	x	x	x	x
Holcus lanatus L.	x			x	x
Aira praecox L.	x	x	x	x	x
Poa pratensis L.	x	x		x	x
Poa annua L.				x	
Dactylis glomerata L.	x			x	
Agrostis tenuis Sibth.*				x	x
Anthoxanthum odoratum L.				x	x
Vulpia fasciculata (Forskål)Samp.	x	x			
Phleum arenarium L.	x	x			
Ammophila arenaria (L) Link	x	x	x	x	x
Arrhenatherum elatius (L) Beav.ex. J. and C. Presl.				x	x
Cyperaceae:					
Carex arenaria L.	x	x	x	x	x
Juncaceae:					
Luzula sp.	x	x	x	x	x
Others:					
Ononis repens L.	x	x	x	x	x
Salix repens L.	x	x	x		x
Rubus caesius L.	x	x	x	x	x
Lotus corniculatus L.	x				x
Betula sp.	x				x
Pinus nigra Arnold				x	
Taraxacum officionale (Dahlst.) Weber	x			x	x
Senecio jacobaea L.	x	x	x		x
Viola canina L.	x	x			
Vicia cracca L.		x		x	x
Chamaenerion angustifolium (L)Scop.					x
Hieracium pilosella L.					x
Geranium robertianum L.		x			
Sedum acre L.	x	x	x		
Equisetum sp.				x	
Unidentified pteridophyte					x
Unidentified bryophytes	x	x	x	x	x

between site 1 and its enclosures (Table 2.3): this supports the choice of the enclosures as being representative of the surrounding site. Differences were caused only by species rare on the site, such as the dune annuals, and also Dactylis glomerata, which was found only in the part of the site which had been added to the original area in 1982.

The dominant grass at each site except site 2, and in each enclosure, was Festuca rubra (Table 2.2) [although at site 3 some of this may have been F.ovina (K. Payne, pers. comm.)]. Site 2 differed by having Agrostis tenuis as its dominant grass, though this was less dominant than was Festuca at the other sites (Table 2.2). Site 2, therefore, had a greater diversity of grasses and was not as heavily dominated by one species as were the other sites (and the enclosures). Consequently, the composition of grass species at site 2, having taken into account their relative abundances, was least like that at the other sites and enclosures (Table 2.3).

Besides grasses, other plants including mosses, dewberry (Rubus caesius), sand sedge (Carex arenaria), restharrow (Ononis repens), and a woodrush (Luzula sp.) were present and not uncommon on all sites and in both enclosures (Table 2.1). In addition, horsetails (Equisetum sp.) became abundant at site 2 from June onwards. The only indication that the grasshoppers might resort to non-grasses in poor feeding conditions came from three observations of C.brunneus feeding on Rubus leaves during the dry summer of 1983 (R. Cullen, pers. comm.), and from occasional sightings of Carex leaves which had had small pieces taken out from their edges. I have no evidence, however, to indicate that non-grasses formed a significant part of their diet

TABLE 2.2: Berger-Parker dominance indices for grasses at each site and enclosure.

Site (enclosure)	Dominant species	Nmax	NT	Nmax/NT
1	*Festuca rubra*	10	14	0.71
1(1)	*Festuca rubra*	5	8	0.63
1(2)	*Festuca rubra*	5	5	1.00
2	*Agrostis tenuis*	15	30	0.50
3	*Festuca* spp	23	37	0.62

Nmax = the number of pins touched by the most abundant grass

NT = the sum of the number of pins touched by each grass

TABLE 2.3: Sorensen's coefficients of similarity of grass species (modified to take into account species abundance) between pairs of sites and enclosures.

Site (enclosure)	1	1(1)	1(2)	2	3
1	-				
1(1)	0.79	-			
1(2)	0.83	0.83	-		
2	0.41	0.32	0.25	-	
3	0.47	0.47	0.43	0.36	-

(see also Bernays and Chapman, 1970b; Monk, 1981).

2.5.3. Vegetation structure

The differences in the structure of the grassy herb vegetation between the sites are shown in Fig. 2.4. Site 1 and the enclosures had mainly very sparse vegetation with bare areas of ground (vegetation type I), whereas site 3 had high proportions of vegetation types **IV** and **V**, and site 2 showed an intermediate vegetational structure (mainly types **II** to **IV**). The frequency of vegetation types in the enclosures resembled that of the original site 1 more closely than that of the extended site, which had a higher proportion of taller, denser vegetation (Fig. 2.4).

The canopy over the grassy vegetation developed during May and June, and started to die back in mid-August (Fig. 2.5). The main cause of this seasonal change is the leaf production and loss by Rubus. At site 3, Salix formed a large part of the canopy and was in leaf by the end of April. Consequently, the seasonal increase in canopy was not as marked as at the other sites (Fig. 2.5). Although site 3 had the tallest and densest grassy vegetation, it tended to have a slightly lower percentage cover of canopy species than the other sites (Table 2.4, Fig. 2.5). Site 2 had slightly more than the extended site 1, which had more than the original unextended site 1 (Table 2.4, Fig. 2.5).

Figure 2.6 illustrates the profile of vegetation heights for each site and enclosure. The measures, derived from the point-intercept method (Section 2.5.1), combine the relative abundances of all plants (grassy herb, canopy species, mosses, and rosettes) at each height interval to demonstrate that the vegetation was

FIGURE 2.4: **Frequency distributions of the six "vegetation types" at each site and in each field enclosure**

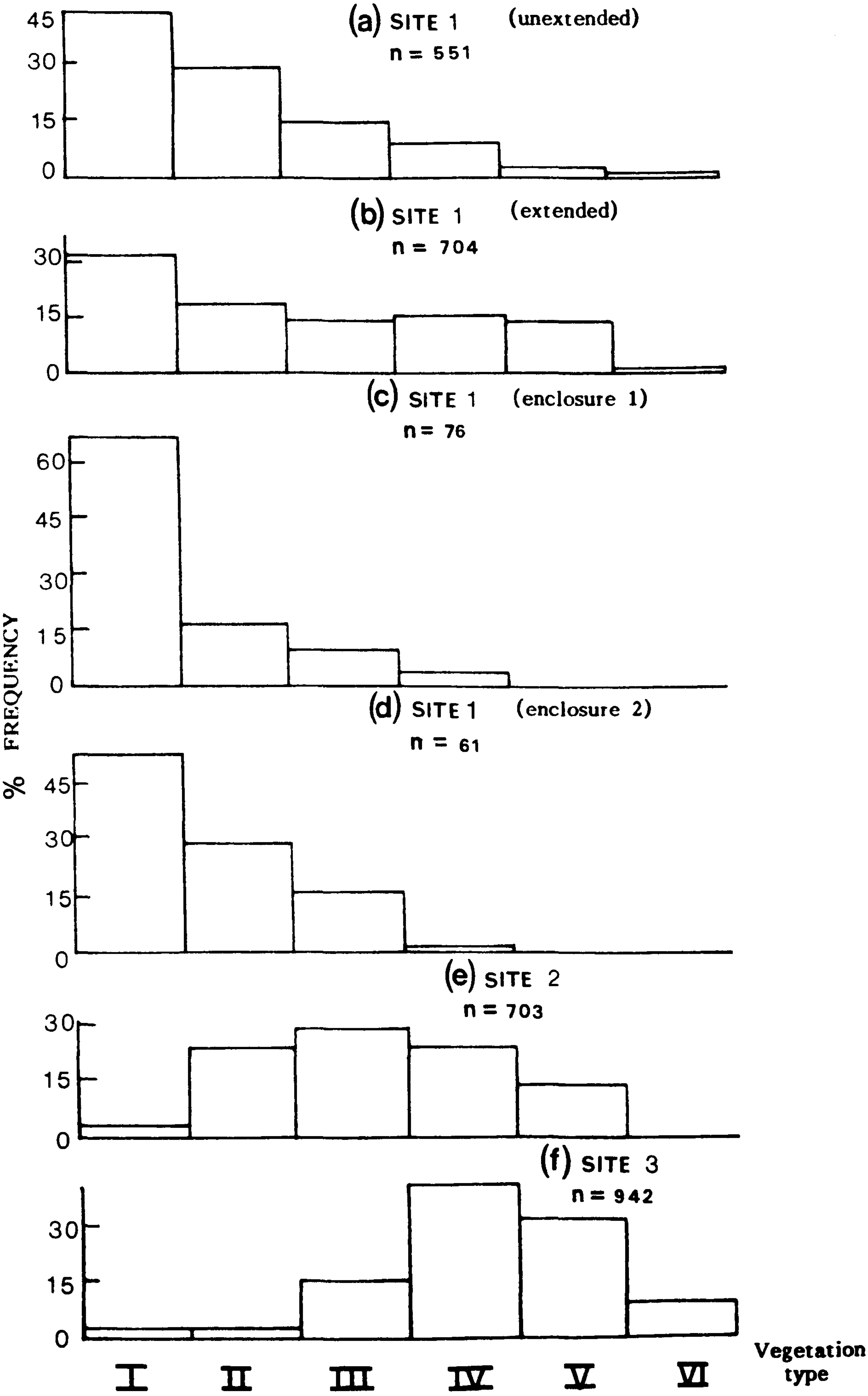

(a) SITE 1 (unextended)
n = 551
45
30
15
0
(b) SITE 1 (extended)
n = 704
30
15
0
(c) SITE 1 (enclosure 1)
n = 76
60
45
30
15
0
(d) SITE 1 (enclosure 2)
n = 61
45
30
15
0
(e) SITE 2
n = 703
30
15
0
(f) SITE 3
n = 942
30
15
0
% FREQUENCY
I
II
III
IV
V
VI
Vegetation type

FIGURE 2.5: **Seasonal changes in the amount of cover of canopy species at each site and in each field enclosure in 1982**

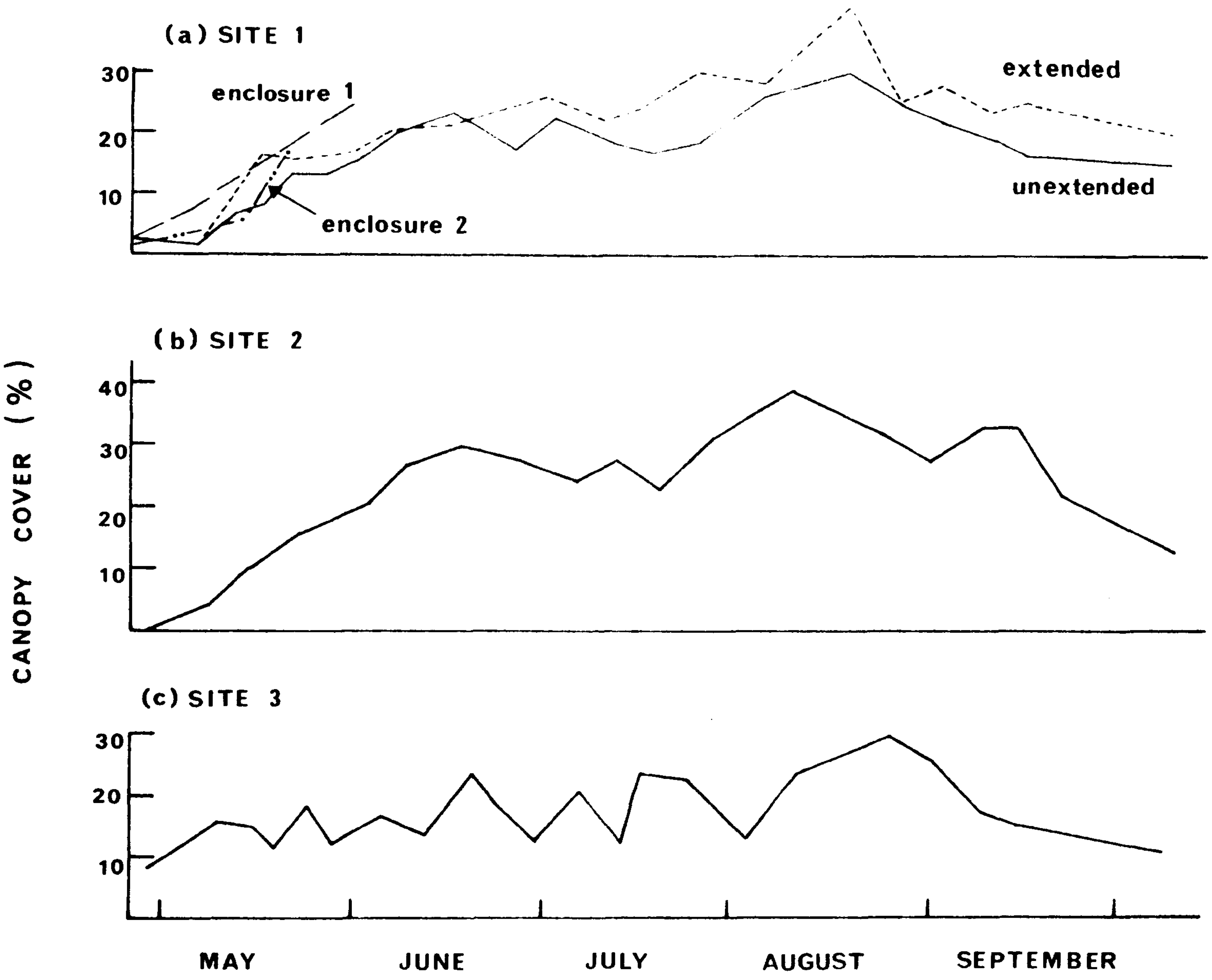

(a) SITE 1
30
20
10
enclosure 1
enclosure 2
extended
unextended
(b) SITE 2
40
30
20
10
CANOPY COVER (%)
(c) SITE 3
30
20
10
MAY
JUNE
JULY
AUGUST
SEPTEMBER

TABLE 2.4: Amounts of canopy and bare sand, and the slopes of metre-square quadrats at each site and enclosure.

Site (enclosure)	Percentage canopy[1] mean (+range)	Percentage sand[1] mean (+ 95% CL)	n[1]	Percentage sand[2]	Slope[1] (°) mean (+range)
1 unextended	17.2(1.9-30.8)	34.9 (31.6-38.2)	21	-	12.4(0-40)
1 extended	21.4(1.5-41.7)	27.7 (25.3-30.1)	21	26	12.2(0-40)
1(1)	-	51.2 (45.3-57.1)	5	28	16.3(1-40)
1(2)	-	50.0 (46.5-53.5)	4	22	14.6(0-30)
2	22.7 (0.7-38.4)	3.1 (2.5- 3.7)	21	1	5.3(0-15)
3	17.2 (8.0-29.8)	7.1 (6.3- 7.9)	23	2	11.1(0-70)

1. Data obtained using estimates from randomly-located metre-square quadrats on n visits

2. Data obtained using the "point-intercept" method

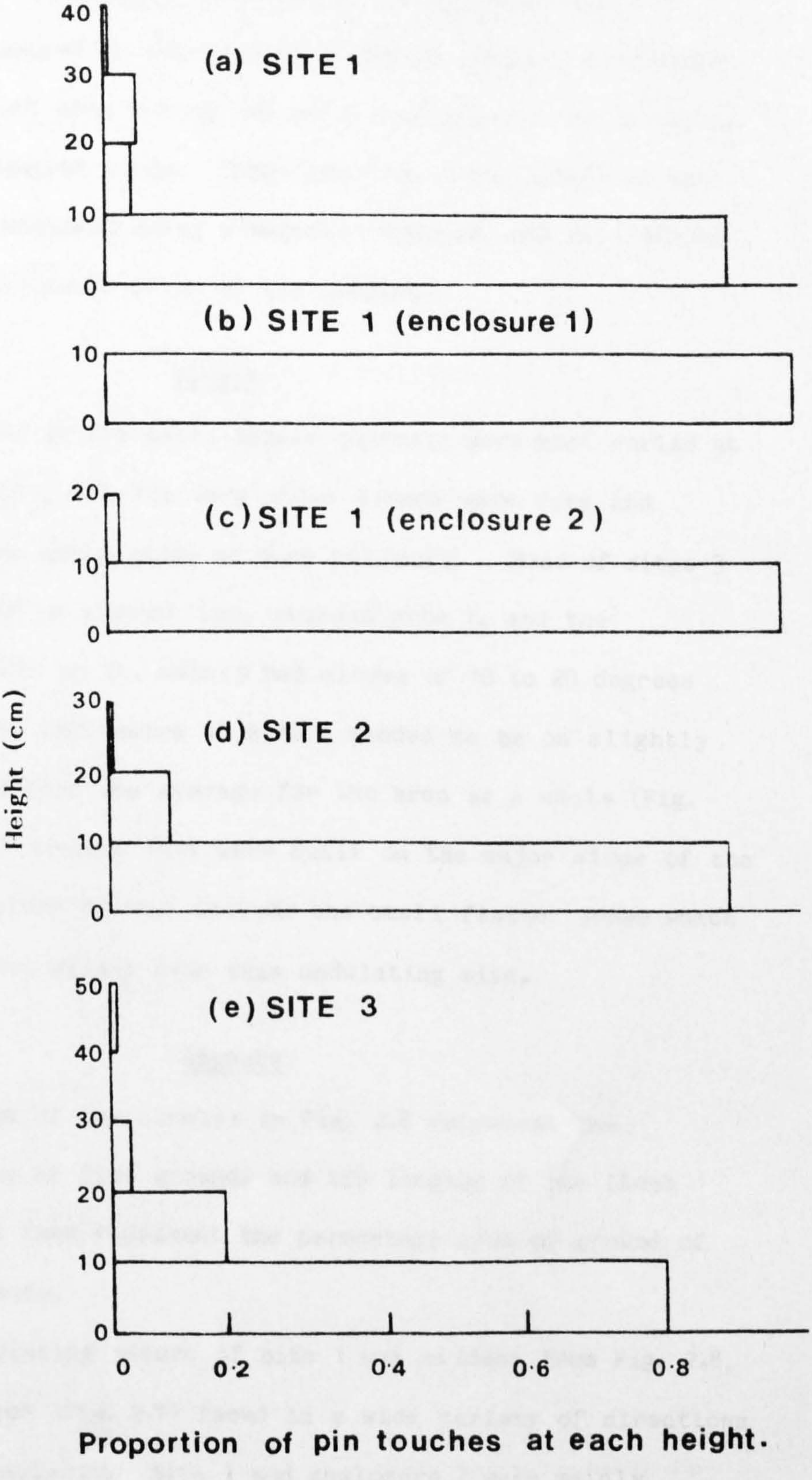
mainly very short (less than 10cm) at all sites, but that site 3 had both the highest vegetation and the highest proportion above 10cm. The difference between the extended site 1 (with the additional areas of taller vegetation) and the enclosures, is also evident (Fig. 2.6). This difference may have meant that the microclimate in the enclosures was more stressful for C.brunneus than that of the surrounding site, since this species tended to move into the denser vegetation of site 1 during its development (see also Chapter 3).

2.5.4. Bare sand

The differences in the amount of bare sand at the three sites was very marked - site 1 having much more than site 3, which had slightly but significantly more than site 2 (Table 2.4; SNK multiple range test, $p_{crit} = 0.05$), and these differences remained despite large discrepancies between the two types of estimate (Table 2.4).

The discrepancies between the two types of estimate were probably due to differences in the methods rather than to any differences between years, since I noticed no change in the amounts of bare sand between 1982 and 1983. One explanation might come from the effect of wind on the lateral movement of leaves which may have caused some to touch the pin as it was lowered to the ground, thus giving a spuriously high measure of the percentage cover of vegetation (and, conversely, a low measure of the amount of bare ground). Also, visual estimates of the amount of bare sand may have been overestimates, since the large extent of bare sand under a canopy can usually be seen in the often-large gaps between the leaves of the canopy. Thus, although the vertical pin would usually touch the canopy, the

FIGURE 2.6: Vegetational height profile for each site and enclosure



roving eye could see the sand beneath.

2.6. SITE TOPOGRAPHY

2.6.1. Methods

The major slope of each randomly-chosen square metre of ground was measured to the nearest 5 degrees using a clinometer placed parallel with the top of the box-quadrat in the direction giving the steepest slope. This direction - the aspect of the square - was measured using a magnetic compass, and recorded to the nearest sixteenth point of the compass.

2.6.2. Slopes

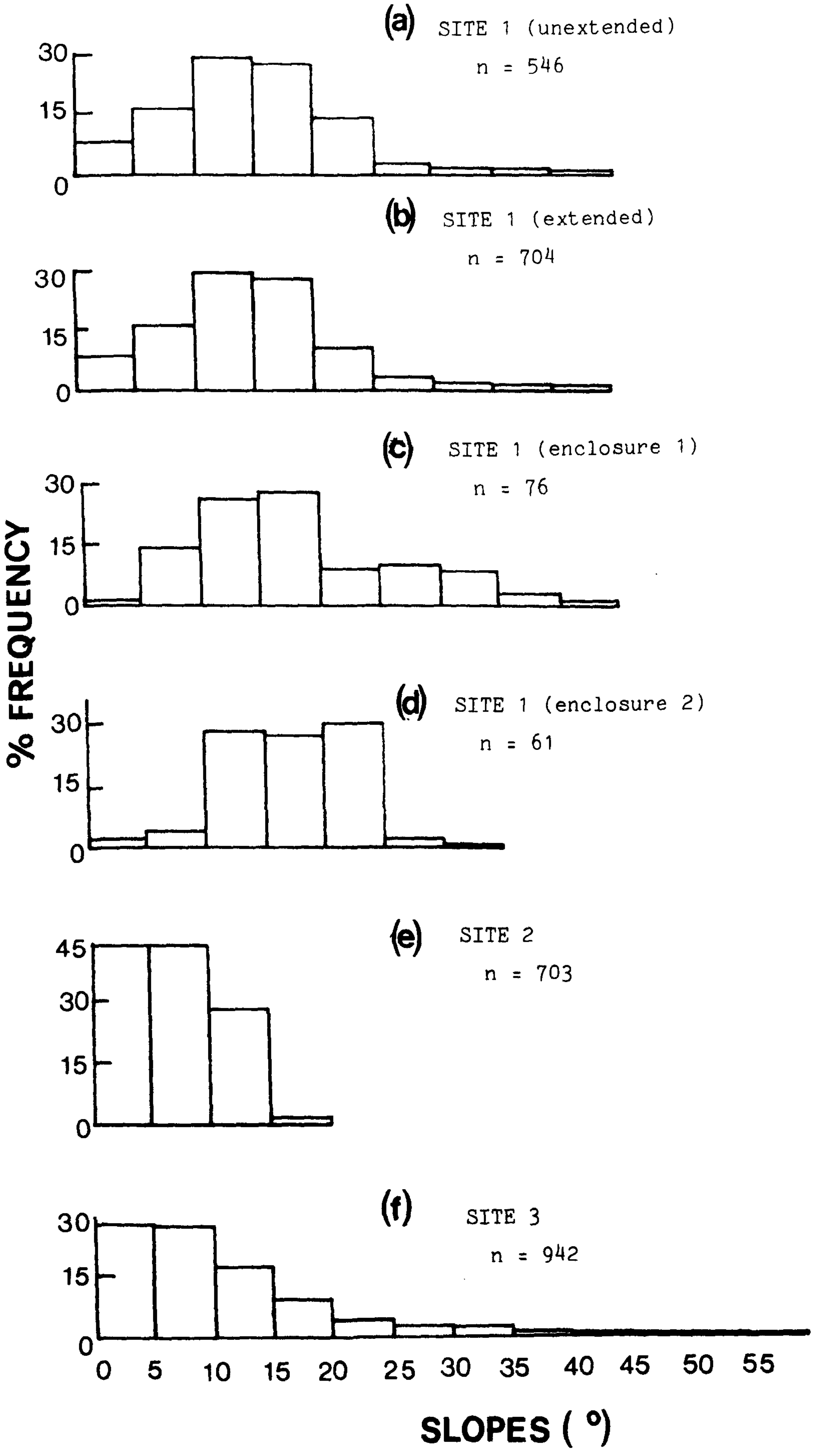
The slopes of the metre-square quadrats were most varied at site 3 (Fig. 2.7), but the very steep slopes were rare and represented the steep sides of dune hillocks. Most of sites 3 and 2 were flat or almost flat, whereas site 1, and the enclosures built on it, mainly had slopes of 10 to 20 degrees (Fig. 2.7). The enclosures at site 1 tended to be on slightly steeper ground than the average for the area as a whole (Fig. 2.7, Table 2.4) because they were built on the major slope of the site and therefore did not include the small flatter areas which were distributed widely over this undulating site.

2.6.3. Aspects

The radius of the circles in Fig. 2.8 represent the percentage area of flat ground, and the lengths of the lines emanating from them represent the percentage area of ground of different aspects.

The undulating nature of site 1 was evident from Fig. 2.8, since the slopes (Fig. 2.7) faced in a wide variety of directions besides southeasterly. Site 1 and enclosure 2 were mainly

FIGURE 2.7: Percentage frequency of slopes at each site and enclosure



(a) SITE 1 (unextended) n = 546

(b) SITE 1 (extended) n = 704

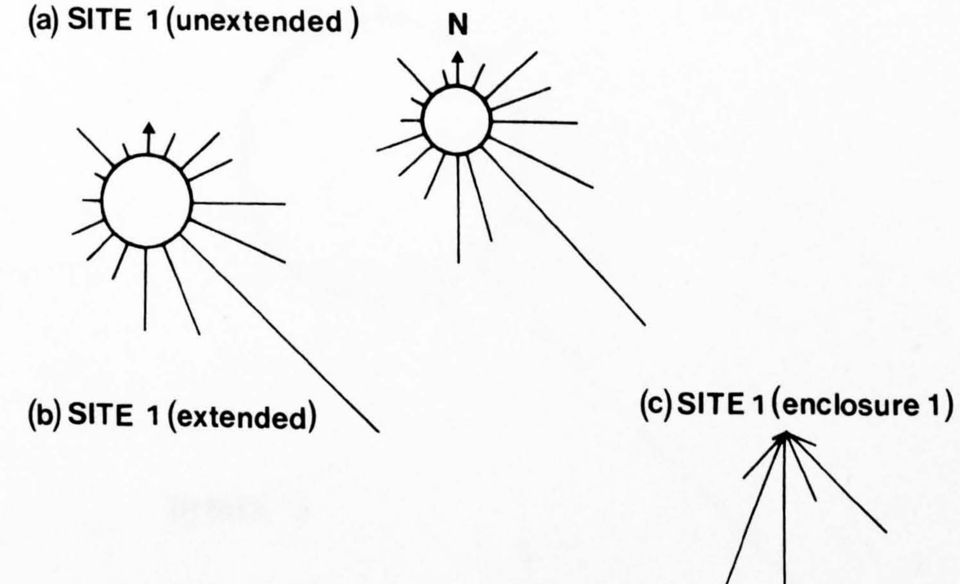
(c) SITE 1 (enclosure 1) n = 76

(d) SITE 1 (enclosure 2) n = 61

(e) SITE 2 n = 703

(f) SITE 3 n = 942

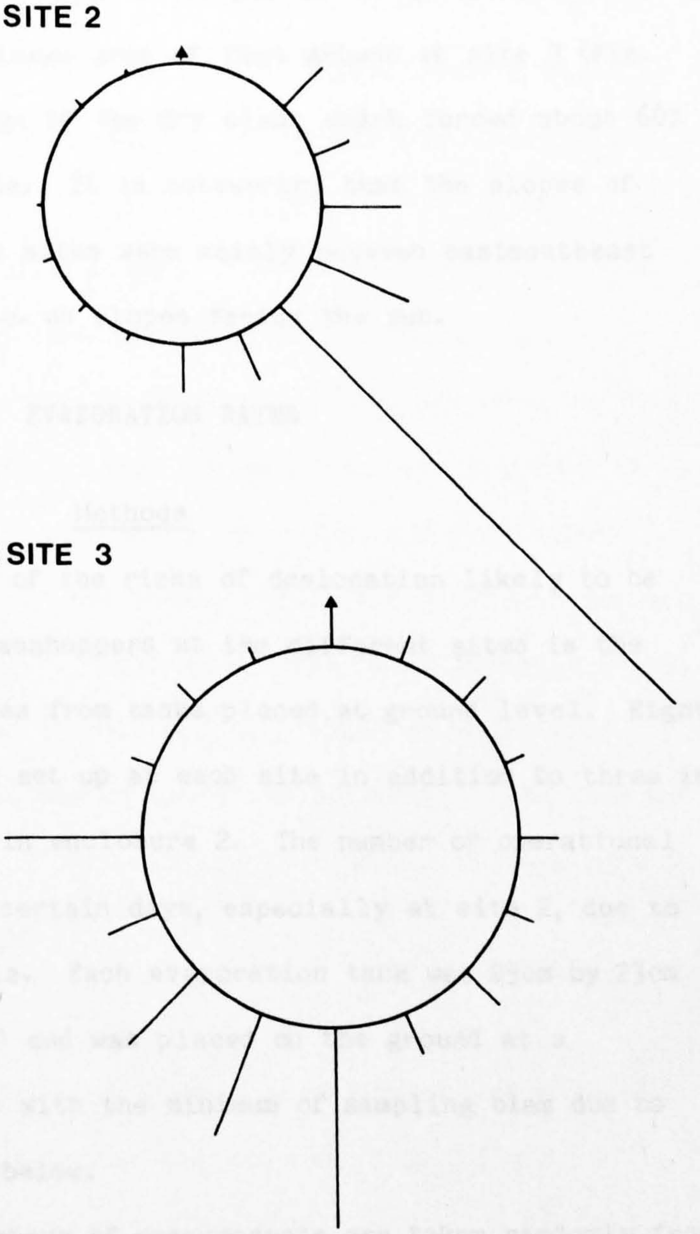
FIGURE 2.8: The distribution of aspects of the metre-square quadrats in each site and enclosure



(All drawings to same scale)

The lengths of the lines and the radii of the circles represent the proportion of each site (or enclosure) comprising slopes of the aspect indicated. The circles in the centres refer to the proportion of flat ground.

FIGURE 2.8. continued.



(e) SITE 2

(f) SITE 3

southeast-facing, whereas enclosure 1 was mainly south- and southsouthwest-facing with no flat ground. Enclosure 1 was therefore more likely to experience more solar radiation than the other enclosure and the site as a whole. The main slope of site 2 (albeit shallow; Fig. 2.7, Table 2.4) was towards the southeast, whereas the dune slopes at site 3 were mainly southerly with a large number of slopes in the quadrant between south and west. The large area of flat ground at site 3 (Fig. 2.8) was due to the edge of the dry slack which formed about 60% of the area of the site. It is noteworthy that the slopes of quadrats at all of the sites were mainly between eastsoutheast and westsouthwest, i.e. on slopes facing the sun.

2.7. EVAPORATION RATES

2.7.1. Methods

A direct measure of the risks of desiccation likely to be experienced by the grasshoppers at the different sites is the daily evaporation rates from tanks placed at ground level. Eight tanks were originally set up at each site in addition to three in enclosure 1 and four in enclosure 2. The number of operational tanks was reduced on certain days, especially at site 2, due to disturbance by vandals. Each evaporation tank was 23cm by 23cm in area (and 9cm high) and was placed on the ground at a randomly-chosen point with the minimum of sampling bias due to chance, as I explain below.

When small numbers of measurements are taken randomly from an area with an environmental gradient, one part of the gradient may be measured disproportionately often due to chance aggregation of the sample squares, and may produce a biased view of the degree of desiccation at the site. Therefore, in order to reduce such sampling bias, each site was split into three to five sections along the major habitat gradient (slope or vegetation structure) and each section sampled randomly with the same intensity. This stratified random sampling programme was used to choose the location of the evaporation tanks at each site. If the ground sloped at the spot on which the tank was placed, it was levelled. The vegetation type (Section 2.5.1.) at this spot was also recorded, since the structure of vegetation is known to influence both microclimate (Ruscoe, 1970) and the distribution of grasshoppers (Lensink, 1963; Von Sanger, 1977). It was therefore possible to examine more closely the desiccation risk experienced by first instars by taking into account their distribution in relation to vegetational structure (Chapter 6).

The daily evaporation rates for each tank was recorded on six occasions between 29 May and 9 June 1983, and then after changing the positions of the tanks, on another four days between 16 June and 20 June 1983. Evaporation rates were measured using a meteorological gauge for determining changes in water level; the depth of water lost per 24 hours was measured to the nearest 0.02mm, and the amount of rainfall in that period at each site was then subtracted from it.

2.7.2. Results

Site 1 was more desiccating than site 2 which was slightly but not significantly more desiccating than site 3 (Table 2.5 and below).

Most desiccating Least desiccating

1(2) 1 1(1) 2 3

(Wilcoxon Matched Pairs Signed Ranks Tests; $p_{crit} = 0.01$).

TABLE 2.5: **Rates of evaporation of water from randomly-positioned tanks at each site and in each field enclosure**

(All measurements in $mm.day^{-1}$)

	SITE 1			SITE 1 (enclosure 1)			SITE 1 (enclosure 2)			SITE 2			SITE 3		
Date	mean	range	n	mean	range	n	mean	range	n	mean	range	n	mean	range	n
29 May	3.50	1.62-6.38	7	3.66	2.62-6.63	4	4.02	3.13-3.49	3	2.23	1.61-2.76	8	1.80	1.20-2.51	8
2 June	2.01	0.69-3.14	7	2.34	1.99-2.70	4	2.58	2.35-2.87	3	2.17	1.83.2.53	5	2.10	1.60-2.58	8
5 June	2.92	1.84-3.93	8	3.03	2.54-3.65	4	3.26	2.68-3.79	3	2.75	2.16-3.22	7	2.50	1.95-2.95	8
6 June	6.59	4.52-8.60	8	6.09	5.20-6.96	4	6.30	5.90-6.70	2	5.69	4.80-6.94	8	5.30	3.48-6.06	8
8 June	3.86	2.70-5.38	8	3.70	3.51-3.82	4	4.01	3.30-4.61	3	3.30	2.72-3.55	8	3.01	2.20-3.69	8
9 June	2.83	2.30-3.46	8	3.00	2.34-3.38	4	3.49	2.50-4.10	3	1.44	1.08-1.84	8	2.61	2.11-3.27	8
16 June	1.79	1.17-2.65	8	1.42	0.99-2.01	3	1.50	1.43-1.57	4	1.04	0.80-1.22	3	0.79	0.21-1.61	8
18 June	4.40	3.20-5.98	8	4.61	4.45-4.77	2	4.46	4.10-4.78	4	3.15	2.62-3.73	4	3.37	2.30-4.57	7
19 June	5.32	4.26-6.10	8	5.15	4.66-5.68	3	5.06	4.54-5.82	3	4.74	4.20-4.98	7	4.21	2.88-5.54	8
20 June	6.35	5.00-7.62	8	5.50	5.06-6.34	3	5.97	5.46-6.34	4	5.62	4.84-6.84	7	4.83	3.60-6.80	8
	Grand Mean	95%CL	n	Grand Mean	95% CL	n	Grand Mean	95% CL	n	Grand Mean	95% CL	n	Grand Mean	95% CL	n
	3.99	2.94-5.04	10	3.79	2.89-4.69	10	3.99	3.07-4.91	10	3.38	2.36-4.40	10	3.05	2.17-3.93	10

Underlining joins together those groups which do not have significantly different daily evaporation rates. A more stringent significance level than usual was applied in order to reduce type I errors. The only other pair which showed a significant difference at the 0.05 probability level was the pair of enclosures at site 1 ($z = -2.344$, $p = 0.019$, $n=10$).

During the periods in which these evaporation measurements were made, wind speeds and directions, maximum daily temperatures, cloud cover, and rainfall varied considerably (Unpublished meteorological data, Ainsdale Sand Dunes NNR; pers. obs.). Therefore, the observed relative differences in evaporation rates probably reflected general summer differences between the sites.

2.8. SITE CHARACTERISTICS AND RESOURCES FOR THE GRASSHOPPERS

2.8.1. Microhabitat, microclimate, and grasshopper fitness

Lensink (1963) summarizes the major effects of vegetational structure on microclimate. Temperature variations tend to be most extreme on and just above bare ground and in very sparse low-growing vegetation (vegetation types I and II), whereas taller and denser vegetation provides shade and moisture. However, because the grasshoppers can climb up grass stems, they will be able to choose their preferred ambient temperature (and humidity). Anderson *et al.* (1979), M. A. Parker (1982), Begon (1983), Chappell (1983), and Gillis and Possai (1983) have noted the thermoregulatory behaviour of grasshoppers in the field. The difference in humidity between tall dense vegetation and bare ground (Lensink, op. cit.) is likely to be especially marked in the sand dunes where the bare ground is almost entirely quickdraining sand. In addition to the effects of vegetational structure, the grasshoppers may find shade and protection from the wind by locating ground with a suitable slope and aspect. This will be achieved more easily on the more undulating sites. Table 2.6 compares the site characteristics and the expectations that grasshoppers will be able to successfully regulate their water loss and body temperatures on these sites. These expectations correspond closely with the rates of evaporative water loss from the sites. Site 1, with the sparsest vegetation and no protective barrier of trees on any side (unlike the other two) was the most desiccating, and would seem to be the most physically stressful of the sites. Consequently, if all other things were equal, we would expect that grasshoppers from this site would have a lower lifetime reproductive success, or specific adaptations to withstand physical stresses, or both.

2.8.2. Other effects of habitat on grasshopper fitness

Tall dense vegetation can provide hiding places from some visual predators but may also provide concealment for some invertebrate predators. We cannot therefore predict the relative degrees of predation at the different sites, and this problem is cuurently being studied in detail at Ainsdale by A. J. Cherrill.

In addition to the effects of vegetational structure, the vegetation provides food for the grasshoppers. The diversity of plant species is known to influence grasshopper distribution (Otte, 1977), and mixed diets tend to be more beneficial to grasshoppers than single species diets (Uvarov, 1966; MacFarlane and Thorsteinson, 1980). Therefore, if all other things were equal, grasshoppers from site 2 would grow better than those from sites 1 and 3 (see Table 2.6).

TABLE 2.6: **Summary of site and field enclosure characteristics**

SITE (enclosure)	1	1(1)	1(2)	2	3
Topography	Undulating, mainly SE-facing	Mainly south-facing	Mainly SE-facing	Almost flat	Largely flat but with some very steep slopes
Vegetational structure	Mainly low-growing and sparse	Mainly low-growing and sparse	Mainly low-growing and sparse	Intermediate between sites 1 and 3	Has the tallest and densest vegetation
therefore...	Little scope for behavioural homestasis by less motile animals	Very little scope for behavioural homeostasis	Very little scope for behavioural homeostasis	Intermediate scope for behavioural homeostasis	Considerable scope for behavioural homeostasis
This corresponds with daily evaporation rates, thus:	High	High	High	Low	Lowest
Amount of grass ('food')	Low	Low	Low	Intermediate	High
Grass diversity	Intermediate between site 2 and enclosures	Low	Lowest	Highest	Intermediate between site 2 and enclosures
Amount of bare sand	High	High	High	Lowest	Low

Grass, as food, may be a limiting resource for which the grasshoppers compete to different extents at the different sites. Although there are marked differences in the amounts of grass at the sites, indices of competition cannot be produced until we know the relative densities of grasshoppers at the three sites. Similarly, the amount of sandy ground may be limiting if adults compete over such areas in order to secure an oviposition site, but the relative densities of adults must first be known before the relative degrees of competition can be assessed. In Chapter 3, I describe the relative densities of grasshoppers at the three sites, and how they change with time. From this data and from the data in this chapter, I can then compute (in Chapters 4 and 6) measures of the density of competitors in relation to the abundance of different resources.

CHAPTER 3: **Variation in density, mortality and developmental rates in the grasshoppers, *Chorthippus brunneus* and *Myrmeleotettix maculatus***

SUMMARY

1. Grasshopper densities increased from 1981 to 1982. The marked increase in 1982 in the enclosures at site 1 corresponded with the higher mean temperatures within them.
2. The sex ratios of the adults of five of the populations were significantly male- or female-biased, but no consistent relationships between the sex ratio and site were detected.
3. Adults were lost from the populations (by mortality and emigration) at a greater rate than juveniles.
4. *C.brunneus* were lost at a lower rate from the populations than *M.maculatus*, and this was likely to be due to differences in survivorship rather than emigration, since *C.brunneus* tended to emigrate more than *M.maculatus* from the sites.
5. Losses of grasshoppers from the populations were more rapid in the cooler, wetter 1981 season than in 1982.
6. There was no consistent effect of site on the rate at which grasshoppers were lost from the populations, and the effects of density-related factors were not conclusive.
7. Differences in the losses of grasshoppers among the enclosures and the surrounding site were consistent with the rates of evaporation of water from them - the more desiccating areas having a higher rate of loss.
8. The larger *C.brunneus* had a longer developmental period than *M.maculatus*, and developmental periods were shorter in the warmer 1982 spring than in 1981.

9. For each species in each year, the time period (t) between the date a given proportion of a population moulted into second instars (t_{ii}) and the date the same proportion had moulted into adults (t_v) decreased in those populations where t_{ii} was late. This relationship held even though the relative moulting dates at the sites varied from species to species and from year to year, but also from one proportion of a population to another: it correlates with a general increase in mean temperature as the season advanced.

3.1. INTRODUCTION

The primary objective of this study is not to show how the amounts of resources affect population size and changes in the numbers of grasshoppers, but to investigate how all of these, and other factors, affect the phenotypes of the grasshoppers.

Many studies have shown a link between population density and the phenotype of acridids which swarm (review in Uvarov, 1977), and a major body of life-history theory predicts specific evolutionary responses to selection at high densities (Pianka, 1970; Stearns, 1976). Changes in the intensity of competition may also result from changes in the amounts of particular resources (Dempster and Pollard, 1981), and clearly any comparison of density-dependent relationships should include some measurement of the amount of limiting resource, especially if it varies considerably between the populations under investigation. In this study, the density of particular stages of the life history and the amounts of several resources are related to specific phenotypic traits such as adult size (Chapter 4) and egg size (Chapter 6). The data on grasshopper density required for this purpose are presented in this chapter. In addition, some ecological correlates of population density are briefly described.

At high density, a greater proportion of the population may die or emigrate, and this possibility, too, will be examined, especially in relation to the amounts of particular resources at the sites.

Because the nature of a life history depends on the timing of events such as hatching and moulting, I will also, in this chapter, describe the correlates of moulting date and nymphal developmental period.

3.2. GENERAL METHODS

3.2.1. Grasshopper sampling

Sampling by sweep-netting underestimates the numbers of first instars in the population (Richards and Waloff, 1954) and may vary in efficiency depending on the structure of the vegetation (Clark, 1948). An absolute method of assessing grasshopper abundance was therefore used in which all the grasshoppers were counted in randomly-chosen 1m^2 units. In order to avoid the disproportionate sampling of certain parts of those sites with a strong environmental gradient (which may occur due to chance aggregation of the sample units when small numbers of samples are taken) each site was split into three to five sections along the major habitat gradient (slope or vegetation structure) and each section sampled randomly and with the same intensity. Wooden pegs were positioned every 5 or 10m, depending on the site topography, in the form of a grid from which co-ordinates were produced. Random co-ordinates used for sampling in 1981 were obtained from Fisher and Yates (1953), and in 1982 were generated by a computer random number generator.

Each site was sampled on sixteen successive occasions in 1981 and on twenty-one occasions, with two supplementary visits to site 3, in 1982. On each occasion the numbers of each instar of each species were recorded in usually not less than thirty $1m^2$ quadrats. For the third and later instars the grasshoppers' sex was also noted. Each quadrat was approached facing the sun to avoid casting a shadow over the grasshoppers, and a $1m^2$ box-quadrat with a fine nylon netting forming a funnel over its area was quickly and quietly placed over the sample square. The funnel allowed me to get my head and arms into the quadrat whilst preventing the grasshoppers' escape. Box-quadrats have also been used for sampling C.brunneus or M.maculatus (or both) by Lensink (1963), Robinson (1973), Bradley (1975), Monk (1983), and Grayson (1984). This method also gives information on the degree of aggregation of grasshoppers which can then be utilized to examine local crowding as well as the overall density of grasshoppers (see Chapter 6). After searching thoroughly for the grasshoppers in each quadrat and identifying any I found, the grasshoppers were released next to their sample square. Samples were not taken on cold overcast or rainy days when the vegetation was wet; this avoided the underestimation of grasshopper numbers, since they remain immobile in cold conditions (Richards and Waloff, 1954), and avoided causing excessive mortality amongst the small early instars which get caught up in water droplets (Lensink, 1963). In order to maintain large enough sample sizes (30+) during periods with intermittent cold wet weather, sampling was sometimes extended into the next suitable day.

Approximately 30% of site 3 had dense vegetation with no or very few early-instar grasshoppers. Therefore, about fifty samples were usually taken from this site early in the season so that the sample size was not reduced in the areas where the grasshoppers did occur.

3.2.2. Measurements of temperature differences

Chapter 2 has described how each of the three nearby sites shows variation in vegetation structure, in their aspects - and therefore in microclimate (Ruscoe, 1970) and in the scope for behavioural thermoregulation by the grasshoppers (Anderson *et al.*, 1979; Begon, 1983; Chappell, 1983; Gillis and Possai, 1983; M.A. Parker, 1982). Less variation was found in the enclosures at site 1, and the presence of metre-high polythene walls may have altered the microclimate within. Consequently, the grasshoppers may have been subjected to a different mean temperature or amount of solar radiation than the surrounding undulating site and may have been unable to find locations with a suitable microclimate. Temperature differences between each of the enclosures and the outside site were therefore measured during one week in mid-August 1983 and repeated during the following week using a total of 119 "Berthet tubes" (Berthet, 1960) containing buffered sucrose solution placed at ground level and at 10cm above the ground. The tubes were covered in aluminium foil to prevent "greenhouse" effects and were attached, one at each height, to canes randomly located in each enclosure (or in the site).

The sucrose inversion method for mean temperature measurements (Berthet, 1960) is particularly apposite for comparing the site and enclosure temperatures experienced by grasshoppers. This is firstly because the rate of inversion, like those of metabolic processes, is not linear with temperature

- higher temperatures are relatively more important. Secondly, the temperature at a large number of stations can be measured since the method is relatively cheap and rapid; this permits a comprehensive comparison between sites and enclosures with samples taken from the full range of microhabitats of each.

Another possible source of major variation in the temperature profiles experienced by grasshoppers in the different populations was the weather differences between years. Differences in grasshopper mortality and developmental rates between the two years were related to the differences in maximum daily temperature at Ainsdale Sand Dunes NNR meteorological station which were kindly made available to me by the warden.

3.3. GRASSHOPPER DENSITY

3.3.1. Variation in density

Figure 3.1 shows the partial population curves for the grasshopper populations. In 1982, sampling from the enclosures ceased before June 2 because the densities within them were then altered for another experiment.

Although site 1 was extended in 1982 in order to avoid the confounding effects of migration and mortality in the analysis of survivorship, especially of *C.brunneus* (Section 3.4) it was more appropriate when comparing densities at the same site between years to consider the density within the same area (i.e. the original unextended site) in the two years.

M.maculatus was more abundant than *C.brunneus* in each site (or enclosure) in each year, and all populations except that of *M.maculatus* at site 2 increased from 1981 to 1982 (Table 3.1). The largest population increases of each species between years

FIGURE 3.1: **Partial population curves for C.brunneus and M.maculatus at each of the three sites and two enclosures in 1981 and 1982.**

(a)-(e): C.brunneus, 1981

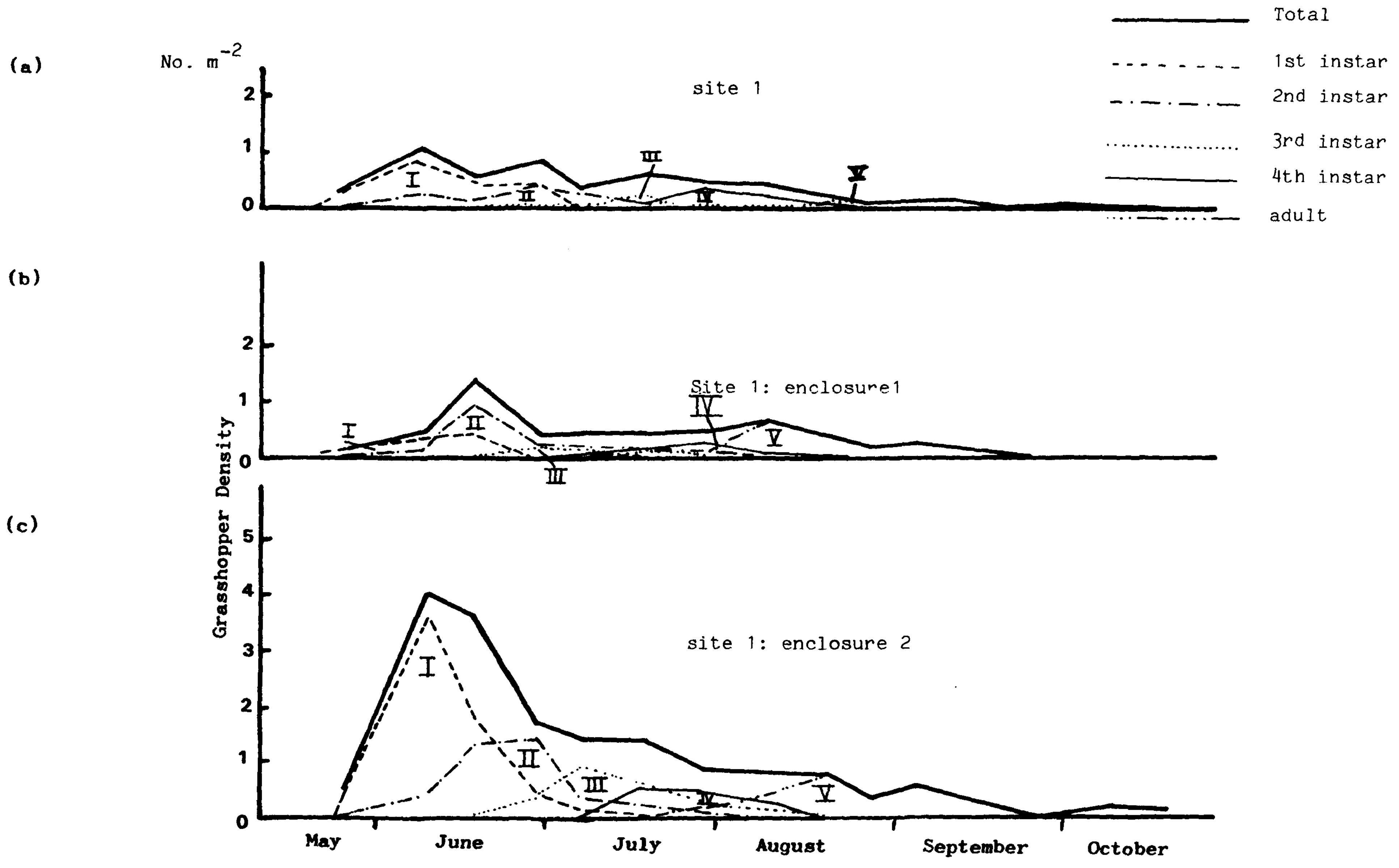
(f)-(j): M.maculatus, 1981

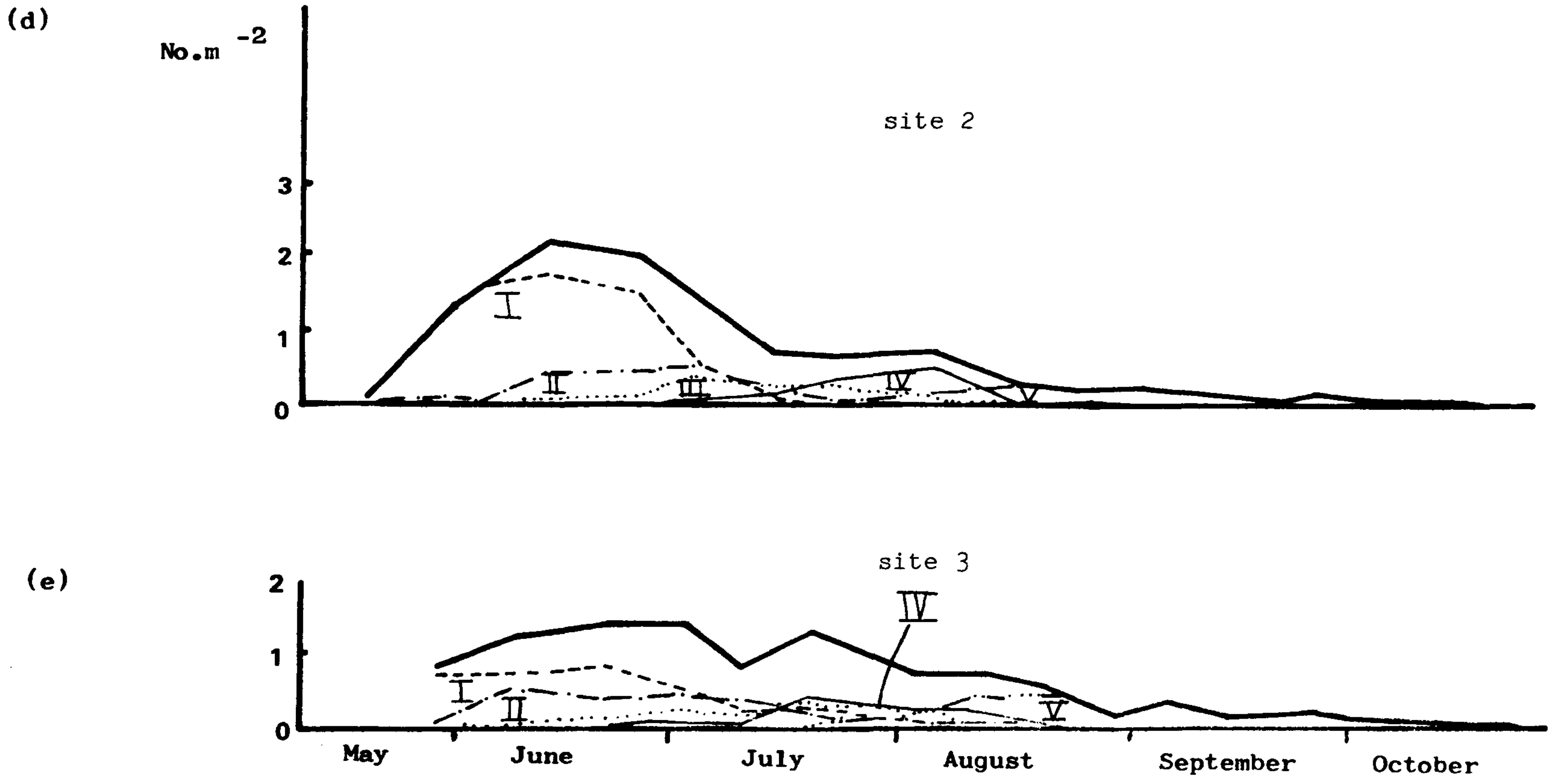
(k)-(o): C.brunneus, 1982

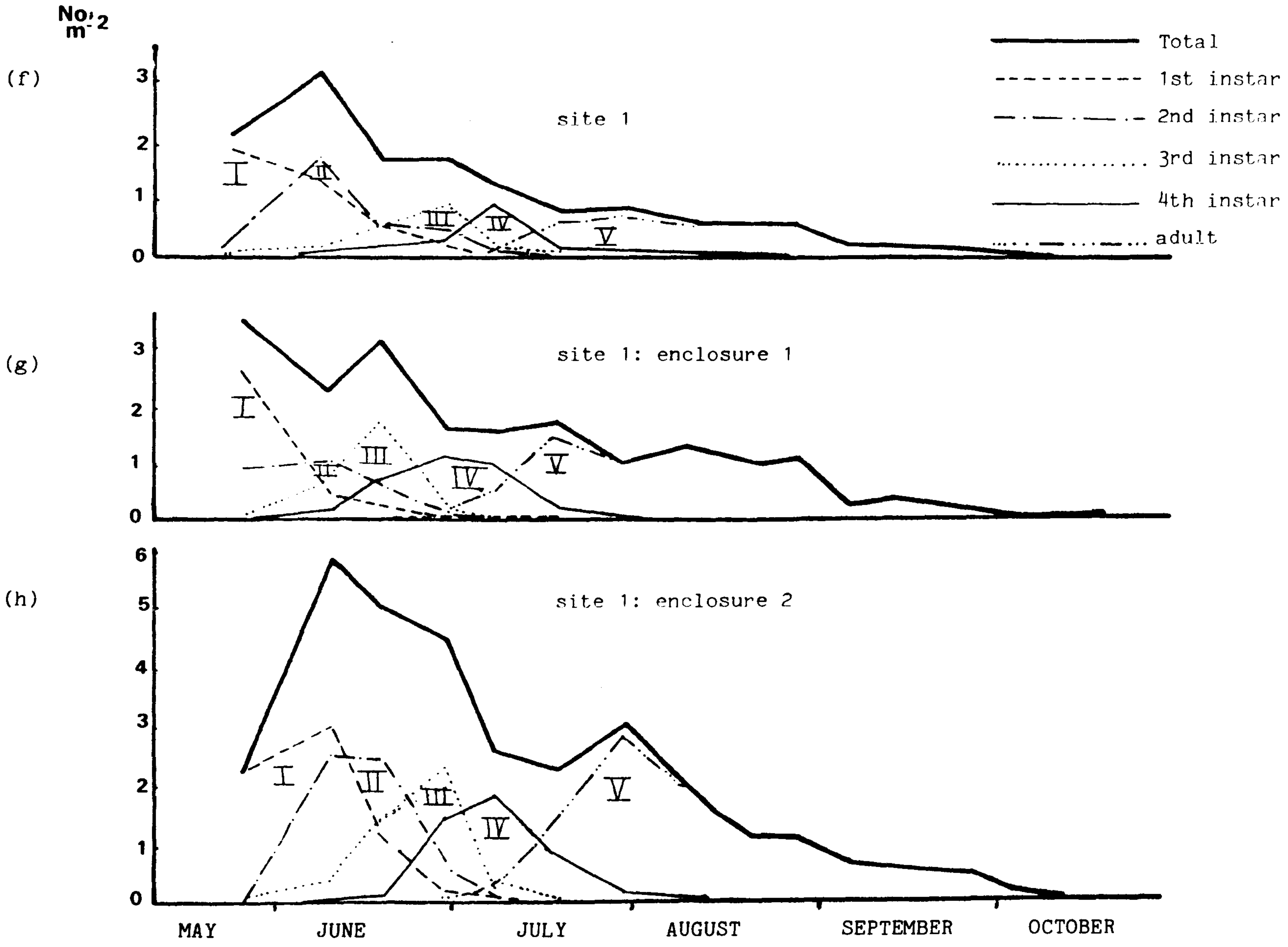
(p)-(t): M.maculatus, 1982

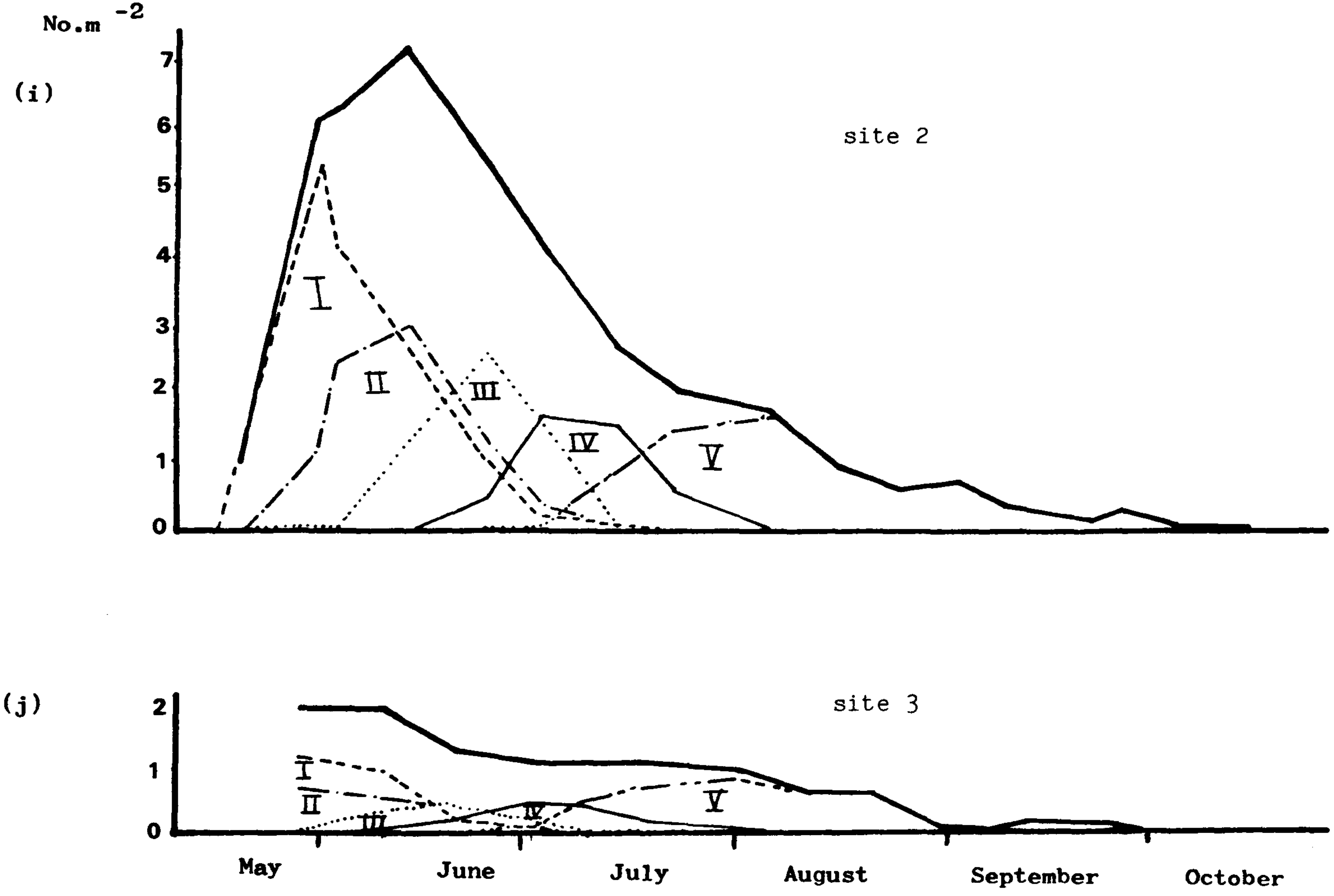
(u) : M.maculatus, 1982 at site 1 (unextended)

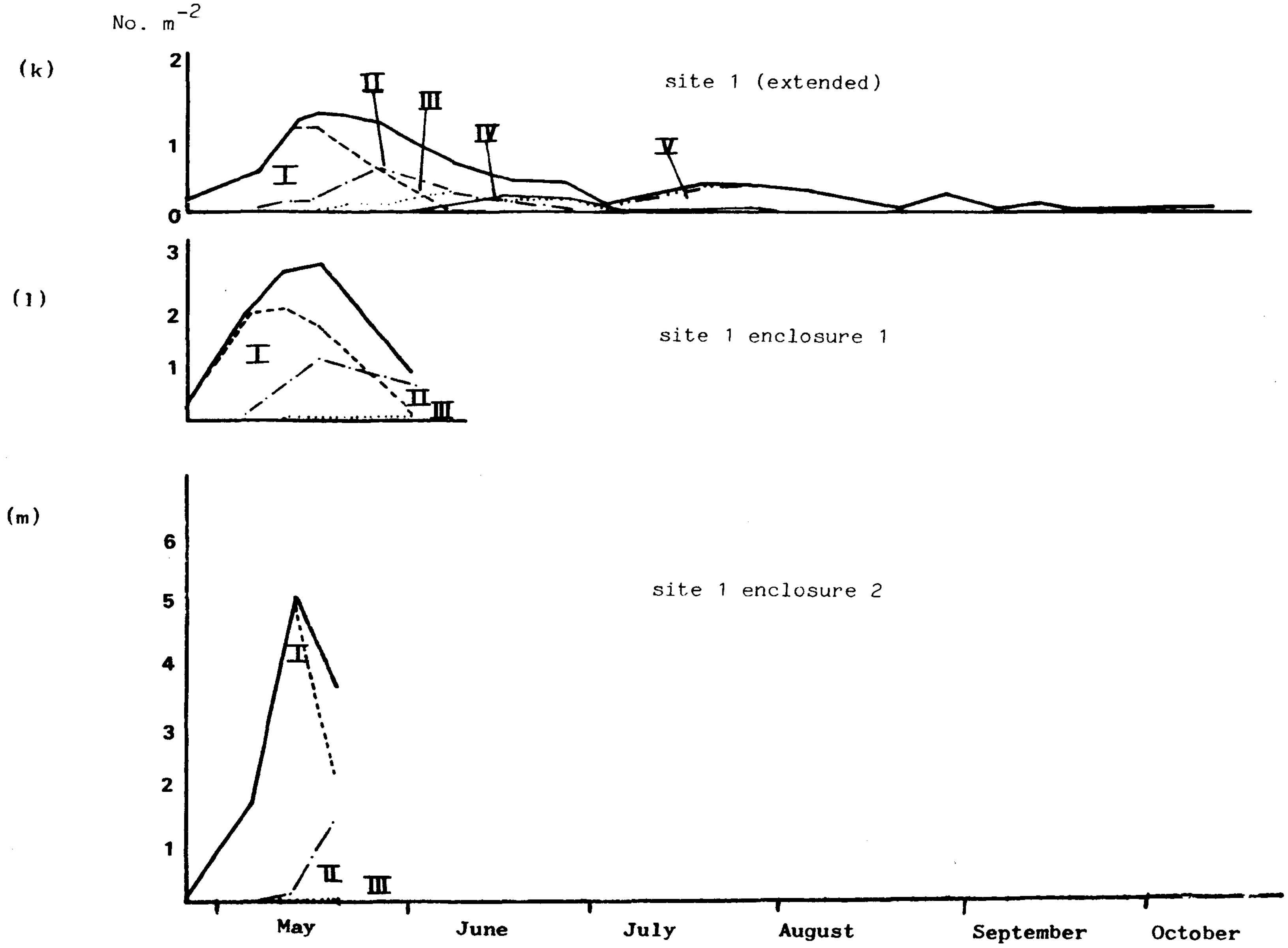
(v) : C.brunneus, 1982 at site 1 (unextended)


(a)
No. m-2
site 1
(b)
Site 1: enclosure1
(c)
site 1: enclosure 2
Grasshopper Density
0
1
2
3
4
5
I
II
III
IV
V
May
June
July
August
September
October
Total
1st instar
2nd instar
3rd instar
4th instar
adult

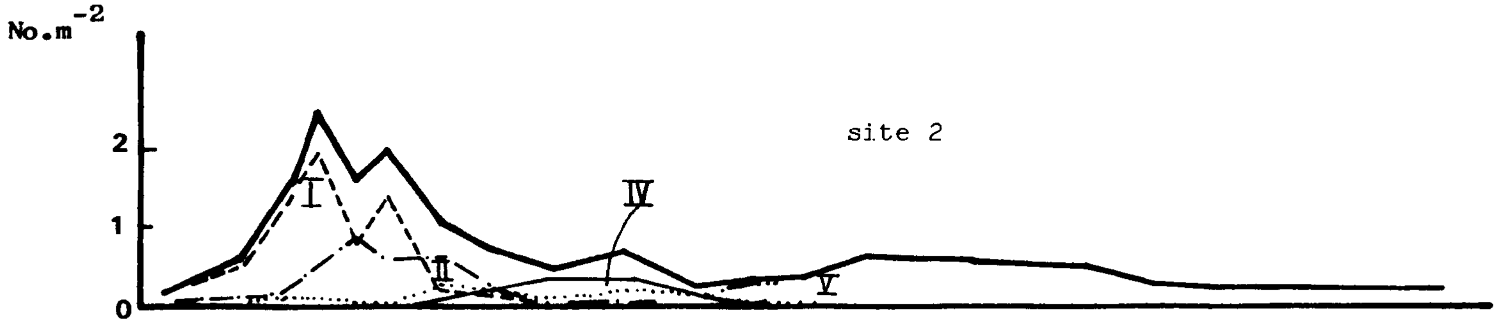

(d)
No.m -2
site 2
3
2
1
0
I
II
III
IV
V
(e)
site 3
2
1
0
I
II
IV
V
May
June
July
August
September
October


No. m-2
(f)
site 1
(g)
site 1: enclosure 1
(h)
site 1: enclosure 2
Total
1st instar
2nd instar
3rd instar
4th instar
adult
I
II
III
IV
V
0
1
2
3
4
5
6
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER

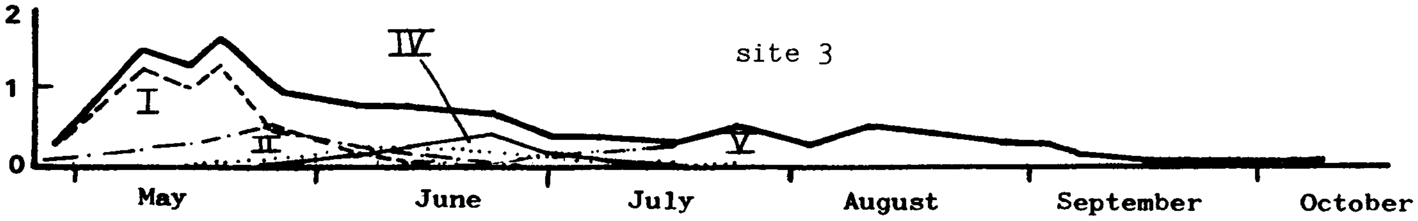

No.m -2
(i)
site 2
7
6
5
4
3
2
1
0
I
II
III
IV
V
(j)
site 3
2
1
0
I
II
III
IV
V
May
June
July
August
September
October

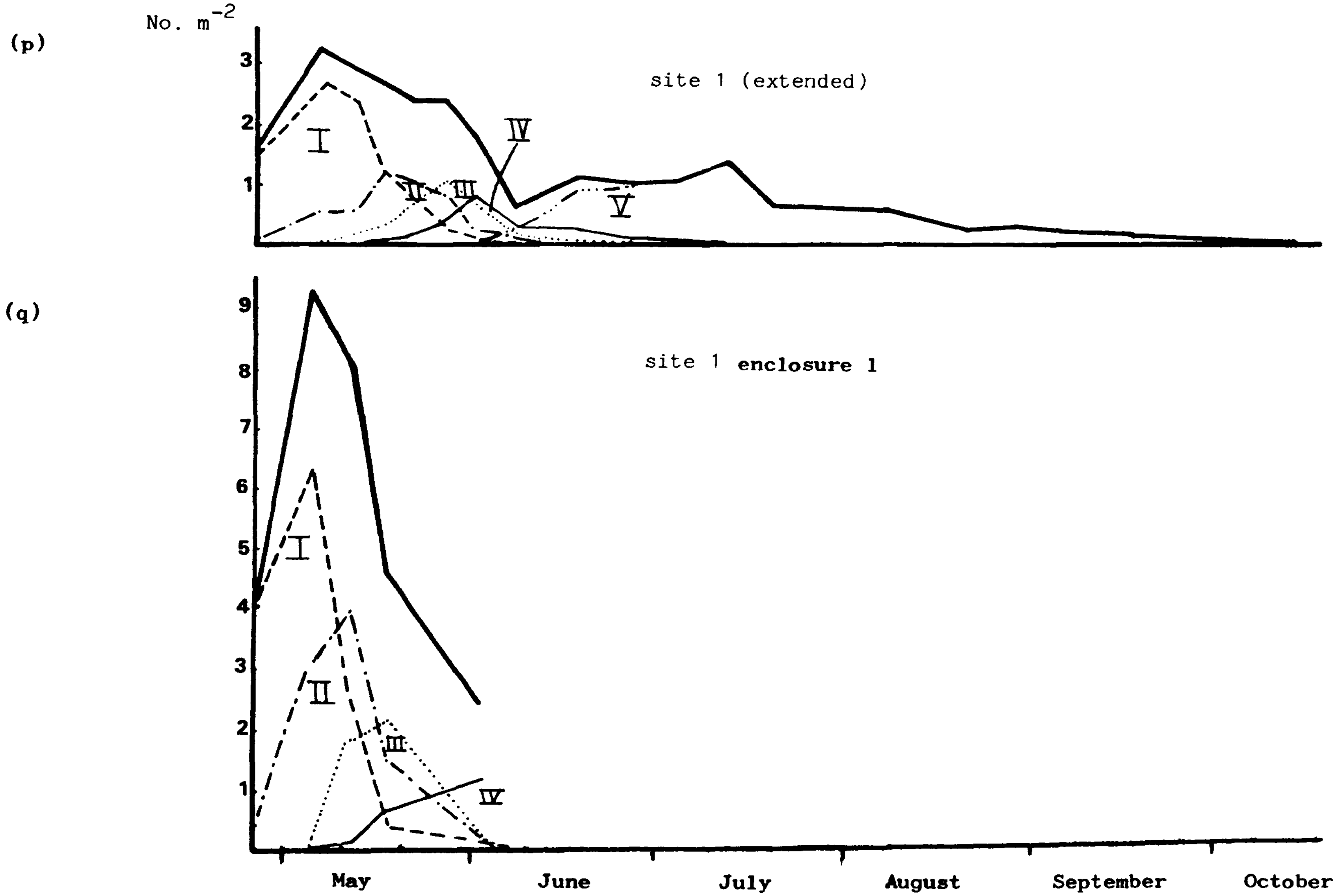

No. m^{-2}
(k)
2
1
0
site 1 (extended)
I
II
III
IV
V
(l)
3
2
1
site 1 enclosure 1
I
II
III
(m)
6
5
4
3
2
1
site 1 enclosure 2
I
II
III
May
June
July
August
September
October

(n)


No.m^{-2}
2
1
0
site 2
I
II
IV
V

(o)


2
1
0
site 3
I
II
IV
V
May
June
July
August
September
October


(p)
No. m^{-2}
3
2
1
site 1 (extended)
I
II
III
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9
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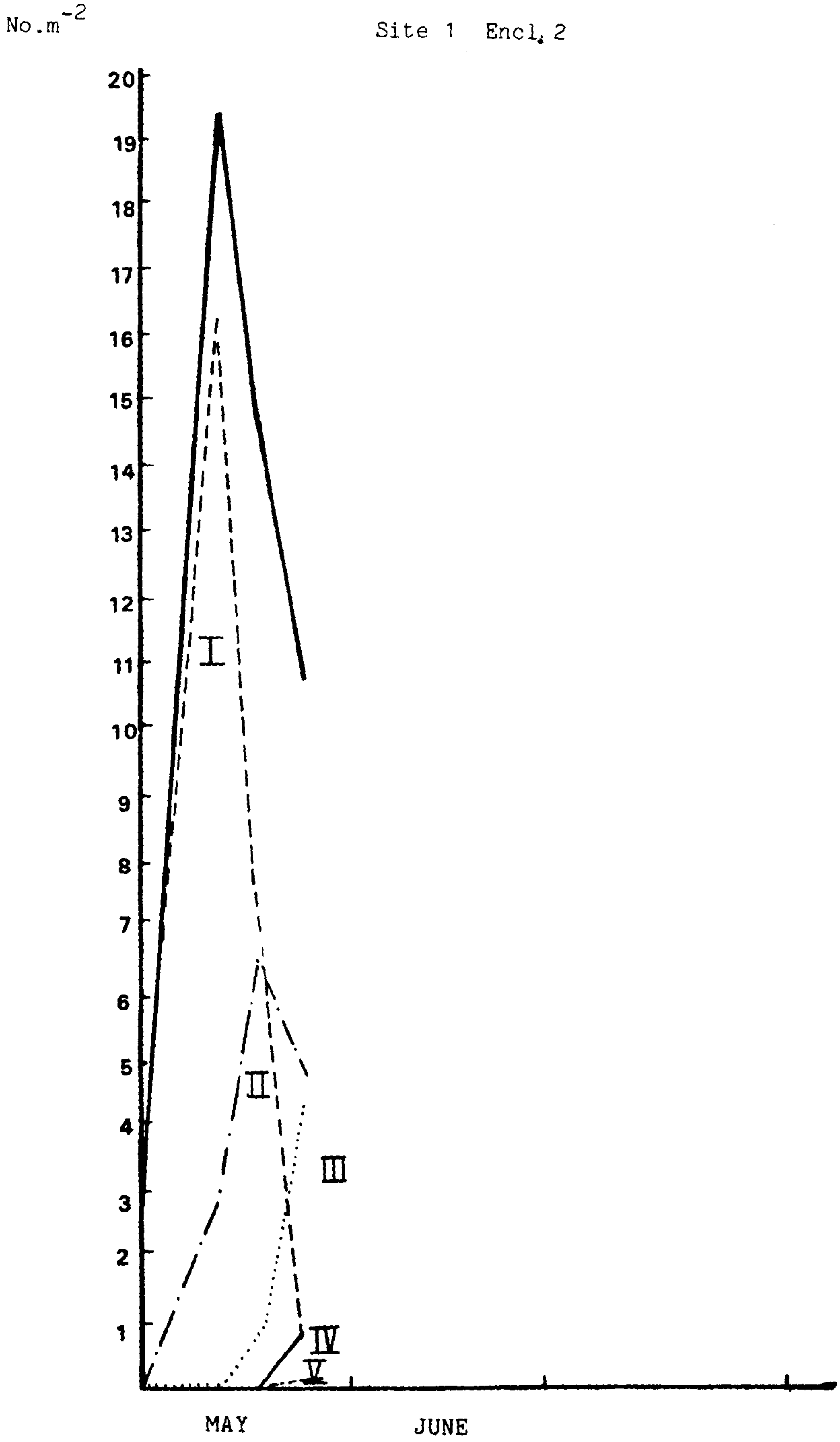
(r)


No.m^{-2}
Site 1 Encl. 2
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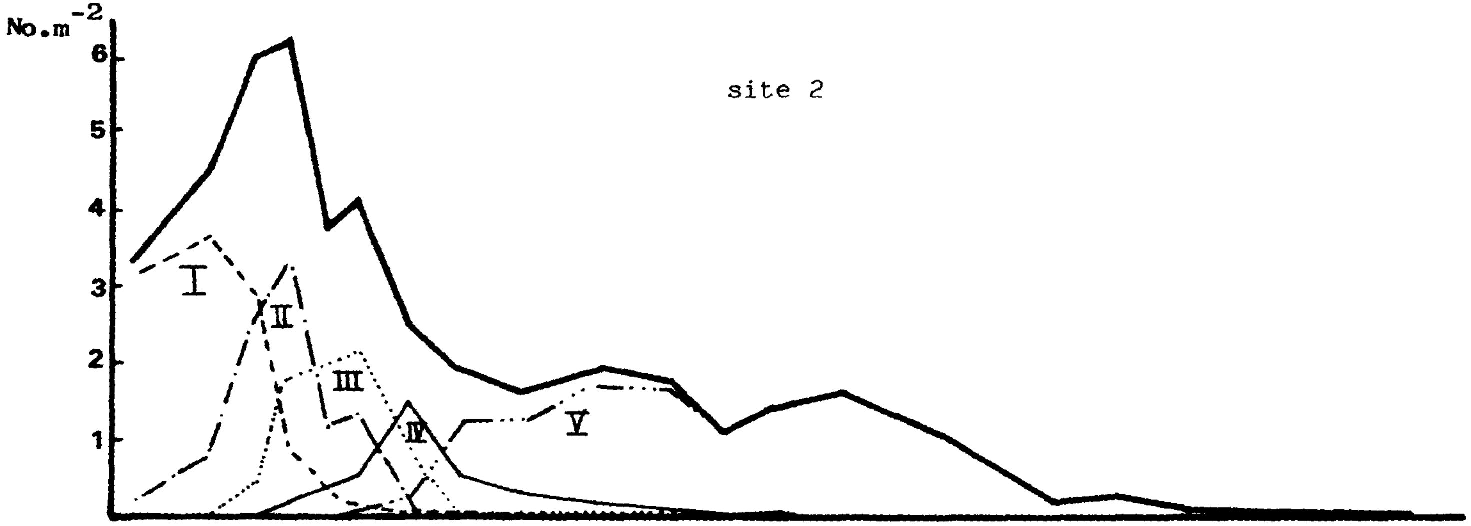
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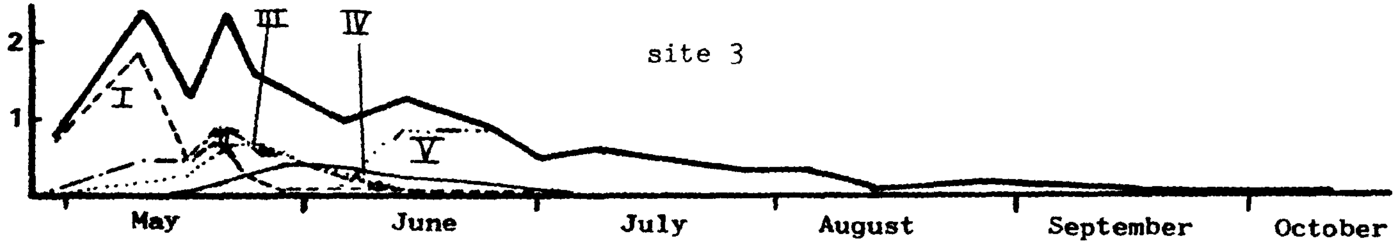
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May
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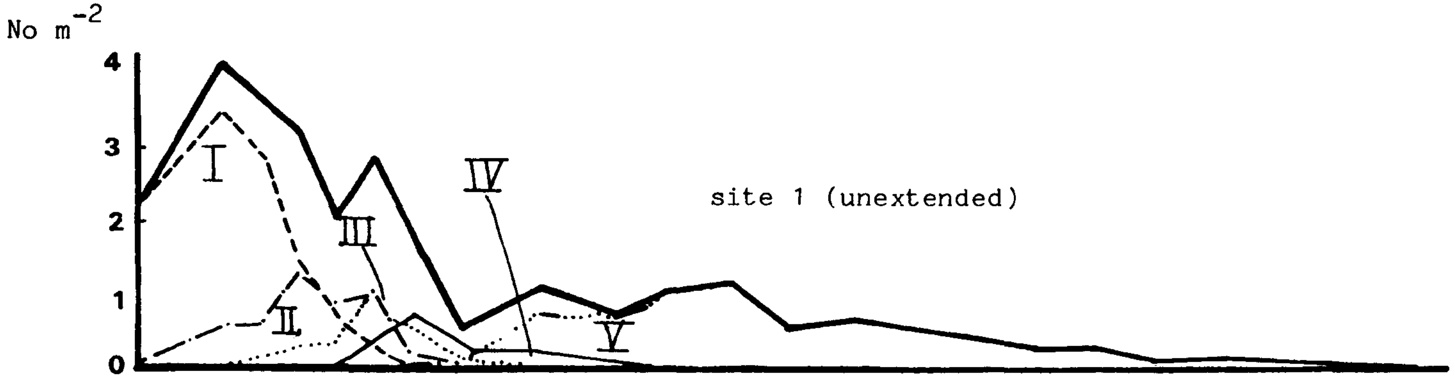
(u)


No m^{-2}
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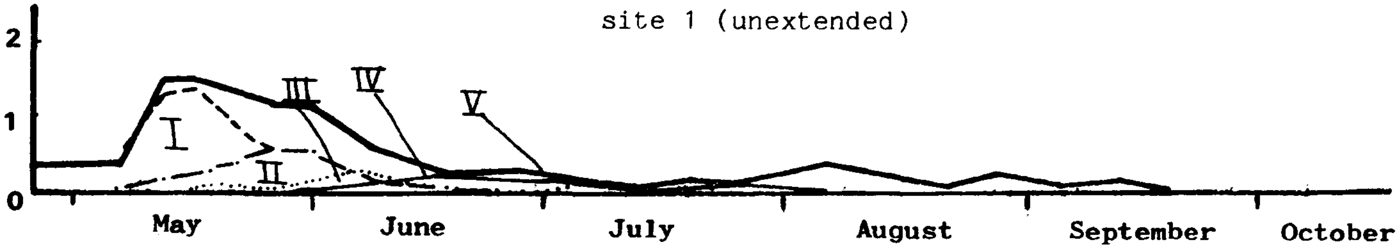
site 1 (unextended)

(v)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site 1 (unextended)
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September
October

TABLE 3.1: Peak densities of each species of grasshopper at each site (or enclosure) in 1981 and 1982.

		Highest density ←				→ Lowest density
M. maculatus 1981						
	site (enclosure)	2	1(2)	1(1)	1	3
	density (no.m^{-2})	7.2	5.8	3.4	3.1	1.9
M. maculatus 1982						
	site (enclosure)	1(2)	1(1)	2	1	3
	density	19.4	9.2	6.3	4.0	2.4
C. brunneus 1981						
	site (enclosure)	1(2)	2	3	1(1)	1
		4.0	2.2	1.4	1.3	1.0
C. brunneus 1982						
	site (enclosure)	1(2)	1(1)	2	3	1
	density	5.1	2.6	2.5	1.6	1.4

were in the enclosures at site 1: this was especially marked in M.maculatus which increased about three-fold between years (Table 3.1). The reasons for such large increases in the enclosures are investigated in Section 3.3.2.2.

When the field enclosures are excluded from the comparison, the rank order of sites from highest density to lowest density of each species remained the same in the two years, with site 2 having the highest density of both species and site 1 having more M.maculatus than site 3 but fewer C.brunneus (Table 3.1).

Some populations showed significant differences in the density of the sexes of the adults, though no consistent relationships with species, site or year were detected (Table 3.2). A strongly male-biased sex ratio may lead to a strong selection pressure on males for large size and competitive ability. The data presented in the present chapter can therefore be used to examine whether sexual selection on male size is likely to be an important determinant of male size differences among the populations (Chapter 4).

3.3.2. Correlates of density differences

3.3.2.1. Vegetation

Although this study is chiefly concerned with the effects of environment on grasshopper phenotype, there are a few points relating to variation in density which can be made by referring to the data collected.

Predicting the density of grasshoppers in an area will depend upon whether they are normally at the carrying capacity of the site or frequently have their density perturbed by density-independent factors or some other destabilizing influences. In the case of the former, the density of grasshoppers would depend

TABLE 3.2: **Mean adult sex ratios of M.maculatus and C.brunneus at each site and field enclosure in 1981 and 1982**

Data were obtained from sequential random samples of the grasshopper populations.

[1] Statistical significance of the sex ratios were tested using Wilcoxon's Matched-Pairs, Signed-Ranks test ($p_{crit} = 0.05$).

Species	Site (enclosure)	Year	No. visits	No. adults	Sex ratio (M/F)	P^1
M. maculatus	1	1981	10	102	1.170	0.314
	1(1)	1981	13	104	0.962	1.000
	1(2)	1981	10	146	0.896	0.151
	2	1981	11	222	0.740	0.050
	3	1981	11	180	0.782	0.131
	1	1982	14	206	1.675	0.006
	2	1982	14	360	1.278	0.124
	3	1982	16	196	0.980	0.861
C.brunneus	1	1981	8	25	2.125	0.183
	1(1)	1981	5	24	0.500	0.138
	1(2)	1981	9	44	1.200	0.529
	2	1981	8	37	0.947	0.933
	3	1981	12	100	1.778	0.019
	1	1982	12	65	1.600	0.158
	2	1982	13	108	1.634	0.011
	3	1982	16	121	1.574	0.004

on the amount and availability of limiting resources. The dual requirements of acridids - for vegetation, to provide food and shelter, and for bare ground, to provide oviposition sites - limit the areas in which the animals can live. Dempster (1963) mentions not only that high density populations develop in areas with mosaic vegetation but also that the limiting requirement is likely to depend on the habitat occupied. The following example makes this point. The fact that both species of grasshopper were most abundant at site 2 - which had the least amount of bare sand (Chapter 2) - suggests that the avaiability of oviposition sites was not the main cause of differences in density between site 2 and the rest. However, this does not preclude the possibility that it is only the amount of bare sand which prevents the population at site 2 being even larger.

Site 2 also did not have the most grass, though it did have more grass with thin-edged blades (grasses excluding Festuca) than the other sites (Chapter 2). [The amount of thin-edged grasses may be a more realistic measure of food abundance, especially for the very small nymphs which cannot easily feed on the rounded leaves of Festuca (Bernays and Chapman, 1970a; see also Section 3.4.4.1)]. Population densities might therefore be influenced by the quality as well as the abundance of grass.

Differences in the density of the two species at each site and between sites are likely to be influenced, in part at least, by the structure of the vegetation. This is supported by the observation that within each site nymphs of C.brunneus moved into taller and denser vegetation than M.maculatus, and that C.brunneus was relatively more abundant at the sites with denser vegetation (Table 3.1 and Chapter 2). The relationship between grasshopper distribution and the structure and composition of vegetation has been well documented in other grasshoppers (Vestal, 1913; Clark, 1948; Dempster, 1955; Lensink, 1963; Otte, 1977; Uvarov, 1977; Von Sanger, 1977; Joern, 1982).

3.3.2.2. Temperature

The most notable change in density was the increase in the enclosures between 1981 and 1982, particularly of M.maculatus in enclosure 2 (Table 3.1; Fig. 3.1). A number of factors could have affected survivorship and fecundity inside the enclosures, including reduced predation, a change in food quality - resulting from either a reduction in rabbit grazing (Grayson, 1984) or an alteration in microclimate - or an increased temperature.

Any exclusion of predators was probably negligible since the enclosed areas were likely to have enclosed some invertebrate predators as well as the grasshoppers. Also, the walls were taken down for the winter period, and birds were free at any time of year to land inside the enclosures.

Unlike the experiment described by Grayson (op. cit.) in which the vegetation structure changed markedly where rabbits were excluded, the only noticeable effect on the enclosed vegetation was an apparent increase in the number of flowering heads of the grasses. Food quality rather than quantity may have been affected, and grass samples have been collected as part of a larger study by M. Begon and myself in which nitrogen contents will be compared.

The mean temperature was significantly different among the enclosures and the site, both at ground level and at 10cm above ground (Table 3.3). The pattern was the same at both heights:

TABLE 3.3: Analysis of variance table to show the differences in air temperatures among enclosures and site 1

Ground Temp.

Source of Variation	Df	MS	F	P
Enclosure/Site	2	22.695	6.311	0.004
Expt.	1	0.580	0.161	0.690
Encl./Site x Expt.	2	0.725	0.202	0.818
Error	48	3.596	-	-
Total	53	4.165	-	-

Temp. at 10 cm

Source of Variation	Df	MS	F	P
Encl./Site	2	10.424	6.106	0.004
Expt.	1	0.728	0.426	0.516
Encl./Site x Expt.	2	1.084	0.635	0.534
Error	59	1.707	-	-
Total	64	1.950	-	-

Temp. = temperature; Expt. = Experiment (I or II)
Encl. = Enclosure (1 or 2)

Site (enclosure)	1(1)	1(2)	1
Mean ground temperature (deg.C)	22.39	22.11	20.43

Site (enclosure)	1(1)	1(2)	1
Mean temperature at 10cm above ground (deg.C)	20.54	19.71	19.14

A common underlining joins together those areas between which no significant difference in mean temperature was detected (SNK multiple range test, $p_{crit} = 0.05$).

The tendency, therefore, was for the most south-facing enclosure (enclosure 1) to be slightly, though not significantly, warmer than enclosure 2, and for the surrounding site to be cooler than both on average.

Since the metabolism of poikilotherms is generally faster at higher-than-average environmental temperatures, and since *C.brunneus*, at least, needs a higher body temperature than the normal range of ambient temperatures in order to reproduce (Begon, 1983), it is possible that the grasshoppers in the enclosures were able to feed *and* reproduce faster. However, because the ranges of vegetation types and topographies in the enclosures were smaller than those of the sites (Chapter 2), the grasshoppers may have been less able to regulate their water loss, and this may have adversely affected the animals which failed to find a suitable microclimate.

The densities of grasshoppers in enclosure 1 are not strictly comparable between years because the adult females were temporarily removed on several occasions in 1981 in order to collect egg pods from them (Chapter 6). We would therefore expect that any increase in population size in enclosure 1 between years would be relatively lower than in other areas. In enclosure 2, conditions seemed to have been more favourable for

M.maculatus than C.brunneus. This may have been because the enclosures lacked the dense vegetation into which C.brunneus tended to move. Tall and dense vegetation not only provides a less desiccating microenvironment (Ruscoe, 1970) but also the means by which grasshoppers could potentially regulate their body temperature since the air was significantly cooler at 10cm above ground than at ground level ($t=6.72$, $p<0.001$, $n=49$ pairs).

When there is variation in grasshopper density among sites, the potential for differences in the degree of competition is obvious. Competition has been postulated as one of the major causes of life-history variation (Pianka, 1970), and this will be considered in more detail in chapters 4 and 6.

Variation in density may also affect the differences in mortality or emigration rates among populations. This possibility will be investigated in the next section.

3.4. MORTALITY AND EMIGRATION

3.4.1. A comparison of adult and juvenile losses

3.4.1.1. Estimating differences in rate of loss

In 1981, emigration from site 1 was noticed during the juvenile period. (This was probably associated with occasional movements of adults back to the sandy areas of the study site to lay eggs - leading to apparent population increases during the adult phase). Because of this, the area of site 1 was extended in 1982 to include more of the denser vegetation where the later instars and adults gathered. There may also have been some migration of M.maculatus out of the original site and into the adjacent vegetation in 1981 (Fig. 3.2). Movement of C.brunneus

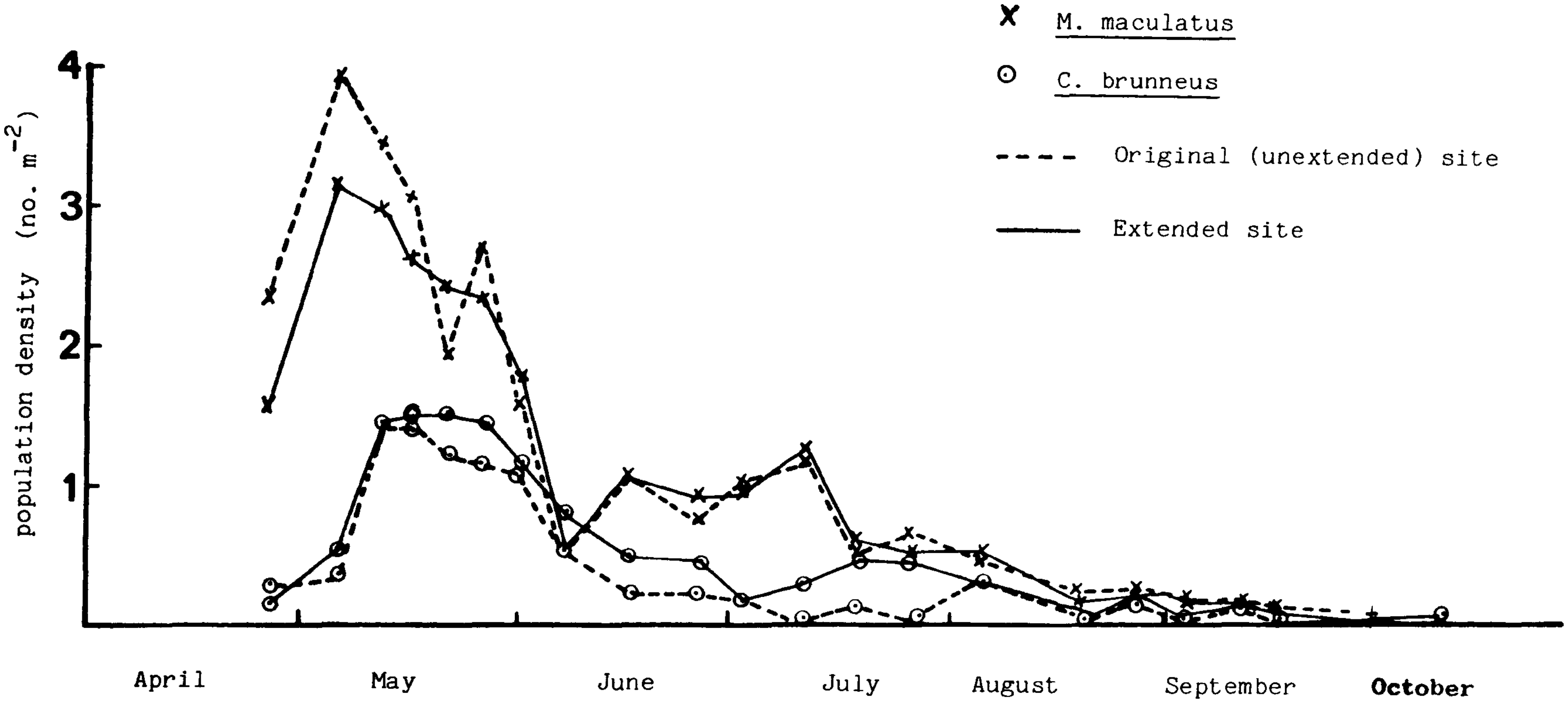


FIGURE 3.2: Seasonal changes in densities of *M.maculatus* and *C.brunneus* in 1982 in the original and the extended site 1.

from site 2 into adjacent denser vegetation was noticed in 1982, but it is possible that this had also occurred in 1981. Therefore, although precautions were taken when choosing the sites to minimize net movement of grasshoppers into or out of them (Chapter 2), some migration may have occurred, and this should be borne in mind when interpreting analyses of so-called mortality losses.

The problems of estimating mortality rates from stage-frequency data have been discussed by Southwood (1978) and Mills (1981b). All existing methods either (i) require some other information in addition to the data on stage frequencies, and/or (ii) make a number of assumptions concerning the shape of the recruitment curves, and/or (iii) require that samples be taken at regular intervals. In the analysis presented here, care was taken to avoid making unjustifiable important assumptions. Consequently, a simple comparison of adult and juvenile losses was performed. The analysis allowed me to establish whether there were qualitative differences between populations in the rates at which adults and juveniles were lost. A modification of the method of Richards and Waloff (1954) was used which derived mortality-emigration estimates by regressing log population density against time, starting from the peak density of the stage in question. Accumulated totals of second or later instars were used to derive the peak density since this avoided erroneous estimates due to confusing moulting with mortality or emigration (Southwood, 1978). The slope of this line gives an average rate of loss of second and subsequent instars, including adults. The only assumption the method makes, therefore, is that the shapes of the recruitment curves into the second instar were not very dissimilar in the different populations, and the importance of this assumption has been minimized anyway because the density data of all subsequent stadia were combined in the analysis of grasshopper losses so that the period of recruitment was relatively small in relation to the period over which the losses were being measured.

A small constant value (0.01) was added to every density measure in the analysis so that the data from those visits which gave zero counts of animals (yet the populations proved subsequently to have some individuals left) could be used.

Also, each point on each "survivorship" curve was weighted in the regression analysis according to the number of samples taken divided by the mean number of samples per point for the whole line. The slope was then compared with the slope of the survivorship curve derived for adults only. If it was steeper, a greater juvenile mortality or emigration rate (or both) must have contributed to this difference.

The rate of loss from the peak number of first instars was not calculated for three populations because some of the first-instar frequency distributions were incomplete. However, in those populations where a distinct increase to a peak density of first instars was recorded, the average daily rate of loss of all stages was also estimated using this regression technique. In these populations the slope of the log survivorship curve for all stadia was compared with that of second and subsequent stadia (to determine whether the loss of first instars was greater than the average for subsequent stages), and with that of the adults (for a comparison of adult losses with that of all juvenile stadia).

3.4.1.2. Results

Linear regression models provided good fits to the data

($p<0.008$ for every "survivorship" curve except three, two of which were not significant; Table 3.4 - discussed below). However, such a good fit does not necessarily imply that the daily survival rate is approximately constant for all stages. Gross changes in mortality rate would produce kinks in the negatively sloping survivorship curves, but these curves will nonetheless show almost perfect rank correlations since the population size declines with each visit after the peak. Pearson's regressions are also, therefore, likely to be highly significant.

The two non-significant regressions were obtained for C.brunneus adults in 1981 from sites 1 and 3 (Table 3.4). At least two factors contributed to this result. First, adult "survivorship" curves were produced from fewer points than the juvenile-and-adult curves, so that any outlying point would have a relatively greater proportional effect on the significance of the regression. Second, the more motile C.brunneus was not contained within the boundaries of the sites.

Of sixteen pairs of regressions, fourteen indicated that the rate at which adults were lost from the populations exceeded that of the juveniles after moult into the second instar (Table 3.4). Of the two pairs of regressions showing the opposite trend, one pair included one of the two non-significant regressions (C.brunneus 1981, site 1) and the other showed the smallest difference between slopes (0.0002; C.brunneus 1981, site 3). This latter population lost first instars at a low rate, which reduced the slope of the juvenile-and-adult "survivorship" curve below that of the adults. Therefore, in the comparisons of the daily rates of adult losses with the daily rates of juvenile

TABLE 3.4: **Estimates of rates of loss of grasshoppers from each population** (3 pages)

The "% mortality" estimates are rates of loss of animals per day; they may include some losses due to emigration (see text).

"II+" refers to all stages of the life history subsequent to, and including, the second instar (i.e. "All" stages minus the first instar).

Species	Year	Site (enclosure)	Stage	Log (survival)	Correlation coefficient	N	P	% mortality
M. maculatus	1981	1	All	-				
			II+	-0.01424	-0.903	14	<0.00001	3.2
			Adult	-0.02198	-0.904	9	0.0004	4.9
		1(1)	All	-				
			II+	-0.01275	-0.939	14	<0.00001	2.9
			Adult	-0.01653	-0.916	11	0.00004	3.7
		1(2)	All	-0.01608	-0.876	14	0.00002	3.6
			II+	-0.01815	-0.861	12	0.00016	4.1
			Adult	-0.02588	-0.875	9	0.00101	5.8
		2	All	-0.01605	-0.927	16	<0.00001	3.6
			II+	-0.01834	-0.919	13	<0.00001	4.1
			Adult	-0.02465	-0.889	9	0.00067	5.5
		3	All	-				
			II+	-0.02270	-0.933	11	0.00001	5.1
			Adult	-0.02432	-0.920	10	0.00008	5.4
	1982	1	All	-0.01215	-0.937	20	<0.00001	2.8
			II+	-0.01255	-0.923	16	<0.00001	2.8
			Adult	-0.01848	-0.936	10	0.0003	4.2
		2	All	-0.01570	-0.954	20	<0.00001	3.6
			II+	-0.01646	-0.937	18	<0.00001	3.7
			Adult	-0.02189	-0.950	12	<0.00001	4.9

Species	Year	Site (enclosure)	Stage	Log (survival)	Correlation coefficient	N	P	% mortality
		3	All	-0.01607	-0.961	21	<0.00001	3.6
			II+	-0.01735	-0.956	18	<0.00001	3.9
			Adult	-0.01987	-0.940	15	<0.00001	4.5
C. brunneus	1981	1	All	-0.01090	-0.866	15	0.00002	2.5
			II+	-0.01297	-0.777	11	0.00245	2.9
			Adult	-0.00993	-0.360	6	0.241	2.3
		1(1)	All	-0.01214	-0.734	11	0.00504	2.8
			II+	-0.01122	-0.704	11	0.00784	2.6
			Adult	-0.03131	-0.851	6	0.0158	7.0
		1(2)	All	-0.01339	-0.848	15	0.00003	3.0
			II+	-0.01308	-0.777	13	0.0009	3.0
			Adult	-0.01515	-0.547	8	0.080	3.4
		2	All	-0.01711	-0.907	14	<0.00001	3.8
			II+	-0.01696	-0.854	12	0.0002	3.8
			Adult	-0.02032	-0.724	8	0.02109	4.6
		3	All	-0.01160	-0.959	14	<0.00001	2.6
			II+	-0.01328	-0.962	11	<0.00001	3.0
			Adult	-0.01308	-0.923	8	0.00055	3.0

Species	Year	Site (enclosure)	Stage	Log (survival)	Correlation coefficient	N	P	% mortality
C. brunneus	1982	1	All	-0.01101	-0.929	18	<0.00001	2.5
			II+	-0.01070	0.864	14	0.00003	2.4
			Adults	-0.01402	-0.820	9	0.00343	3.2
		2	All	-0.00780	-0.902	18	<0.00001	1.8
			II+	-0.00588	-0.852	15	0.00003	1.3
			Adults	-0.00978	-0.820	8	0.00636	2.2
		3	All	-0.00959	-0.909	20	<0.00001	2.2
			II+	-0.00978	-0.811	15	0.00012	2.2
			Adults	-0.01146	-0.710	11	0.00723	2.6

losses, adults suffered more severe rates of loss in twelve out of thirteen populations (Table 3.4).

A qualitative difference in daily losses between adults and juveniles similar to that described here, has been found by Monk (1985). She recorded that the daily mortality rate of nymphs of Chorthippus parallelus, and of C.brunneus, was less than that of adults in nine out of the ten "populations" ("species-site-year" combinations) which showed unambiguous qualitative differences between nymphal and adult mortality.

Dempster (1963) in his review of the causes of mortality in acridids examined the effects of a number of factors at different stages of the life history. Both adults and juveniles appear to be most susceptible to the effects of weather. Generally speaking, mortality is greater in cool wet conditions than in warm dry weather, though this effect may be confounded if drought reduces the amount of green food available. Therefore, it might be expected that differences in mortality rate between adults and juveniles would not normally exhibit any clear pattern over a period of years since the weather during the hatching, juvenile, and adult periods, and its relationship to the condition of the vegetation, are likely to differ unpredictably between years.

In the five populations of M.maculatus in which the rate of loss of all grasshoppers was compared with that of second instars and later stages, the difference in every case indicated that the daily losses of first instars were less than the average for subsequent stages (Table 3.4). In C.brunneus, however, five of the eight comparisons indicated the opposite trend (Table 3.4). Chapman and Page (1979) report negligible mortality of newly-hatched animals in the African grasshopper, Zonocerus variegatus, but Pickford (1960) found that early nymphal mortality in Melanoplus bilituratus was variable and highly dependent on weather conditions.

3.4.2. Effects of species, site, year and density

3.4.2.1. Analysis

Differences in the rate of loss of adults and of second and subsequent instars between populations, years and species were examined together with the effects of initial density by performing simultaneous analyses of variance and covariance on the slopes of the "survivorship" curves. To do this, the Generalised Linear Interactive Modelling (GLIM) computer package (Baker and Nelder, 1977) was used. I shall explain the use of GLIM in a little detail below since it will be used extensively here and in later chapters, especially Chapter 6.

The main advantage of GLIM over most other statistical packages for this particular analysis is that it is "interactive" and therefore allows the user to make decisions and to retain control of the statistical tests throughout the procedure. The method adopted here examines the effect on grasshopper losses of each factor (e.g."species") and its interaction effects with other factors (e.g. "year", "site") by adding these terms to the original model (that with only the Grand Mean). This analysis is an analysis of variance: the GLIM package calculates the deviance (residual sum of squares) and the degrees of freedom associated with the addition of each term in the model, and from these the F-statistic can be calculated, thus:

$$F = \frac{\text{reduction in deviance}}{\text{deviance of new model}} \times \frac{\text{degrees of freedom of new model}}{\text{change in degrees of freedom}}$$

$$= \frac{\text{reduction in the mean squares}}{\text{mean squares of new model}}$$

The statistical significance of the improvement in fit could therefore be found.

The fraction of the variance explained by a particular model can also be calculated simply by dividing the reduction in deviance by the deviance of the original model.

As well as examining the effects of discrete factors on the rate of loss of animals from the populations, the method also examines the effect of a continuous variable ("density") by adding this term to the original model. This is a linear regression analysis.

Because density could have a different relationship to the y-variate (grasshopper losses) for different levels of a factor (e.g. for each species), "density" was also added to the original model as interaction terms with all combinations of the factors. In other words, the method permits the testing for different slopes in an analysis of covariance.

The analysis was continued further by adding each factor and variable (both singly and as interaction terms) to the new model. Thus, if the initial best-fit model included the effects of density, the addition of factors to this model determined whether the curves had different intercepts for each level of each factor (e.g. each species, each site, or each year). Thus by testing for different intercepts, the analysis of covariance is completed.

Table 3.5 provides an example of the procedure. The best initial improvement in the fit of the model to the data was due to the addition of the "species-year" interaction term to the model with only the Grand Mean. The remaining factors were then

TABLE 3.5: **Effects of species, site (or enclosure), year and density on the log "survivorship" of second instars and all subsequent stages**

(Two pages)

[1] All deviances are "deviances x 10^3"

The best-fit model is asterisked.

Abbreviations:

df	degrees of freedom
Sp.	species
Site	site (or enclosure)
Yr.	year
Dens.	initial density of IInd+ instars

Model: Grand Mean (GM); Deviance[1] = 0.2664, df = 15

Variables added	Reduction in deviance[1]	Reduction in df	F	df	P
Sp.	0.0860	1	6.674	1,14	0.025-0.01
Site	0.0258	4	0.295	4,11	NS
Yr.	0.0684	1	4.836	1,14	0.05-0.025
Dens.	0.0581	1	3.905	1,14	NS
Sp. x Site	0.1727	9	1.229	9,6	NS
Sp. x Yr.	0.1630	3	6.306	3,12	0.01-0.005*
Sp. x Dens.	0.0875	2	3.179	2,13	NS
Site x Yr.	0.0968	7	0.652	7,8	NS
Site x Dens.	0.1179	5	1.588	5,10	NS
Yr. x Dens.	0.0865	2	3.125	2,13	NS
Sp. x Site x Yr.	-	15	-	-	-
Sp. x Site x Dens.	0.1736	10	0.936	10,5	NS
Sp. x Yr. x Dens.	0.1683	4	4.716	4,11	0.025-0.01
Site x Yr. x Dens.	0.1591	8	1.297	8,7	NS
Sp. x Site x Yr. x Dens.	-	15	-	-	-

Model: GM + Sp. x Yr.; Deviance[1] = 0.1034, df = 12

Variables added	Reduction in deviance[1]	Reduction in df	F	df	P
Site	0.0214	4	0.522	4,8	NS
Dens.	0.0003	1	0.317	1,11	NS
Sp. x Site	0.0767	8	0.958	8,4	NS
Site x Yr.	0.0284	6	0.379	6,6	NS
Site x Dens	0.0395	5	0.865	5,7	NS
Yr. x Dens.	0.0003	2	0.149	2,10	NS
Sp. x Site x Yr.	-	12	-	-	-
Sp. x Site x Dens.	0.0848	10	0.909	10,2	NS
Sp. x Yr. x Dens.	0.0008	4	0.177	4,8	NS
Site x Yr. x Dens.	0.0549	8	0.566	8,4	NS
Sp. x Site x Yr. x Dens.	-	12	-	-	-

Therefore, best fit model = GM + Sp. x Yr.

Parameter Estimates (+ SE)

GM		-0.01807	(0.001313)
M. maculatus	1982	0.002764	(0.002144)
C. brunneus	1981	0.003506	(0.001857)
C. brunneus	1982	0.009287	(0.002144)

added to the new model, both singly and as interaction terms, but there was no further significant improvement in fit to the data.

3.4.2.2. Variation in losses of second instar and later stages

The strongest effect on the variation in average rate of loss of second instars and later stages was the combination of "species" and "year" (Table 3.5): this model explained 61% of the variance. The rates at which M.maculatus was lost from the populations were higher than those of C.brunneus; both species lost a lower proportion of their population per day in 1982 than in 1981; and the difference between species was greater in 1982 than 1981 (Table 3.5). The addition of further terms to the model did not explain significantly more of the variation in log "survivorship".

3.4.2.3. Variation in adult losses

The rate of adult loss was density dependent when the two species were analyzed together (Table 3.6; Fig. 3.3), but there was also a clear relationship between "species" and both "density" and "the rate at which adults were lost from each population" (Table 3.6). M.maculatus generally occurred at higher densities and suffered higher losses (Fig. 3.3). The effects of "density" explained 32% of the variance in adult losses, whereas the effect of "species" explained almost 28% of the variance.

When the effect of "density" was examined on each species separately, the relationship was found to be not significant (M.maculatus, r=-0.386, p=0.173, n=8; C.brunneus, r=-0.270, p=0.29, n=8).

When the effect of "density" was controlled, no other factor

TABLE 3.6: **Effects of species, site (or enclosure), year, and density on the log "survivorship" of adult grasshoppers**

(2 pages)[1]

[1] All deviances are "deviances x 10^3"

Abbreviations: As for Table 3.5.

Model: Grand Mean (GM); Deviance = 0.6267, df = 15

Variables added	Reduction in deviance	Reduction in df	F	df	P
Sp.	0.1732	1	5.347	1,14	0.05-0.025
Site	0.1018	4	0.533	4,11	NS
Yr.	0.0975	1	2.579	1,14	NS
Dens.	0.2007	1	6.596	1,14	0.025-0.01*
Sp. x Site	0.5236	9	3.386	9,6	NS
Sp. x Yr.	0.2737	3	3.101	3,12	NS
Sp. x Dens.	0.2028	2	3.110	2,13	NS
Site x Yr.	0.1621	7	0.399	7,8	NS
Site x Dens.	0.2020	2	0.951	2,13	NS
Yr. x Dens.	0.2384	2	3.991	2,13	0.05-0.025
Sp. x Site x Yr.	-	15	-	-	-
Sp. x Site x Dens.	0.5051	10	2.077	10,5	NS
Sp. x Yr. x Dens.	0.3077	4	2.653	4,11	NS
Site x Yr. x Dens.	0.2773	8	0.694	8,7	NS
Sp. x Site x Yr. x Dens.	-	15	-	-	-

Model: GM + Dens.; Deviance = 0.4260, df = 14

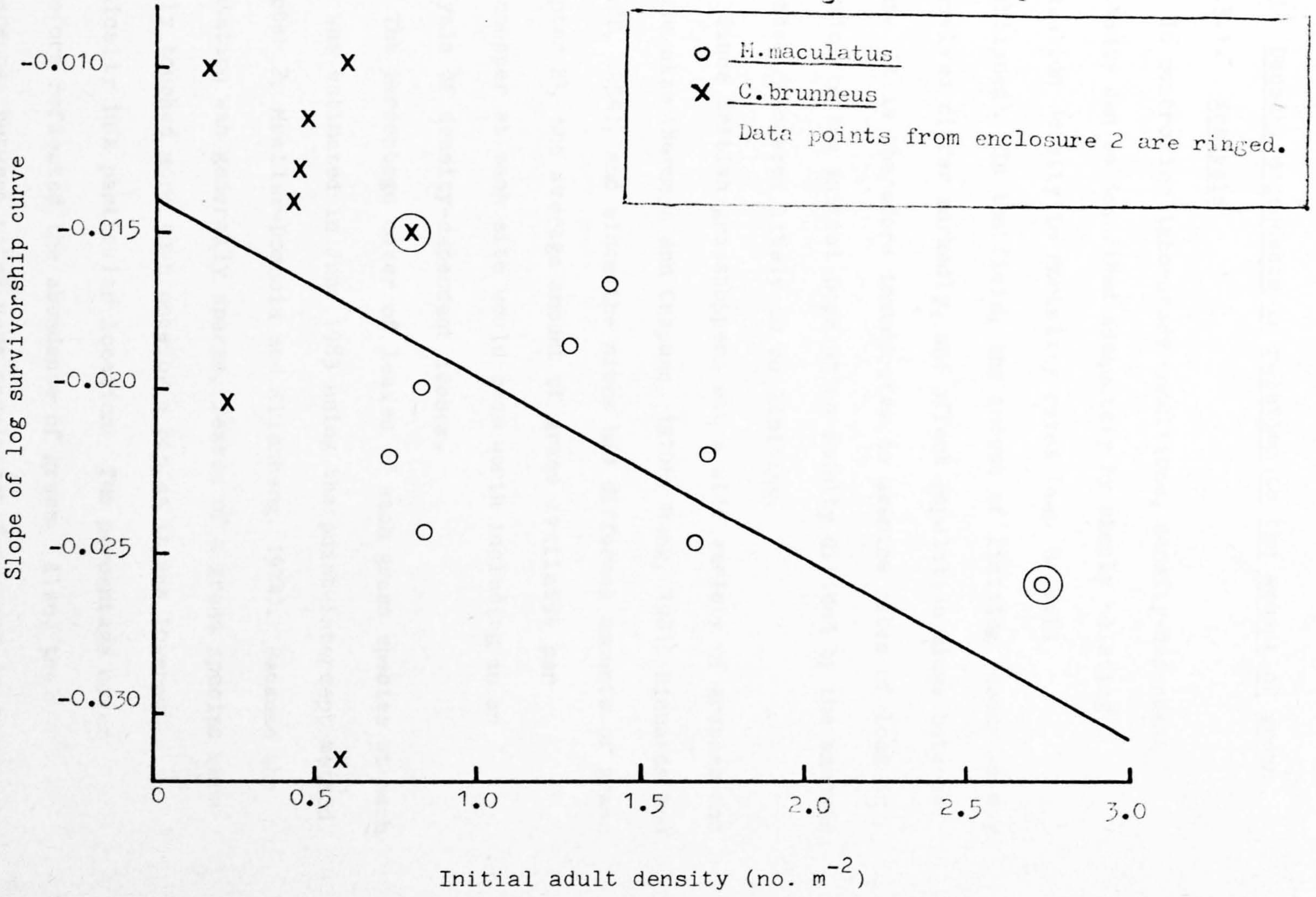
Variables added	Reduction in deviance	Reduction in df	F	df	P
Sp.	0.0142	1	0.448	1,13	NS
Site	0.0401	4	0.260	4,10	NS
Yr.	0.0865	1	3.312	1,13	NS
Sp. x Site	0.3673	9	3.478	9,5	NS
Sp. x Yr.	0.1094	3	1.267	3,11	NS
Sp. x Dens.	0.0002	1	0.064	1,13	NS
Site x Yr.	0.1299	7	0.439	7,7	NS
Site x Dens.	0.0001	4	0.031	4,10	NS
Yr. x Dens.	0.0377	1	1.262	1,13	NS
Sp. x Site x Yr.	-	14	-	-	-
Sp. x Site x Dens.	0.3044	9	1.391	9,5	NS
Sp. x Yr. x Dens.	0.1070	3	1.230	3,11	NS
Site x Yr. x Dens.	0.0766	7	0.219	7,7	NS
Sp. x Site x Yr. x Dens.	-	14	-	-	-

Therefore, best fit model = GM + Dens.

Parameter Estimates (+ SE)

GM	-0.01360	(0.002448)
Dens.	-0.005049	(0.001966)

FIGURE 3.3: The relationship between initial adult density and log "survivorship"



was able to explain a significant amount of variation in log "survivorship" (Table 3.6).

3.4.3. Density dependence in relation to the amount of grass

3.4.3.1. Analysis

In controlled laboratory conditions, density-dependent mortality can be described adequately by simply relating population density to mortality rates (e.g. R. Wall, unpublished). In the field, the amount of limiting resources may themselves differ markedly, and affect population sizes between sites. It is therefore instructive to examine rates of loss in relation to the initial population density divided by the amounts of those resources likely to be limiting.

Since British grasshoppers eat a wide variety of grasses and little else (Bernays and Chapman, 1970b; Monk, 1981; Richards and Waloff, 1954), and since the sites had different amounts of grass (Chapter 2), the average amount of grass available per grasshopper at each site would seem worth including in an analysis of density-dependent losses.

The percentage cover of leaves of each grass species at each site was estimated in June 1983 using the point-intercept method (Chapter 2; Mueller-Dombois and Ellenberg, 1974). Because the vegetation was generally sparse, leaves of a grass species were rarely touched more than once by a pin as it was lowered vertically in a particular location. The percentage cover therefore reflected the abundance of grass. Also, the differences between sites were consistent from year to year.

The effects of potential competition for grass on the losses of grasshoppers were examined by performing a GLIM analysis as described in Section 3.4.2.1 but substituting for the initial density of animals (second instars and later stages for one analysis, and adults for the second) the same population density divided by the percentage cover of grass at the respective site.

3.4.3.2. Effects on the average rate of loss of second instars and later stages

The effects of competition for grass on the average rate of loss of second instars and subsequent stages (Table 3.7) were weaker than the effects of the combination of "species" and "year" (Table 3.5). Further addition of terms to the model, controlling for the different species' loss rates in the two years, did not explain any more of the variance in log "survivorship" (Table 3.7).

3.4.3.3. Effects on adult loss

When initial adult density *per se* was excluded from the analysis but replaced by the density divided by the amount of grass at the respective site, the only significant effect was the difference between species - adult *M.maculatus* having a higher average daily rate of loss than adult *C.brunneus* (Table 3.8). Therefore, the effects of competition on the loss of adults is less likely to occur because of insufficient grass *per capita* than it is due to simple crowding.

3.4.4. Density dependence in relation to the amount of "preferred" grasses

3.4.4.1. Analysis

Studies of the diet of British grasshoppers have shown that they are often more selective than would be expected if they consumed grasses in amounts proportional to their relative abundances. Monk (1981) and Young (1979) found that *C.brunneus* tended to avoid the leaves of *Festuca*. A detailed examination of

TABLE 3.7: **Effects of "initial density divided by grass abundance" on log "survivorship" of second instars and subsequent stages**

[1] All deviances are "deviances x 10^3"

[2] The variables added to the model (Dens./grass and its interactions with other factors) do not explain a significant amount of the variation in log "survivorship". The significance levels from this analysis were compared with those in Table 3.5.

[3] The best-fit model is the best-fit model of Table 3.5.

Abbreviations: As for Table 3.5.

Model: Grand Mean (GM); Deviance[1] = 0.2664, df = 15

Variables added[2]	Reduction in deviance[1]	Reduction in df	F	df	P
Dens./grass	0.0195	1	1.066	1,14	NS
Sp. x Dens./grass	0.0961	2	3.482	2,13	NS
Yr. x Dens./grass	0.0399	2	1.101	2,13	NS
Sp. x Yr. x Dens./grass	0.1456	4	3.082	4,11	NS

Model[3]: GM + Sp. x Yr.; Deviance[1] = 0.1034, df = 12

Variables added	Reduction in deviance[1]	Reduction in df	F	df	P
Dens./grass	0.00136	1	0.171	1,11	NS
Sp. x Dens./grass	0.00214	2	0.123	2,10	NS
Yr. x Dens./grass	0.0028	2	0.163	2,10	NS
Sp. x Yr. x Dens./grass	0.0195	4	0.281	4,8	NS

TABLE 3.8: **Effects of "initial density divided by the amount of grass" on log "survivorship" of adults**

Notes [1], [2], [3], as for Table 3.7.

Abbreviations: As for Table 3.5.

Model: Grand Mean (GM); Deviance[1] = 0.6267, df = 15

Variables added[2]	Reduction[1] in deviance	Reduction in df	F	df	P
Dens./grass	0.0491	1	1.190	1,14	NS
Sp. x Dens./grass	0.0774	2	0.916	2,13	NS
Yr. x Dens./grass	0.1074	2	1.344	2,13	NS
Sp. x Yr. x Dens./grass	0.2202	4	1.490	4,11	NS

Model[3]: GM + Sp.; Deviance[1] = 0.4535, df = 14

Variables added	Reduction in deviance	Reduction in df	F	df	P
Site	0.1018	4	0.724	4,10	NS
Yr.	0.0974	1	3.556	1,13	NS
Dens./grass	0.0156	1	0.463	1,13	NS
Sp. x Site	0.3504	8	2.549	8,6	NS
Sp. x Yr.	0.0955	2	1.601	2,12	NS
Sp. x Dens./grass	0.0661	2	1.024	2,12	NS
Site x Yr.	0.162	7	0.556	7,7	NS
Yr. x Dens./grass	0.0535	2	0.803	2,12	NS
Sp. x Site x Yr.	-	14	-	-	-
Sp. x Yr. x Dens./grass	0.2098	4	2.152	4,10	NS

Therefore, best fit model = GM + Sp.

Parameter Estimates (+SE)

GM	-0.02209	(0.002012)
C. brunneus	0.006579	(0.002846)

TABLE 3.9: **Effects of species, site (or enclosure), year and "initial density divided by the amount of non-*Festuca* grass" on log "survivorship" of second instars and subsequent stages**

[1] All deviances are "deviances x 10^3

Abbreviations: D/nFg, density divided by the amount of non-*Festuca* grass at the site (enclosure)

The rest are described for Table 3.5.

Model: Grand Mean (GM); Deviance[1] = 0.2251, df = 13

Variables added	Reduction[1] in deviance	Reduction in df	F	df	P
Sp.	0.0616	1	4.521	1,12	NS
Site	0.0145	3	0.230	3,10	NS
Yr.	0.0581	1	4.175	1,12	NS
D/nFg	0.0263	1	1.588	1,12	NS
Sp. x Site	0.1314	7	1.202	7,6	NS
Sp. x Yr.	0.1339	3	4.892	3,10	0.025-0.01*
Sp. x D/nFg	0.0859	2	3.394	2,11	NS
Site x Yr.	0.0852	6	0.711	6,7	NS
Yr. x D/nFg	0.0494	3	1.546	3,10	NS
Sp. x Site x Yr.	-	13	-	-	-
Sp. x Yr. x D/nFg	0.1417	4	3.823	4,9	0.05-0.025

Model: GM + Sp. x Yr.; Deviance[1] = 0.09122, df = 10

Variables added	Reduction[1] in deviance	Reduction in df	F	df	P
Site	0.02044	3	0.674	3,7	NS
D/nFg	0.00386	1	0.398	1,9	NS
Sp. x Site	0.06453	6	1.612	6,4	NS
Site x Yr.	0.02743	5	0.430	5,5	NS
Yr. x D/nFg	0.00400	2	0.183	2,8	NS
Sp. x Site x Yr.	-	10	-	-	-
Sp. x Yr. x D/nFg	0.00988	4	0.182	4,6	NS

Therefore, best fit model = GM + Sp. x Yr.

Parameter Estimates (+SE)

GM		-0.01739	(0.001510)
M. maculatus	1982	0.002077	(0.002307)
C. brunneus	1981	0.002448	(0.002136)
C. brunneus	1982	0.008601	(0.002307)

the feeding behaviour of Chorthippus parallelus by Bernays and Chapman (1970a) also revealed that leaves of Festuca were rejected, especially by the young nymphs whose small gapes were unable to cope with the lack of leaf edges because the leaves were rolled up. A further GLIM analysis of losses was therefore performed but this time substituting for population density the population density divided by the percentage cover of all grasses minus that of Festuca spp. The abundance of non-Festuca grass was obtained from the point-intercept method of examining vegetation structure and composition (Chapter 2). This method did not detect any other grass besides Festuca in enclosure 2, so there was no data from this enclosure for use in this third analysis.

3.4.4.2. Effects on the average rate of loss of second instars and subsequent stages

Even when a third and more sophisticated estimate of competition intensity for food was included in the analysis of losses of second instars and subsequent stages, there was no stronger effect than the difference between species in the two years (Table 3.9).

Therefore, the average rate of loss of C.brunneus was less than that of M.maculatus, yet the former species was more motile and tended to move out of some of the sites more than M.maculatus (Fig. 3.2 and pers. obs.). It is likely, therefore, that C.brunneus lived longer on average than M.maculatus. Also, some difference in conditions between 1981 and 1982, other than density or its relation to the amount of grass (Table 3.7) or non-Festuca grass (Table 3.9), caused a higher rate of loss in 1981. The relationship between grasshopper losses and weather is briefly examined in Section 3.4.5.

3.4.4.3. Effects on the loss of adults

The initial amount of non-Festuca grass per adult did have an effect on the rate of loss of adults from the populations, but the effect was only significant in M.maculatus (Table 3.10, Fig.3.4). Those populations of M.maculatus with higher initial densities of adults in relation to the amounts of non-Festuca grass lost individuals at a slower rate than populations with lower relative densities. In C.brunneus, the trend was in the opposite direction but was not significant.

In order to determine whether initial density alone or initial density in relation to the amount of non-Festuca grass shows a stronger relationship to adult losses, it is appropriate to compare the significance levels of the F-values of the relationships. However, to make the comparison valid, the relationships should apply to the same set of sites and enclosures. Therefore, F-values were re-calculated for the relationships between density and rate of adult loss using all sites and enclosures except enclosure 2; these values are included as an addendum to Table 3.10.

When enclosure 2 was excluded from the analysis, the effect of the combination of "species" and "density in relation to the amount of non-Festuca grass" was stronger than the effect of "density" alone - explaining 45% and 18% of the variance respectively. A comparison of Fig. 3.4 with Fig. 3.3, excluding the points from enclosure 2 (ringed) demonstrates the difference. This final analysis of the effects of competition for food, therefore, identifies an effect of competition which is common to only one species - M.maculatus.

This result may at first appear counter-intuitive since it

TABLE 3.10: **Effects of species, site (or enclosure), year and "initial density divided by the amount of non-*Festuca* grass" on log "survivorship" of adult grasshoppers.**

(1 page + an addendum)

[1] All deviances = "deviances x 10^3"

Abbreviations: As for Table 3.9.

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Model: Grand Mean (GM); Deviance[1] = 0.5071, df = 13

Variables added	Reduction[1] in deviance	Reduction in df	F	df	P
Sp.	0.1077	1	3.236	1,12	NS
Site	0.0776	3	0.602	3,10	NS
Yr.	0.0778	1	2.175	1,12	NS
D/nFg	0.0494	1	1.295	1,12	NS
Sp. x Site	0.4040	7	3.359	7,6	NS
Sp. x Yr.	0.1978	3	2.132	3,10	NS
Sp. x D/nFg	0.2287	2	4.518	2,11	0.05-0.025
Site x Yr.	0.1378	6	0.435	6,7	NS
Yr. x D/nFg	0.1139	2	1.593	2,11	NS
Sp. x Site x Yr.	-	13	-	-	-
Sp. x Yr. x D/nFg	0.2604	4	2.375	4,9	NS

Model: GM + Sp. x D/nFg; Deviance[1] = 0.2784, df = 11

Variables added	Reduction[1] in deviance	Reduction in df			
Sp.	0.0273	1	1.087	1,10	NS
Site	0.0445	3	0.507	3,8	NS
Yr.	0.0355	1	1.460	1,10	NS
Sp. x Site	0.2212	7	2.209	7,4	NS
Sp. x Yr.	0.0692	3	0.882	3,8	NS
Site x Yr.	0.0891	6	0.392	6,5	NS
Yr. x D/nFg	0.0305	1	1.230	1,10	NS
Sp. x Site x Yr.	-	11	-	-	-
Sp. x Yr. x D/nFg	0.0317	2	0.578	2,9	NS

Therefore, best fit model = GM + Sp. x D/nFg

Parameter Estimates (+SE)

GM	-0.02176	(0.003249)
M. maculatus D/nFg	0.00006521	(0.002764)
C. brunneus D/nFg	0.01796	(0.008389)

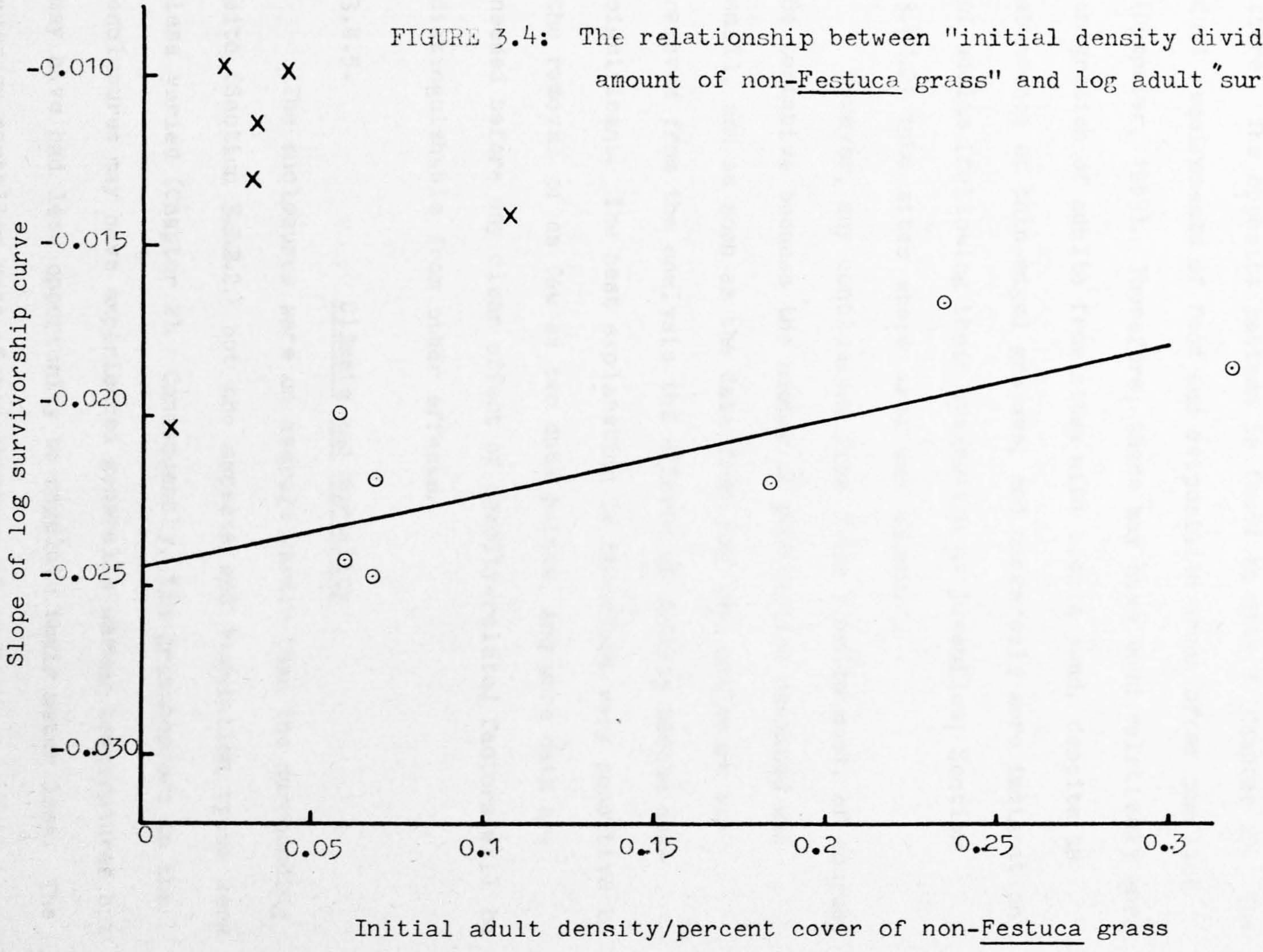
ADDENDUM TO TABLE 3.10

Effects of density, and its interactions with other factors, on the adult egression rate when enclosure 2 is excluded from the analysis

Model: Grand Mean (GM); Deviance[1] = 0.5071, df = 13

Variables added	**Reduction in deviance**	**Reduction in df**	F	df	**P**
Dens.	0.0932	1	2.640	1,12	NS
Sp. x Dens.	0.0935	2	1.215	2,11	NS
Site x Dens.	0.0945	4	0.503	4,9	NS
Sp. x Site x Dens.	0.4155	7	2.564	7,6	NS
Sp. x Yr. x Dens.	0.2464	4	2.050	4,9	NS
Site x Yr. x Dens.	0.1433	7	0.329	7,6	NS
Sp. x Site x Yr. x Dens.		13	-	-	-

FIGURE 3.4: The relationship between "initial density divided by the amount of non-*Festuca* grass" and log adult "survivorship"



(Symbols, as for Fig. 3.3.) The linear relationship applies only to *M. maculatus* populations.

seems to indicate that the rate at which adults are lost from the populations increases when there is more food for the grasshoppers (inverse density dependence). However, the site with the most non-Festuca grass (site 2) had the least bare sand (Chapter 2), so that oviposition sites may have been limiting there. The opposite pattern is found at site 1 (Chapter 2). The dual requirements of food and oviposition areas often conflict (Dempster, 1963). Therefore, there may have been relatively more emigration of adults from sites with little sand, despite an abundance of thin-edged grasses, and conversely more immigration of adults (following their emigration as juveniles; Section 3.4.1.2) into sites where sand was abundant.

However, any conclusions from these results must, of course, be tentative because the number of populations examined was small, and as soon as the data from just one enclosure was removed from the analysis the effects of density became non-significant. The best explanation is therefore very sensitive to the removal of as few as two data points, and more data are needed before any clear effect of density-related factors will be distinguishable from other effects.

3.4.5. Climate and mortality

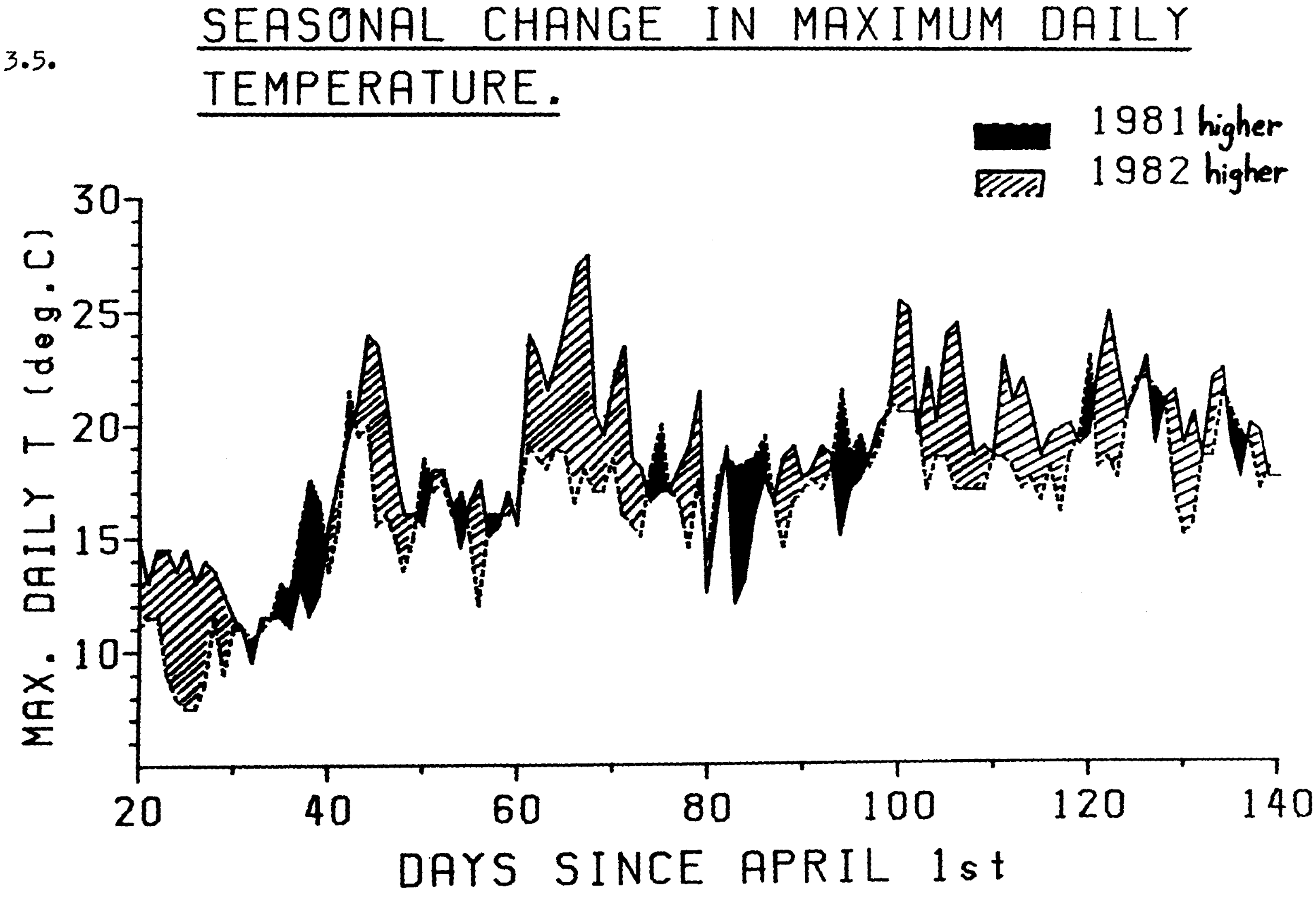
The enclosures were on average warmer than the surrounding site (Section 3.2.2.2.) but the aspects and vegetation types were less varied (Chapter 2). Consequently, the grasshoppers in the enclosures may have experienced generally warmer temperatures but may have had less opportunity to regulate their water loss. The average mortality rate of grasshoppers of each species after moulting into the second instar was lower in enclosure 1, but higher in enclosure 2, than the losses from the surrounding site

(Table 3.4), so no general relationship between ambient temperature and mortality was evident.

However, the combination of temperature and humidity may be more crucial to the grasshoppers than just temperature on its own (Hamilton, 1950). The evaporation rates in enclosure 2 were significantly greater (at the 5% probability level) than in enclosure 1, with the surrounding site having an intermediate rate of evaporation (albeit not significantly different from each enclosure; Section 2.7.2). Therefore, the mortality rates of grasshoppers in the enclosures and in the surrounding area may have differed due to differences water loss by the animals.

In 1981 the weather was cooler (Fig. 3.5) and wetter (unpublished data, Ainsdale Sand Dunes NNR meteorological station) during the period the grasshoppers were developing than in 1982. This cooler weather was associated with a higher average mortality-emigration rate in all populations of each species (Table 3.4). This result is therefore consistent with the findings from mortality analyses of other acridid populations which show that a higher mortality occurs generally in cooler weather (Dempster, 1963). Emigration, on the other hand, appears to be greater in hotter drier years (as in this study, pers. obs.), especially when the vegetation is parched (Dempster, 1955, 1963). This suggests that the more important cause of differences in the losses of grasshoppers between years was mortality differences rather than differences in emigration rates.

FIGURE 3.5.



SEASONAL CHANGE IN MAXIMUM DAILY TEMPERATURE.

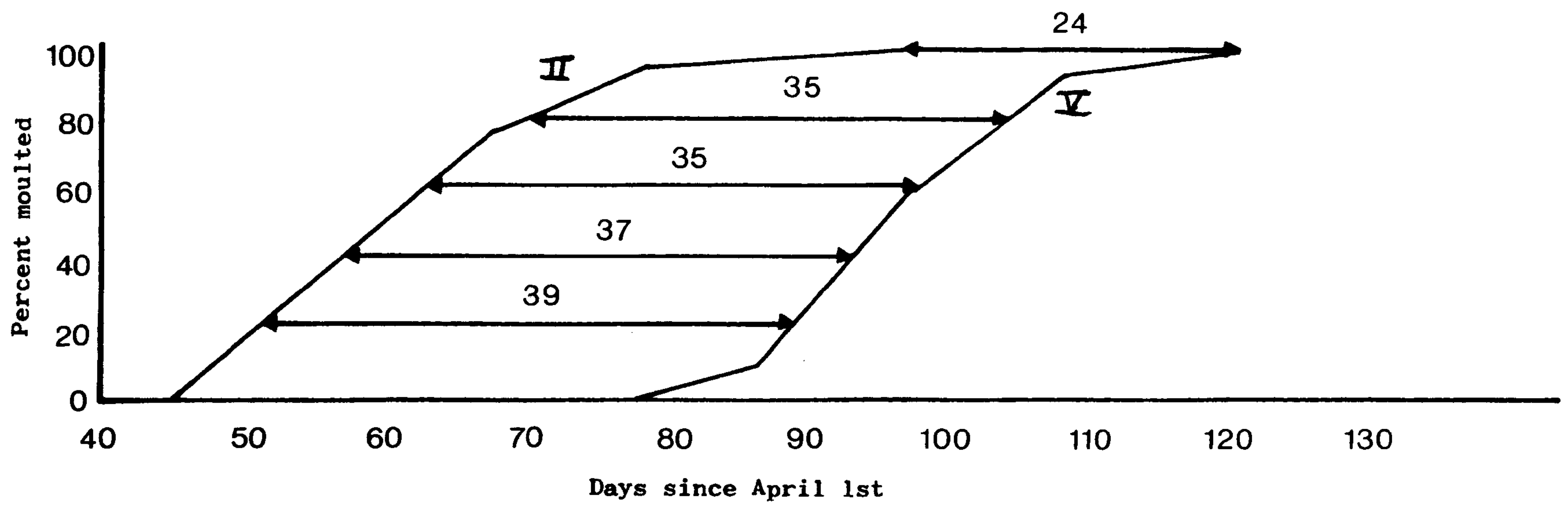
3.5. DEVELOPMENTAL PERIOD

3.5.1. Analysis

All the methods for estimating developmental period from stage-frequency data discussed by Southwood (1978) and Mills (1981a) either make a number of assumptions which are difficult to justify for the populations in this study or require additional information. There is no assumption-free method for estimating developmental period without directly measuring the development of particular individuals, but in order to at least reduce the probability of finding differences which may be spurious because of the assumptions used, I have adopted a simple and conservative method of analysis which is a modification of that of Begon (1983).

The analysis concentrated on the period from the moult into the second instar until the time the adults emerged; it therefore excluded the first instars for which incomplete stage-frequency distributions were obtained for some populations. On each visit the proportion of the population comprising second or later instars was calculated so that a cumulative recruitment curve could be drawn. A cumulative recruitment curve for the adult stage was also drawn, and the period between points on the two curves for a particular cumulative frequency was measured. 20, 40, 60, 80 and 100% cumulative frequencies were used (Fig. 3.6 provides an example). A mean developmental period was calculated using these five estimates for each species at each site or enclosure in each year, and the data analyzed by analysis of variance to determine the effects of species, site (or enclosure), and year on developmental period. If the distance between only one pair of points had been used to estimate

FIGURE 3.6: Calculating a "developmental period" from the difference between the curves of cumulative frequencies moulted into adults (V) and second instars (II)



developmental period, differences among populations could have arisen in the analysis which were undetectably spurious - arising either from sampling error or from disproportionate mortality or speed of development among animals on different parts of the recruitment curves. By using a range of cumulative frequencies in the analysis therefore, such spurious differences were much reduced.

Simultaneous analyses of variance and covariance were then performed using the GLIM statistical package to investigate, for each of the five cumulative frequencies of moulted animals, the effects of "species", "site (or enclosure)", "year" and "date of moult into the second instar" ($\mathbf{t_{ii}}$) on the subsequent developmental period ($\mathbf{t}$).

The date of moult of animals corresponding to, say, the 40% cumulative frequency is, of course, partly dependent on the date of moult of the "20% animals", so that each analysis is not a strict replicate of the others. However, if a particular relationship is found to occur over all the "replicates" when the rank order of the moulting dates of the populations changes, then this result supports the relationship more strongly than if a single cumulative frequency was analyzed. This is because the relationship holds despite changes in rank order of moulting dates for the sites and enclosures.

3.5.2. Variation in developmental period

Significant differences in developmental period, **t**, were found between species and years though the magnitude of the effect of "year" was different in the two species (Table 3.11). The larger C.brunneus had a longer developmental period than M.maculatus, and grasshoppers developed faster in 1982 than in

TABLE 3.11: Effects of species, site (or enclosure), and year on grasshopper developmental period.

Model: Grand Mean (GM); Deviance = 796.7, **df** = 15

Variables added	**Reduction in deviance**	**Reduction in df**	**F**	**df**	**P**
Sp.	497.3	1	23.254	1,14	<0.001
Site	74.4	4	0.283	4,11	NS
Yr.	204.6	1	4.838	1,14	0.05 - 0.025
Sp. x Site	588.6	9	1.886	9,6	NS
Sp. x Yr.	715.55	3	35.270	3,12	<0.001
Site x Yr.	253.5	7	0.533	7,8	NS
Sp. x Site x Yr.	-	15	-	-	-

"Developmental period" refers to the period between the time a given percent of a population **had moulted into second (or later) instars** and the time the same percent had moulted **into adults. For each population,** the mean of five replicates (percentages) was used.

1981 (Table 3.12). No effect of "site (or enclosure)" was noted on the developmental period of the grasshoppers (Table 3.11).

The developmental periods also differed significantly between the cumulative frequencies (Table 3.13). The rank order of developmental periods for the five cumulative frequencies were the same in both species in 1981 - the early animals either developing slower than later ones or suffering less mortality (Table 3.13). This latter explanation is consistent with the results of R. Wall (unpublished) who has shown that under conditions of competition poor competitors moult later and are more likely subsequently to die as juveniles. Since those late-moulting nymphs which survive in Wall's experiments also have a longer developmental period than good competitors, the data of Wall contradict the first explanation - that the early-moulting animals actually develop more slowly. In 1982, the pattern is reversed in C.brunneus, though there were no significant differences among cumulative frequencies.

Faster development can result if animals are subject to fewer constraints (e.g. reduction in the effects of competition, higher temperatures) or if they make a "strategic" decision to speed up development (both can occur). These alternative explanations are examined in the next section.

3.5.3. Causes of variation in developmental rate

3.5.3.1. Species, site (enclosure), year, date of moult

Table 3.14 presents the GLIM analysis of the effects of "species", "site (or enclosure)", "year" and "date of moult into second instar (t_{ii})" on developmental period (t) for each cumulative frequency. For every cumulative frequency (except the 100% one in which no effect was significant) the same model provided the

TABLE 3.12: Mean estimated developmental periods between second instar and adulthood for each population.

Species	Year	Site	1	1(1)	1(2)	2	3
		(enclosure)	Mean developmental period (days)				
<u>M. maculatus</u>	1981		37.0	37.2	34.0	38.2	35.4
	1982		27.0	-	-	27.0	27.2
<u>C. brunneus</u>	1981		51.2	49.8	44.0	42.6	42.8
	1982		40.6	-	-	39.4	41.8

TABLE 3.13:

Relative "developmental periods" of early- and late-moulting animals

Species	Year	Cumulative frequency of population (%)				
		Fastest				Slowest
M. maculatus	1981	100	80	60	40	20
	1982	60	40	20	100	80
C. brunneus	1981	100	80	60	40	20
	1982	20	40	60	80	100

Underlining joins together those cumulative frequencies which do not differ significantly in their "developmental periods" (SNK multiple range test, $p_{crit}=0.05$).

TABLE 3.14: **Effects of species, site (or enclosure), year, and date of moult into second instar on the period between second instar moult and adult moult**

(9 pages)

(a) All values of T_{ii} and "developmental period", t, were calculated using data for the first 20% of each population to moult into second instars and into adults.

(b) All values of T_{ii} and t, calculated using data from the second 20% to moult.

(c) All values of T_{ii} and t, calculated using data from the third 20% to moult.

(d) All values of T_{ii} and t, calculated using data from the fourth 20% to moult.

(e) All values of T_{ii} and t, calculated using data from the last 20% to moult.

Abbreviations: Sp., species

Site, site or enclosure

Yr., year

T_{ii}, date on which the respective percentage of a given population had moulted into at least second instars.

(a)

Model: Grand Mean (GM); Deviance = 1950, df = 15

Variables added	Reduction in deviance	Reduction in df	F	df	P
Sp.	729.0	1	8.359	1,14	0.025-0.01
Site	128.0	4	0.193	4,11	NS
Yr.	968.3	1	13.809	1,14	0.005-0.001
Tii	916.0	1	12.402	1,14	0.005-0.001
Sp. x Site	889.0	9	0.559	9,6	NS
Sp. x Yr.	1702.7	3	27.541	3,12	<0.001
Sp. x Tii	1002.1	2	6.872	2,13	0.01-0.005
Site x Yr.	1180	7	1.751	7,8	NS
Site x Tii	1500.3	5	6.672	5,10	0.01-0.005
Yr. x Tii	1175.5	2	9.865	2,13	0.005-0.001
Sp. x Site x Yr.	-	15	-	-	-
Sp. x Site x Tii	1578.5	10	2.124	10,5	NS
Sp. x Yr. x Tii	1811.4	4	35.940	4,11	<0.001*
Site x Yr. x Tii	1863.7	8	18.905	8,7	<0.001
Sp. x Site x Yr. x Tii	-	15	-	-	-

Model: GM + Sp. x Yr. x Tii; Deviance = 138.6, df = 11

Variables added	Reduction in deviance	Reduction in df	F	df	P
Sp.	29.00	1	2.646	1,10	NS
Site	71.30	3	1.854	3,8	NS
Yr.	2.60	1	0.191	1,10	NS
Sp. x Site	135.56	9	9.919	2,9	NS
Sp. x Yr.	47.99	3	1.412	3,8	NS
Site x Yr.	102.08	7	1.597	7,4	NS
Sp. x Site x Yr.	-	11	-	-	-

Therefore, best fit model = GM + Sp. x Yr. x Tii

Parameter Estimates (+ SE)

GM			82.16	(11.48)
M. maculatus	1981	Tii	-0.8727	(0.2510)
M. maculatus	1982	Tii	-1.430	(0.3040)
C. brunneus	1981	Tii	-0.4423	(0.1982)
C. brunneus	1982	Tii	-0.9103	(0.2480)

(b)

Model: Grand Mean (GM); Deviance = 1313, df = 15

Variables added	Reduction in deviance	Reduction in df	F	df	P
Sp.	576.0	1	10.942	1,14	0.01-0.005
Site	62.0	4	0.136	4,11	NS
Yr.	552.1	1	10.158	1,14	0.01-0.005
Tii	729.4	1	17.498	1,14	<0.001
Sp. x Site	742.0	9	0.866	9,6	NS
Sp. x Yr.	1137.7	3	25.960	3,12	<0.001
Sp. x Tii	762.4	2	9.000	2,13	0.005-0.001
Site x Yr.	613.0	7	1.001	7,8	NS
Site x Tii	940.5	5	5.050	5,10	0.025-0.01
Yr. x Tii	778.0	2	9.452	2,13	0.005-0.001
Sp. x Site x Yr.	-	15	-	-	-
Sp. x Site x Tii	1025.3	10	1.782	10,3	NS
Sp. x Yr. x Tii	1190.1	4	26.630	4,11	<0.001*
Site x Yr. x Tii	1043.0	8	3.380	8,7	NS
Sp. x Site x Yr. x Tii	-	15	-	-	-

Model: GM + Sp. x Yr. x Tii; Deviance = 122.9, df = 11

Variables added	Reduction in deviance	Reduction in df	F	df	P
Sp.	14.60	1	1.348	1,10	NS
Site	32.92	4	0.640	4,7	NS
Yr.	10.10	1	0.895	1,10	NS
Sp. x Site	70.42	9	0.298	2,9	NS
Sp. x Yr.	27.20	3	0.758	3,8	NS
Site x Yr.	50.26	7	0.395	7,4	NS
Sp. x Site x Yr.	-	11	-	-	-

Therefore, best fit model = GM + Sp. x Yr. x Tii

Parameter Estimates (+ SE)

GM	78.75	(13.44)
M. maculatus 1981 Tii	-0.7412	(0.2544)
M. maculatus 1982 Tii	-1.244	(0.3180)
C. brunneus 1981 Tii	-0.4106	(0.1919)
C. brunneus 1982 Tii	-0.7321	(0.2544)

(c)

Model: Grand Mean (GM); Deviance = 1101, df = 15

Variables added	Reduction in deviance	Reduction in df	F	df	P
Sp.	625.0	1	18.382	1,14	<0.001
Site	169.8	4	0.501	4,11	NS
Yr.	248.1	1	4.072	1,14	NS
Tii	491.8	1	11.302	1,14	0.005-0.001
Sp. x Site	827.5	9	2.017	9,6	NS
Sp. x Yr.	897.1	3	17.599	3,12	<0.001
Sp. x Tii	642.5	2	9.109	2,13	0.005-0.001
Site x Yr.	378.0	7	0.598	7,8	NS
Site x Tii	698.0	5	3.464	5,10	0.05-0.025
Yr. x Tii	491.9	2	5.249	2,13	0.025-0.01
Sp. x Site x Yr.	-	15	-	-	-
Sp. x Site x Tii	876.3	10	1.950	10,5	NS
Sp. x Yr. x Tii	989.9	4	24.502	4,11	<0.001*
Site x Yr. x Tii	925.5	8	4.614	8,7	0.05-0.025
Sp. x Site x Yr. x Tii	-	15	-	-	-

Model: GM + Sp. x Yr. x Tii; Deviance = 111.1, df = 11

Variables added	Reduction in deviance	Reduction in df	F	df	P
Sp.	8.30	1	0.807	1,10	NS
Site	20.21	4	0.195	4,7	NS
Yr.	2.50	1	0.230	1,10	NS
Sp. x Site	74.42	9	0.451	9,2	NS
Sp. x Yr.	25.15	3	0.780	3,8	NS
Site x Yr.	41.64	7	0.343	7,4	NS
Sp. x Site x Yr.	-	11	-	-	

Therefore, best fit model = GM + Sp. x Yr. x Tii

Parameter Estimates (+ SE)

GM	79.29	(11.93)
M. maculatus 1981 Tii	-0.7112	(0.1967)
M. maculatus 1982 Tii	-1.164	(0.2604)
C. brunneus 1981 Tii	-0.4206	(0.1532)
C. brunneus 1982 Tii	-0.6430	(0.2020)

(d)

Model: Grand Mean (GM); Deviance = 798.9, df = 15

Variables added	Reduction in deviance	Reduction in df	F	df	P
Sp.	410.0	1	14.760	1,14	0.005-0.001
Site	128.2	4	0.526	4,11	NS
Yr.	42.5	1	0.787	1,14	NS
Tii	79.5	1	1.547	1,14	NS
Sp. x Site	577.4	9	1.738	9,6	NS
Sp. x Yr.	464.2	3	5.548	3,12	0.025-0.01
Sp. x Tii	356.3	2	5.233	2,13	0.025-0.01
Site x Yr.	194.4	7	0.368	7,8	NS
Site x Tii	234.0	5	0.828	5,10	NS
Yr. x Tii	83.0	2	0.754	2,13	NS
Sp. x Site x Yr.	-	15	-	-	-
Sp. x Site x Tii	560.2	10	1.173	10,5	NS
Sp. x Yr. x Tii	639.9	4	11.067	4,11	<0.001*
Site x Yr. x Tii	503.8	8	0.797	8,7	NS
Sp. x Site x Yr. x Tii	-	15	-	-	-

Model: GM + Sp. x Yr. x Tii; Deviance = 159.0, df = 11

Variables added	Reduction in deviance	Reduction in df	F	df	P
Sp.	19.00	1	1.357	1,10	NS
Site	91.12	4	1.304	4,7	NS
Yr.	0.00	1	0	1,10	NS
Sp. x Site	149.25	9	3.400	9,2	NS
Sp. x Yr.	22.30	3	0.435	3,8	NS
Site x Yr.	107.43	7	1.190	7,4	NS
Sp. x Site x Yr.	-	11	-	-	-

Therefore, best fit model = GM + Sp. x Yr. x Tii

Parameter Estimates (+SE)

GM			80.1	(11.54)
M. maculatus	1981	Tii	-0.6559	(0.1646)
M. maculatus	1982	Tii	-1.015	(0.2312)
C. brunneus	1981	Tii	-0.4346	(0.1328)
C. brunneus	1982	Tii	-0.6068	(0.1825)

(e)

Model: Grand Mean (GM); Deviance = 1098, df = 15

Variables added	Reduction in deviance	Reduction in df	F	df	P
Sp.	169.3	1	2.552	1,14	NS
Site	415.5	4	1.674	4,11	NS
Yr.	51.0	1	0.682	1,14	NS
Tii	102.0	1	1.434	1,14	NS
Sp. x Site	646.0	9	0.953	9,6	NS
Sp. x Yr.	342.9	3	1.816	3,12	NS
Sp. x Tii	340.8	2	2.926	2,13	NS
Site x Yr.	726.0	7	2.230	7,8	NS
Site x Tii	469.4	5	1.493	5,10	NS
Yr. x Tii	103.2	2	0.674	2,13	NS
Sp. x Site x Yr.	-	15	-	-	-
Sp. x Site x Tii	710.7	10	0.918	10,5	NS
Sp. x Yr. x Tii	527.8	4	2.546	4,11	NS
Site x Yr. x Tii	811.9	8	2.483	8,7	NS
Sp. x Site x Yr. x Tii	-	15	-	-	-

best fit to the data, namely, the interaction of "species x year x date of moult into second instar". This model explained between 80% and 93% of the variance in developmental period depending on the cumulative frequency examined (excluding the non-significant 100% cumulative frequency). The lack of any relationship between any of the variables, or factors, and developmental period for the 100% cumulative frequency was probably because the estimates of developmental period were highly dependent on just one - the last - moulting grasshopper, so that errors due to small numbers were relatively more important.

The later the date of moult into second instar the shorter the subsequent developmental period (see also Fig. 3.7). This effect was found for each of the sixteen species-year-cumulative frequency combinations (Table 3.14) and was consistent despite changes in the rank order of moulting dates between populations and cumulative frequencies (Fig. 3.7).

The most obvious explanation is that in those populations with later-moulting second-instar grasshoppers the animals start to catch up in their development. This faster development could conceivably be a "strategic" increase, or may simply result from a progressive increase in the mean temperature as the season advances: the graph of maximum daily temperatures (Fig. 3.5) supports this latter explanation. Pickford (1960) also records that where hatching was later there was a tendency for a shorter developmental period; he, too, suggests that increasing environmental temperatures as the season advanced were the most likely cause of this trend.

The idea that the negative relationship between t_{ii} and t

FIGURE 3.7: **Relationship between "date of moult into second instar" and "the period between second instar moult and adult moult"**

(a) The first 20% of the population to moult, for each population

(b) The second 20%.

(c) The third 20%.

(d) The fourth 20%.

(e) The last 20%.

(i) M.maculatus, 1981

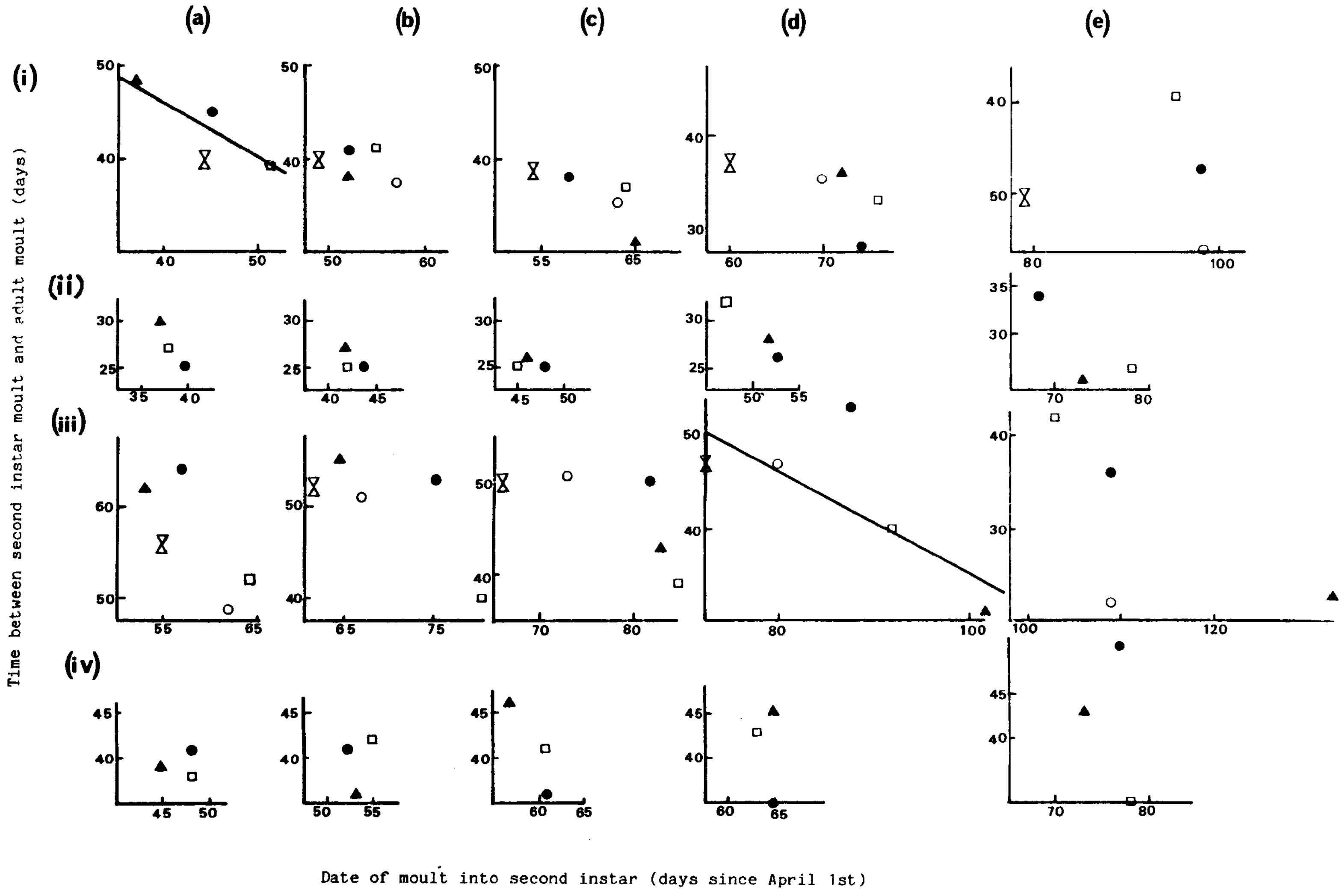
(ii) M.maculatus, 1982

(iii) C.brunneus, 1981

(iv) C.brunneus, 1982

● site 1; ⧖ enclosure 1 at site 1; ○ enclosure 2 at site 1;

◻ site 2; ▲ site 3.


(a)
(b)
(c)
(d)
(e)
(i)
(ii)
(iii)
(iv)
Time between second instar moult and adult moult (days)
Date of moult into second instar (days since April 1st)

is an artefact caused by differential mortality of later-moulting animals within each population would only be plausible if the mortality affected each proportion of each population differentially and in a way which preserved the relationship despite changes in the rank order of t_{ii}.

Such a combination of mortalities might, at first, seem improbable, but there is a mechanism which can produce it. I shall set out the mechanism in the form of a list of premises, with supporting statements for the premises, and conclusions derived from them.

Premise i. The recruitment of animals into the second instar occurs over a longer time period at some sites than others.

Support for premise i. The data plotted in Fig. 3.1, which was used to produce curves for the cumulative frequency of moulted animals, support this. On *a priori* grounds, this is likely to be true also because some sites have a greater range of slopes and aspects than others (Chapter 2), and therefore presumably a greater range of surface soil temperatures and hatching dates.

Consequence. With a flatter and broader recruitment curve, produced by animals moulting both earlier and later than in other populations, it takes longer for the later animals to moult. Therefore, as each successive cumulative frequency is examined, t_{ii} will become relatively later in a population with such a broad recruitment curve than the corresponding t_{ii} for a population with a narrower recruitment curve.

Premise ii. Competition occurs amongst the nymphs.

Support for premise ii. No good evidence - for or against. The results from Chapter 6 are consistent with the notion that hatchling competition has had a selective effect on egg size.

Premise iii. The greater the difference in age or size between nymphs in a population, the more contest-like is the competition, resulting in a greater proportionate mortality of the small, late nymphs.

Support for premise iii. Initial size and developmental stage have been shown to be positively related to subsequent survivorship in laboratory populations of C.brunneus showing the high levels of competition; the relationship is strongest at the highest densities (R. Wall, unpublished). The phenomenon occurs in other taxa - e.g. the creation of large differences in the size and age of chicks by staggering the hatching dates is generally regarded as an efficient means of brood reduction in a number of bird species (Lack, 1954).

Consequence. As each cumulative frequency is examined, the "developmental period", t, will become relatively shorter in those populations with a broad recruitment curve because a relatively greater proportion of the later moulting nymphs do not reach adulthood.

Thus, by combining the two consequences of the premises described we can conclude that populations with broad recruitment curves are likely to start off with an early t_{ii} and a fairly long t, but as each cumulative frequency is examined, t_{ii} will become relatively later than that for populations with a narrower recruitment curve; also the apparent developmental period, t, will become relatively shorter because a larger proportion of the later-moulting nymphs do not reach adulthood.

Thus, the negative relationship between t_{ii} and t may be explained by either the effects of date of moult on subsequent developmental period, or by differential mortality of particular proportions of particular populations.

3.5.3.2. Temperature

The egg is one stage of the life history when grasshoppers would experience the measured differences in temperature between areas, since they would obviously be unable to regulate their temperatures by moving to suitable spots. We would therefore expect that the grasshoppers in the enclosures would hatch earlier than the those in the surrounding site. Incomplete partial population curves for first instars of some populations precluded a proper test of this, but the recruitment curve into the second instar, and also the subsequent developmental period were known for each population (Section 3.5.2).

The grasshoppers in enclosure 1 moulted into the second instar earlier than those in the sites or in the other enclosure (Table 3.15). However, early grasshoppers did not subsequently develop faster (Table 3.12, Fig. 3.7). These results are consistent with the idea that the high temperature in enclosure 1 caused an early hatch and/or possibly a rapid passage through the first instar, but thereafter was less important than the effect on development of moulting early into the second instar (Section 3.5.3.1).

The effect of temperature on development may explain the differences in developmental rates observed between years. The warmer weather in 1982 than in 1981 during the period of nymphal development (Fig. 3.5) corresponds to the early entry into the second instar (Table 3.15) and the faster subsequent developmental rate of grasshoppers from all populations in 1982 (Tables 3.12 and 3.14).

To briefly conclude this chapter; there is considerable variation in density, rates of loss from the populations, and

TABLE 3.15: Dates of moult into the second instar (days since April 1st).

Species	Site (enclosure)	Year	Percent of population comprising second or later instars				
			20	40	60	80	100
			Days since April 1st				
M. maculatus	1	1981	45	52	58	74	98
	1(1)		44	49	54	60	79
	1(2)		51	57	63	70	98
	2		51	55	64	76	95
	3		37	52	65	72	100
	1	1982	40	44	48	53	68
	2		38	42	45	47	78
	3		37	42	46	52	73
C. brunneus	1	1981	57	75	82	87	109
	1(1)		55	62	66	72	98
	1(2)		62	67	73	80	109
	2		64	80	85	92	103
	3		53	65	83	102	133
	1	1982	48	52	61	65	77
	2		48	55	61	63	78
	3		45	53	57	65	73

The population which moults first, for a given "species-year" and cumulative frequency group, is underlined.

developmental periods of the grasshoppers. Mortality is greater in M.maculatus than C.brunneus, and losses were greater in the cooler and wetter 1981 season than in 1982, but the effects of density-related factors on grasshopper losses were not conclusive. The larger C.brunneus grasshoppers, the cooler 1981 season, and populations with earlier-moulting second instars all had relatively slow developmental rates. However, the latter relationship may have been due to the seasonal increase in temperature in the spring, may have been "strategic", or may have been an artefact produced by differential mortality of particular proportions of particular populations. The data on density differences will be used in the analyses of the correlates of size differences in later chapters.

CHAPTER 4: **Ecological correlates of life-history variation in the grasshoppers *Chorthippus brunneus* (Thunb.) and *Myrmeleotettix maculatus* (Thunb.) : I. Size at maturity.**

SUMMARY

1. Consistent significant differences in adult size were found in each species and in each year between sites. Site 3 had the largest, and site 2 the smallest animals. Adults were also bigger in 1982 than in 1981. These relationships were found in both sexes.

2. None of eleven indices of adult competition (for space, grass, grass with thin-edged leaves, and sandy areas) showed a positive correlation with adult size; nor did the degree of evaporative water loss at each site.

3. Sites (or enclosures) and years with earlier-emerging adults tended also to have larger adults. Also, *within* all populations of *M.maculatus* in 1982, and of *C.brunneus* at site 2, earlier-emerging individuals were larger than later ones. No such relationship was found in *C.brunneus* in 1983.

4. Circumstantial evidence suggests that the variation in adult size results largely from the effects of the immediate environment on the amount of resources assimilated by the nymphs.

4.1. INTRODUCTION

Adult size is a life-history characteristic which is likely to have important effects on fitness. Large females are often more fecund than smaller ones (e.g. Berven, 1982; Lawlor, 1976), and large males tend to have a higher mating success (e.g. Howard, 1979; Kodric-Brown, 1977; Ward, 1983). A large size can provide better protection from predators as Seed and Brown (1978) have shown, but the converse may also be true sometimes as Culver (1980) has discussed; he suggested that smaller cladocerans may be less apparent to visual predators such as fish and therefore better protected from them. Being big may improve the animal's ability to compete for resources (MacArthur, 1972; Pianka, 1970), and may reduce water loss as Nevo (1973) found in cricket frogs.

However, in ephemeral environments or those with short growing seasons, it may be more important to rush through development even at the expense of becoming a smaller adult as Harrison (1978), Masaki (1978), Roff (1980) and Schoener and Janzen (1968) have suggested. In addition, Peters (1983) has contended that some of the advantages which are said to be associated with large body size are debatable.

In addition to its direct selective value, body size may, due to design constraints, be unavoidably developmentally correlated with the magnitude of other characters which are under strong selection (Gould and Lewontin, 1979). It may therefore be selected for indirectly (e.g. as Berven (1982) hypothesized to account for adult size variation in a wood frog; see also Chapter 1). Growth rates and adult size may also be constrained simply by the amount of food available.

The forces which can affect adult size or any life-history trait are therefore numerous, and it is not obvious how body size should vary in different ecological circumstances (Chapter 1).

In this chapter I describe the adult size variation, and its relationship to some potential causes of this variation, in the grasshoppers *Chorthippus brunneus* and *Myrmeleotettix maculatus* co-occurring at three study sites at Ainsdale Sand Dunes National Nature Reserve, Merseyside. In particular, I examine how adult size correlates with emergence date, crowding and competition indices, and measures of hydric stress.

4.2. THE STUDY SITES

A detailed account of the site characteristics is given in Chapter 2; the present description represents an outline of the main differences.

Site 1 was in the open dunes and was sandy - 26% of the site area was bare sand. It was the most exposed to sun and wind, and undulating, though mainly SE-facing. Grass leaves covered only 14% of the area at this site. The rest of the area was covered mainly by other herbs and by moss. The structure of the vegetation within each of two enclosures at site 1 was similar to that found in the surrounding site (Chapter 2). Enclosure 1, however, was more south-facing than the predominantly SE-facing enclosure 2 and surrounding site, and was hotter.

Site 2 was the furthest inland; it had the smallest proportion of bare sand (potential oviposition sites) of the three sites (1%); and about 30% of the site was covered with grass blades.

Site 3 was a mainly south-facing dune slope but also included the edge of the adjacent horizontal dry slack. Two percent of this last site was covered by bare sand and 37% by grass leaves.

Estimates of grass cover and the amount of bare sand were made using the point-intercept method described by Mueller-Dombois and Ellenburg (1974). Because there were very few multiple touches of the 2mm diameter pin by grass blades as the pin was lowered to the ground (Chapter 2) the percentage cover of grass indicated the relative amounts of grass at the three sites.

4.3. HIND FEMUR LENGTH AS A MEASURE OF MATURE SIZE

In grasshoppers, adult body weight varies markedly with time, particularly in the female, in which it varies according to the stage in her reproductive cycle as well as with her degree of maturity (Richards and Waloff, 1954; P. de Souza Santos jr., unpublished). Therefore, when using adult weights as a measure of size at maturity, extremely large sample sizes would be needed to reveal any significant differences among different populations because of the large variances in the weight of individuals. However, in arthropods, for which potential maximum weight will be limited by the size of the adult's exoskeleton, a linear measure of the exoskeleton can provide a reliable index of mature size, as has been shown in dipterans (Ward, 1983) for example. Figures 4.1a and 4.1b show the relationship between hind femur length and adult emergence weight in both male and female *C.brunneus*. These data were obtained from closely-observed laboratory animals. A more direct indication of the relationship between hind femur length and mature size is provided by Figures 4.1c and 4.1d which show, for each species, the positive linear correlation between hind femur length and the weight of a female grasshopper brought into the laboratory from enclosure 1. The correlations were performed using only the data from those females which laid egg pods less than 48 hours after being weighed. Also, the weight of the hind legs were subtracted from the total weight to remove any possibility of autocorrelation. Therefore, hind femur length provides an index of body weight both at adult emergence and just before the females lay egg pods

FIGURE 4.1a+b: Relationship between emergence weight and hind femur length in adult *C.brunneus* (a) MALES; (b) FEMALES

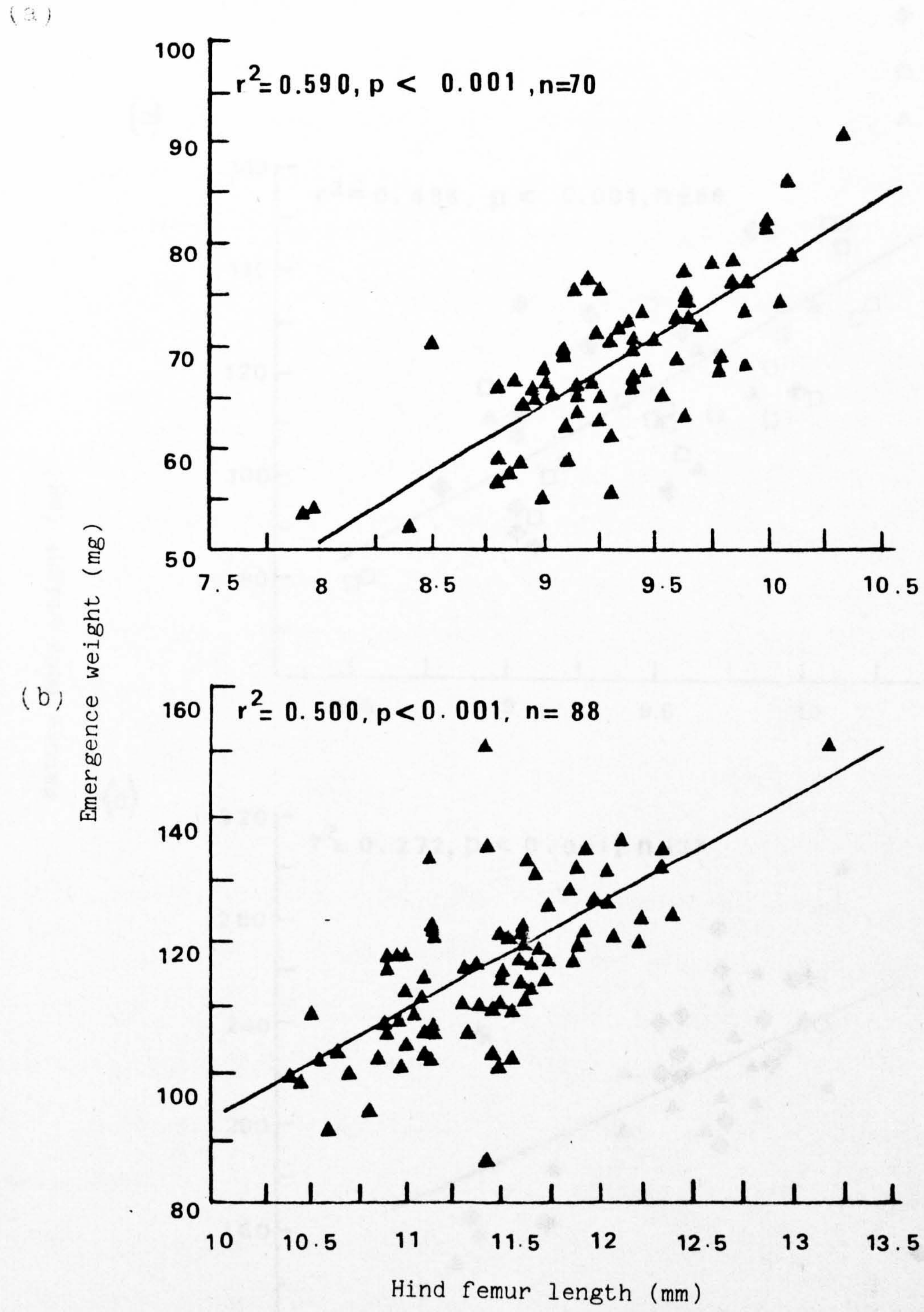
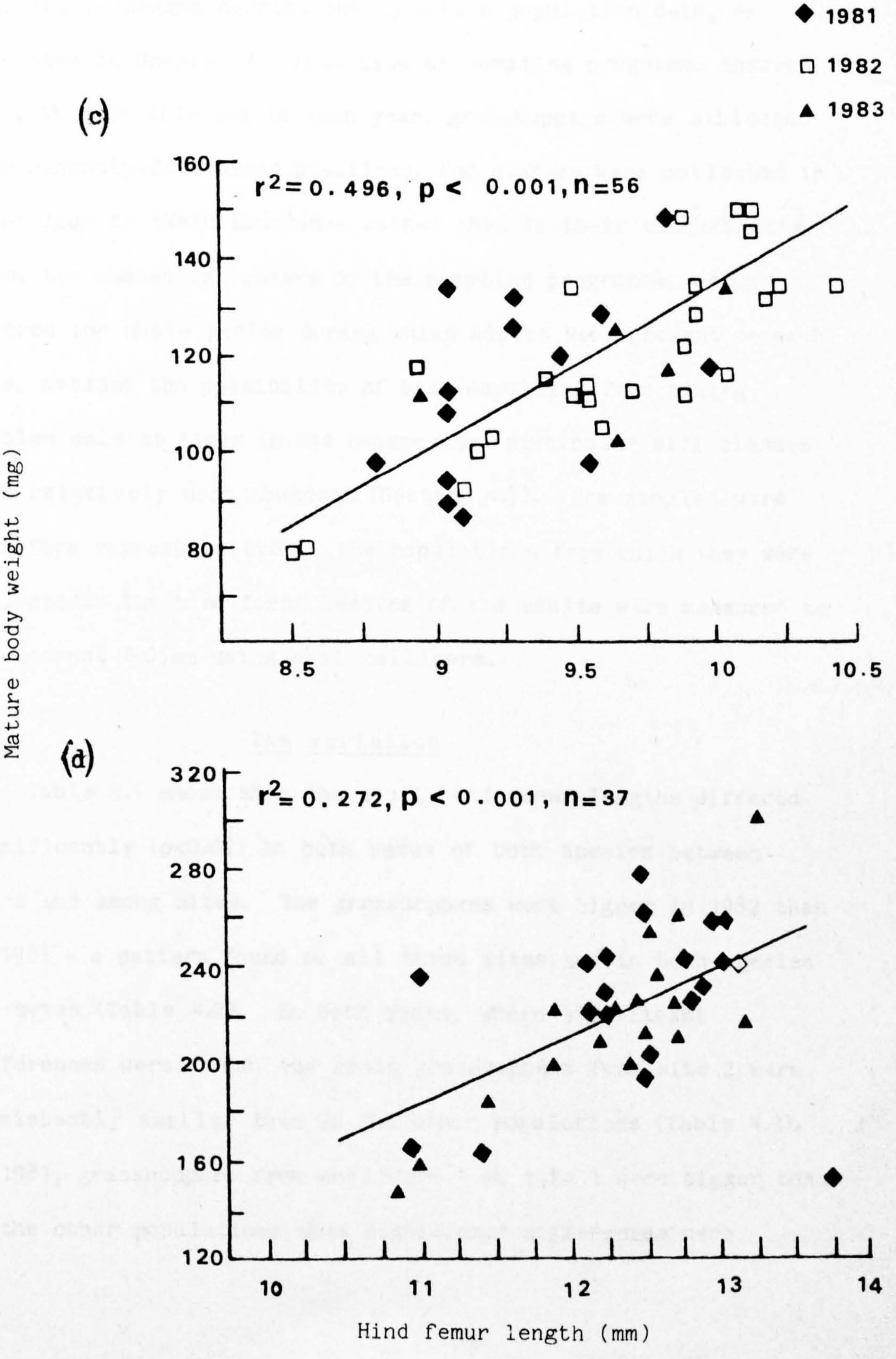


FIGURE 4.1c and d: Relationship between mature weight and hind femur length in adult females (c) M.maculatus (d) C.brunneus



(the mature weight).

4.4. VARIATION IN ADULT SIZE

4.4.1. Sequential random sampling

Throughout the summers of 1981 and 1982, adult grasshoppers were collected from each site as part of a sequential random sampling programme carried out to obtain population data, as described in Chapter 3. This type of sampling programme ensured that, at each site and in each year, grasshoppers were collected from randomly-determined positions, and numbers were collected in proportion to their abundance rather than to their catchability. Also, the sequential nature of the sampling programme, which covered the whole period during which adults were present on each site, avoided the possibility of bias resulting from taking samples only at times in the season when particular size classes were relatively more abundant (Section 4.7). The samples were therefore representative of the populations from which they were collected. The hind femur lengths of the adults were measured to the nearest 0.05mm using dial callipers.

4.4.2. The variation

Table 4.1 shows that the adult hind femur lengths differed significantly ($p<0.05$) in both sexes of both species between years and among sites. The grasshoppers were bigger in 1982 than in 1981 - a pattern found on all three sites and in both species and sexes (Table 4.2). In both years, where significant differences were found, the adult grasshoppers from site 2 were consistently smaller than in the other populations (Table 4.3). In 1981, grasshoppers from enclosure 1 at site 1 were bigger than in the other populations when significant differences were

TABLE 4.1: Analysis of variance tables showing the effects of site and year on adult size

C. brunneus adult males; hind femur length

Source of variation	DF	MS	F	P
Site	2	1.472	7.493	0.001
Year	1	3.061	15.580	<0.001
Interaction	2	0.130	0.662	NS
Error	336	0.196		
Total	341	0.210		

C. brunneus adult females; hind femur length

Source of variation	DF	MS	F	P
Site	2	2.071	4.117	0.017
Year	1	27.083	53.835	<0.001
Interaction	2	1.743	3.465	0.033
Error	235	0.503		
Total	240	0.642		

M. maculatus adult males; hind femur length

Source of variation	DF	MS	F	P
Site	2	2.422	24.476	< 0.001
Year	1	1.203	12.161	0.001
Interaction	2	0.156	1.578	NS
Error	617	0.099		
Total	622	0.108		

M. maculatus adult females; hind femur length

Source of variation	DF	MS	F	P
Site	2	8.344	48.914	< 0.001
Year	1	11.697	68.568	< 0.001
Interaction	2	0.015	0.085	NS
Error	586	0.171		
Total	591	0.216		

TABLE 4.2: Differences in adult size between years.

M. maculatus adult males; hind femur length

	Year	Mean	SE	T	DF	P
Site 1	1981	7.833	0.048	-1.63	175	0.105
	1982	7.9207	0.029			
Site 2	1981	7.6474	0.031	-3.56	288	<0.001
	1982	7.7845	0.022			
Site 3	1981	7.9152	0.038	-0.47	154	0.639
	1982	7.9383	0.032			

M. maculatus adult females; hind femur length

	Year	Mean	SE	T	DF	P
Site 1	1981	9.0160	0.058	-3.20	131	0.002
	1982	9.2860	0.054			
Site 2	1981	8.8399	0.035	-5.95	277	<0.001
	1982	9.1177	0.031			
Site 3	1981	9.2168	0.036	-4.97	160.84	<0.001
	1982	9.5216	0.050			

TABLE 4.2 continued

C. brunneus adult males; hind femur length

	Year	Mean	SE	T	DF	P
Site 1	1981	9.2000	0.069	-3.32	86	0.001
	1982	9.4867	0.046			
Site 2	1981	9.1409	0.082	-1.19	114	0.237
	1982	9.2669	0.058			
Site 3	1981	9.2920	0.053	-2.90	136	0.004
	1982	9.5022	0.049			

C. brunneus adult females; hind femur length

	Year	Mean	SE	T	DF	P
Site 1	1981	11.8864	0.236	-3.96	65	< 0.001
	1982	12.6830	0.077			
Site 2	1981	11.8862	0.160	-2.66	90	0.009
	1982	12.3230	0.083			
Site 3	1981	11.7912	0.143	-6.04	80	<0.001
	1982	12.8177	0.101			

TABLE 4.3: Differences in adult size among sites and enclosures

1981

Species	Sex	Populations (site(enclosure)) of grasshoppers				
		largest				........smallest
M.maculatus	M	1(1)	3	1(2)	1	2
M.maculatus	F	1(1)	1(2)	3	1	2
C.brunneus	M	1(1)	3	1(2)	1	2
C.brunneus	F	1(1)	1(2)	1	2	3

1982

M.maculatus	M	3	1	2
M.maculatus	F	3	1	2
C.brunneus	M	3	1	2
C.brunneus	F	3	1	2

(SNK multiple range test)

recorded (Table 4.3). When differences among the three sites were compared, adults from site 3 were larger than those from site 1 which in turn were larger than adults from site 2. This occurred in each sex of each species in each year: the only exception was provided by the non-significant differences in hind femur length of C.brunneus females between sites in 1981, in which those from site 3 tended to be slightly smaller than those from the other sites. This exception to the general result (albeit non-significant) explains the significant "site x year" interaction effect shown in Table 4.1; that is, the order in which the sizes of C.brunneus adult females differed between sites depended upon the year.

Therefore, despite the fact that the sites were less than 1.5 km apart, and the enclosures were actually built within one of the sites, significant differences in adult size were still observed between them. Because the significant differences in adult size between years and among the sites were consistent in both sexes of both species, I shall look for a single cause of the variation rather than separate ones for each sex. Also, the adult sex ratios, and therefore the potential for differences in sexual selection, did not show any consistent relationship to site (Chapter 3); sexual selection is therefore unlikely to be the main cause of differences in male size.

The first hypothesis I consider is that in populations in which there is intense competition among adults, large adults are favoured by natural selection.

4.5. ADULT SIZE AND INDICES OF COMPETITION

4.5.1. Natural selection and competitive ability

If larger adults are better competitors than smaller ones, larger adults should, as Pianka (1970) proposed, be favoured by natural selection in crowded environments. Indeed, there does seem to be an association in a wide range of taxa between large adults and either crowded conditions (Gadgil and Solbrig, 1972; Law et al., 1977) or competitive ability (Arak, 1983; Howard, 1979; Kodric-Brown, 1977; Ward, 1983). Therefore, larger adults should be found on those sites in which they or their ancestors experienced more intense levels of competition.

Adult grasshoppers of both sexes may compete for space, food, or oviposition sites, and they may compete with other adult conspecifics, other adult grasshoppers of either species, or (for food and space, at least) with all other grasshoppers. In this study, I compare how each of eleven indices of competition differ between sites, and how they correlate with adult size.

Each index of competition was calculated as the density of competitors divided by the amount of resources, as described below.

4.5.2. Crowding (competition for space)

The stage-frequency data for each sex, collected from each population in 1981 (as described in Chapter 3) were used to calculate the indices of the competition for space experienced by adults of each species at their peak density (indices **A1-3**). The density of competitors was used for each of three sets of indices in which the following were considered as potential competitors: (i) all grasshoppers (index=**A1**), (ii) all adults (index=**A2**), or (iii) all adult conspecifics (index=**A3**). Density measurements can be considered as indices of competition for space simply because they incorporate the numbers of competitors divided by the amount of space in which they were sampled.

The relationship between these indices of crowding and adult size in the following year are described in Table 4.4. Site 2, which had the smallest adults of both species, did not have the lowest density of competitors, irrespective of which of the indices of crowding were used. Therefore, if selection for competitive ability was an important determinant of adult size variation between populations, the grasshoppers were unlikely to be competing just for space.

4.5.3. Competition for grass

British grasshoppers eat a wide variety of grasses but little else (Bernays and Chapman, 1970b; Monk, 1981; Richards and Waloff, 1954). The sites had different amounts of grass (Chapter 2), and therefore indices of competition for food should take this into account.

The measures of grass abundance (derived from the estimates of percentage cover obtained using the "point-intercept" method of vegetational analysis; Chapter 2) were summed for grass blades of all species. Each of the crowding indices **A1-3** for each population was divided by the measure of total grass abundance (grass percentage cover expressed as a fraction of 1) of the respective site and labelled **B1-3.** (The same calculation was performed on population density in the analysis of density-dependent losses in Chapter 3).

Site 3, which had the largest grasshoppers (and also the most grass; Section 4.2), did not have the highest estimated levels of competition for grass. This result was found in both species and occurred irrespective of which group of potential competitors was considered (Table 4.4). However, before I discard the idea that the most important influence on adult size

TABLE 4.4: **Adult competition indices in each population, in relation to adult size**

Species			*M.maculatus*			*C.brunneus*		
Site			2	1	3	2	1	3
Adult size			Smallest					Largest
Competitors	Resources	Competition Index						
All grasshoppers	space	A1	2.467	1.233	1.718	1.267	0.371	1.150
All adults	space	A2	1.800	0.733	0.956	1.166	0.371	1.050
All adult conspecifics	space	A3	1.667	0.733	0.826	0.233	0.171	0.450
All grasshoppers	grass	B1	8.223	8.807	4.643	4.223	2.650	3.108
All adults	grass	B2	6.000	5.236	2.584	3.887	2.650	2.838
All adult conspecifics	grass	B3	5.557	5.236	2.232	0.777	1.221	1.216
All grasshoppers	Non-*Festuca* grass	C1	9.868	30.825	12.271	5.068	9.275	8.214
All adults	Non-*Festuca* grass	C2	7.200	18.325	6.829	4.664	9.275	7.500
All adult conspecifics	Non-*Festuca* grass	C3	6.668	18.325	5.900	0.932	4.275	3.214
All adults	Sandy areas	D2	180.000	2.819	47.800	116.600	1.427	52.500
All adult conspecifics	Sandy areas	D3	166.700	2.819	41.300	23.300	0.658	22.500

is the selection pressures on the ability to compete for food, I shall examine the notion that certain grasses are either preferred or avoided by the grasshoppers.

4.5.4. The effect of natural diet restriction

Two studies of C.brunneus (Young, 1979; Monk, 1981) showed that adults tended to feed less on the grass Festuca, than would be expected if the grasshoppers were unselective. Festuca rubra accounted for a large proportion of the grass at sites 1 and 3 (Chapter 2), and Festuca ovina was also present at site 3 (K. Payne, pers. comm.). In the vegetation survey (Chapter 2) grass blades of Festuca were not identified to species level. The percentage abundance of grass blades excluding Festuca were 4% at site 1, 25% at site 2, and 14% at site 3.

In order to take into account the tendency, of C.brunneus at least, to avoid Festuca, I calculated another set of competition indices. Each of the crowding indices **A1-3** for each population was divided by the abundance of potential food (grass leaves minus Festuca) at the appropriate site. These indices of competition for non-Festuca grass were labelled **C1** to **C3**. (The calculations are the like those performed for the analysis of density dependent losses in Chapter 3).

Once again, Table 4.4 shows that the site with the largest grasshoppers (site 3) did not exhibit the highest index of grasshopper competition for any of the indices **C1-3** in either species. Competition for non-Festuca grass, therefore, did not seem to be the most important selective influence on adult size.

Bernays and Chapman (1970a) showed that another grass, Anthoxanthum odoratum, was eaten in smaller amounts by the grasshopper Chorthippus parallelus than would be expected if it was eaten in proportion to its abundance. This grass covered only about 2% of the area of site 2 and 1% of site 3 (Chapter 2). If the grasshoppers avoided this grass, the relationships between adult size and competition indices among the populations (Table 4.4) would tend to become more negative, and therefore counter to the predictions of the hypothesis under test.

4.5.5. Competition for sandy areas

A final set of indices was calculated to examine the idea that adults compete for access to areas with bare sand, where oviposition and much courtship takes place (Young, 1979).

Indices D2 and D3 were calculated by dividing, respectively, the density of adults (A2) and the density of adult conspecifics (A3) by the percentage cover of bare sand (expressed as a fraction of 1) at each site. Estimates of the amount of bare sand were obtained by using the point-intercept method to estimate vegetation cover and, by subtraction, the amount of bare ground (Chapter 2).

Because site 1 had much more bare sand than the other two sites, the indices of competition were much lower (Table 4.4), but the adult grasshoppers at this site were only intermediate in size between those at sites 2 and 3 (Table 4.3).

Therefore, none of the eleven indices of competition showed any tendency which was consistent with the idea that larger adults occurred in populations where competition was most intense because they were favoured by natural selection.

In the next section I discuss the conditions in which adult grasshoppers at different sites are likely to be subject to differences in selection for competitive ability.

4.5.6. Competition and dispersal

It might pay an animal to disperse from an area if there are usually areas surrounding a site in which conditions are more favourable (Baker, 1978), or if the animal can gain a higher inclusive fitness by moving away from close relatives and competing with more distantly-related animals, even when the habitat is uniformally crowded (Hamilton and May, 1977).

Young C.brunneus and M.maculatus do disperse from their hatching sites, since later instars have been found in parts of the study areas where grasshoppers had not been caught before and where no bare sand (hatching sites) occurred (pers. obs.). This would enable the hoppers to move away from their siblings which hatch from the same egg pod. The argument of Hamilton and May (op. cit.) may therefore apply to young hoppers, but once this initial dispersal has been achieved it is likely to be less important. The rest of my discussion focuses on the argument described by Baker (op. cit.), which is more likely to be applicable to this study of adult competition because the grasshoppers are motile, and the sand dunes have a heterogeneous distribution of resources (sand; grass species and vegetation structure; and slopes and aspects; Chapter 2). An example of the grasshoppers moving into another area is provided by the observation that C.brunneus tended to move out of the original sites 1 and 2 into taller and denser vegetation as they got older, apparently only returning briefly to lay pods (Chapter 3).

If grasshoppers are free to move to areas in which competition is less severe, and if they behave so as to maximize their reproductive success (i.e. are "ideal"), they should be distributed so that they all acquire the resources at the same rate. They would therefore follow the "ideal free distribution", described by Fretwell and Lucas (1970) and Parker (1970). Thus, adult grasshoppers may move away from areas of higher than average levels of competition and may not therefore be subject to large differences in selection for the ability to compete for limiting resources. This is consistent with the observations noted in Chapter 3: in some cases the grasshoppers moved out of the study sites and thereby avoided intense competition.

Alternatively, if the nearest underexploited resources are too far away, dispersal would lower lifetime reproductive success, and an ability to compete successfully would be favoured instead. The results of Richards and Waloff (1954), Aikman and Hewitt (1972), and Young (1979) suggest that C.brunneus and M.maculatus tend to move only a few metres, but Dempster (1955) showed that the amount of movement depends on the structure of the habitat.

The argument that adults can move to the nearest underexploited patch of resources (and therefore alter the strength of selection for competitive ability) cannot be extended to the hatchlings without considering their much-reduced motility. We should be wary, therefore, of assuming that just because the adults and juveniles share the same habitat, the variation in life history of both phases can necessarily be explained by theories such as that of r- and K-selection (Pianka, 1970) which assume implicitly that the environment affects all ages similarly. Chapter 6 describes the relationships between a number of competition indices and egg size (and therefore hatchling size; R. Wall, unpublished), and shows whether the relationships differ from those with adult size.

The next section examines the relationship between adult size and another potential selection pressure - desiccation stress.

4.6. ADULT SIZE AND DESICCATING CONDITIONS

4.6.1. Why should large adults be favoured in desiccating conditions ?

Larger adults are likely to be better protected from desiccation stress than smaller ones because larger bodies have smaller surface area-to-volume ratios than smaller ones of the same shape. They therefore have a relatively smaller surface area through which water can be lost. This results from the fact that an increase in length is associated with only a quadratic increase in area but the corresponding increase in volume is cubic.

Anderson *et al.* (1979) provide evidence that different grasshoppers are affected differentially by thermal and hydric stresses. They found that *Psolessa delicatula* displayed thermoregulatory postures and shade-seeking behaviour, and kept its body temperature at a relatively constant level. This contrasted with *Erritettix simplex* which was more abundant in dense vegetation, and the nymphs of which lost water rapidly.

There are, in addititon, a number of studies which suggest that larger animals should occur at the site with the most desiccating conditions. Schoener and Janzen (1968), for example, showed, using data from an interpecific comparison, a significant negative correlation between insect size and environmental humidity. Within a species, larger adult cricket frogs lost less water (Nevo, 1973) and larger fruit flies survived better in desiccating conditions (Barker and Barker, 1980). In grasshoppers, body size has been shown to increase within a species from north to south in the northern hemisphere, and from low to high altitude (Kritskaya, 1972; Litvinova, 1972). Therefore, in some organisms, at least, the effects of desiccation are apparently more important than competition in determining adult size.

4.6.2. Measuring the degree of desiccation

The desiccation stresses likely to be experienced by the grasshoppers at the three sites were measured by recording the daily evaporation rates from randomly-located tanks of water placed at ground level. Measures of temperatures and humidity would have been less satisfactory measures of desiccation risk because they do not take into account the accelerating effect of air movement on evaporation. A fuller account of the measurement of water evaporation rates from the sites is given in Chapter 2.

4.6.3. The relationship between evaporation rates and adult size

The results shown below summarize the findings described in Chapter 2.

Site	1	2	3
Mean daily evaporation rate	3.99	3.38	3.05

(A common underlining joins together the sites with values which were not significantly different using Wilcoxon Matched-Pairs Signed-Ranks Tests, p_{crit}=0.01).

Site 1, therefore, had the highest rate of evaporative water loss but not the largest adults (Table 4.3). Site 3, on the other hand, had the lowest rates of evaporation (albeit not significantly lower than site 2), but had the largest adults

(Table 4.3).

4.6.4. Interpreting correlations between the degree of desiccation and phenotypic characters

In this comparison, the hypothesis under test - that the main cause of adult size variation between sites is selection to withstand the effects of desiccating conditions - is falsified. This is not to say that selection for the ability to withstand desiccation has no effect on adult size, or that it is not the main cause of size variation between two of the sites, namely sites 1 and 2. The result also does not exclude the possibility that desiccation stress has other important morphological effects.

For instance, recent work on C.brunneus and Chorthippus parallelus describes a difference in shape but not in size between hot dry sites (and years), and cool wet ones (Monk, 1983). A canonical variate analysis, performed on 10 independent skeletal measurements, showed that measurements which tended to contribute to body length showed a negative correlation with those measurements contributing to body width. In hotter drier conditions the grasshoppers were shorter and wider; this could give them a smaller surface area-to-volume ratio, so they too might lose water more slowly than longer and thinner animals.

Desiccation stress can also have effects on the behaviour to regulate water loss (Ruscoe, 1970; Anderson et al., 1979). Because the topography and vegetational structure at the sites were varied (Chapter 2), the motile grasshoppers might have been able to find locations which were much less desiccating than the mean for the site as a whole. If this was true, the significant mean differences in desiccation stress between the sites (which seemed to be important in the studies of Schoener and Janzen (1968) and Barker and Barker (1980)) may therefore have been unimportant as selective differences in this study. Adults of C.brunneus show basking behaviour to raise their body temperatures (Begon, 1983), so they may also be able to behaviourally regulate water loss by choosing areas with dense vegetation (which are less desiccating; Ruscoe, 1970), or by moving into other areas sheltered from the wind and direct sunshine.

The observations noted in Chapter 3 - that some C.brunneus, and possibly some M.maculatus too, moved out of the study sites into taller denser vegetation - is also consistent with the idea that the grasshoppers avoid extreme conditions of desiccation by moving into more-humid spots. Thus, as was the case in the analysis of the effects of competition on adult size, the adults may have been able to avoid the potential selection pressure on size by moving into areas within or outside the sites where the selection pressure on size was reduced.

4.7. ADULT SIZE AND EMERGENCE DATE

4.7.1. An expected trade-off with adult size ?

The concept of a trade-off between different behavioural and physiological activities which utilize the same resources is central to theoretical work on adaptive life histories (e.g. reviews in Stearns, 1976; Begon and Mortimer, 1981; Horn and Rubenstein, 1984). Juvenile grasshoppers must allocate resources to growth, moulting, and activities likely to improve the chances of survival (maintenance activities). If different animals devote the same amount of resources to maintenance activities, then any selection for a larger size at moult or adult emergence should be achieved at the expense of developmental rate. Thus, a difference in adult size in natural populations may not only result from differences in direct selection on it but also from differences in selection on developmental rate (i.e. indirect selection on body size; Chapter 1).

If, however, a positive correlation is found between adult size and developmental rate, some organisms will have had more resources than others to allocate to both activities, and the expected trade-off thus becomes obscured. To translate this reasoning to field observations of adult emergence only: a grasshopper which emerges as an adult earlier and at a larger size than another one will have had more resources to allocate to growth and development.

In the following sections, I shall examine the correlation between adult size and emergence date to determine whether the effects of selection pressures on the phenotypes may be masked by the effects of total resources assimilated.

4.7.2. Measurements of adult emergence dates

Since the sex ratio was approximately unity in most of the populations (Chapter 3), the average emergence date for each sex could be estimated by noting the date on which 25% of the total population comprised adult males (or females) (i.e. 50% of the sex had become adult) by interpolation of the stage-frequency data. Thus for eight populations (2 years x 3 sites, +2 enclosures, in 1981) of each species, a value of the mean hind femur length could be related to the average emergence date.

In addition to the comparison among populations, the relationship between hind femur length and emergence date was compared among individuals within a population. Recently-emerged adults could be identified by the absence of any orange or red colouration on the posterior region of the abdomen. Such colouration, which takes two days before it first appears (pers. obs.), is an external indication of sexual maturation (Richards and Waloff, 1954). Enough of the recently-emerged animals were observed in 1982 for regression analyses to be performed for hind femur length against emergence date in all populations of M.maculatus except the males at site 1, and in the populations of C.brunneus at site 3 (and of males only) at site 2. The hind femur lengths and emergence dates of C.brunneus were also monitored in 1983. The slopes and intercepts of the regressions at the different sites were compared using an analysis of covariance of the GLIM (Generalised Linear Interactive Modelling) package (Baker and Nelder, 1977; see also Chapter 3). The package allows one to compare the goodness-of-fit of regression models with separate slopes and intercepts for each site with those which have a common slope and intercept. It calculates the deviance (residual sum of squares) and the degrees of freedom associated with each model. From these the F-statistic can be calculated, and the significance of the improvement in fit to the data can therefore be found.

4.7.3. The covariation

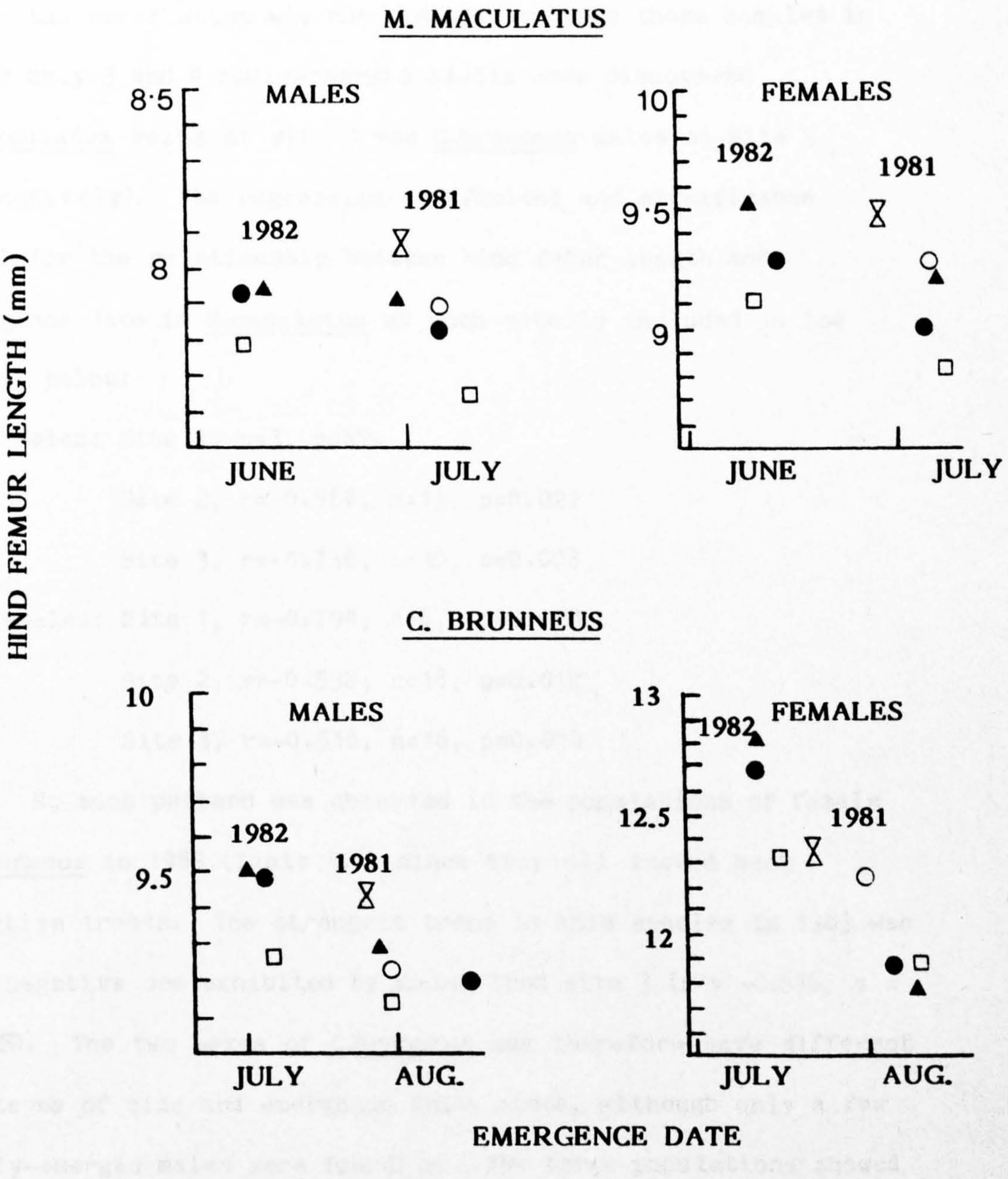
Figure 4.2 shows that grasshoppers in 1982 emerged as adults earlier than in 1981. This difference corresponds with the fact that 1982 had a much warmer spring with a correspondingly earlier hatch and more rapid juvenile development (Chapter 3). Figure 4.2 also shows a broad negative trend of hind femur length with emergence date among the three sites and two enclosures in 1981;

FIGURE 4.2:

RELATIONSHIPS BETWEEN MEAN ADULT SIZE AND EMERGENCE DATE

● SITE 1; □ SITE 2; ▲ SITE 3;

⧗ SITE 1 ENCL. 1; ○ SITE 1 ENCL. 2.



that is, the earlier-maturing populations tended to have larger grasshoppers on average. Thus, the grasshoppers showed differences between sites which suggested that some had had a "head start" over others. This was probably because they either hatched earlier, grew and developed faster, or both.

In 1982, this negative trend was also found within populations of *M.maculatus*, in both sexes (Fig. 4.3), and among males of *C.brunneus* at site 2 (Table 4.6). The only cases in which the correlation was not significant were those samples in which only 3 and 4 newly-emerged adults were discovered (*M.maculatus* males at site 1 and *C.brunneus* males at site 3, respectively). The regression coefficient and significance level for the relationship between hind femur length and emergence date in *M.maculatus* at each site is included in the list, below:

Males: Site 1, n=3, p=NS.
Site 2, r=-0.566, n=13, p=0.022
Site 3, r=-0.736, n=10, p=0.008
Females: Site 1, r=-0.794, n=6, p=0.029
Site 2, r=-0.532, n=18, p=0.012
Site 3, r=-0.516, n=18, p=0.014

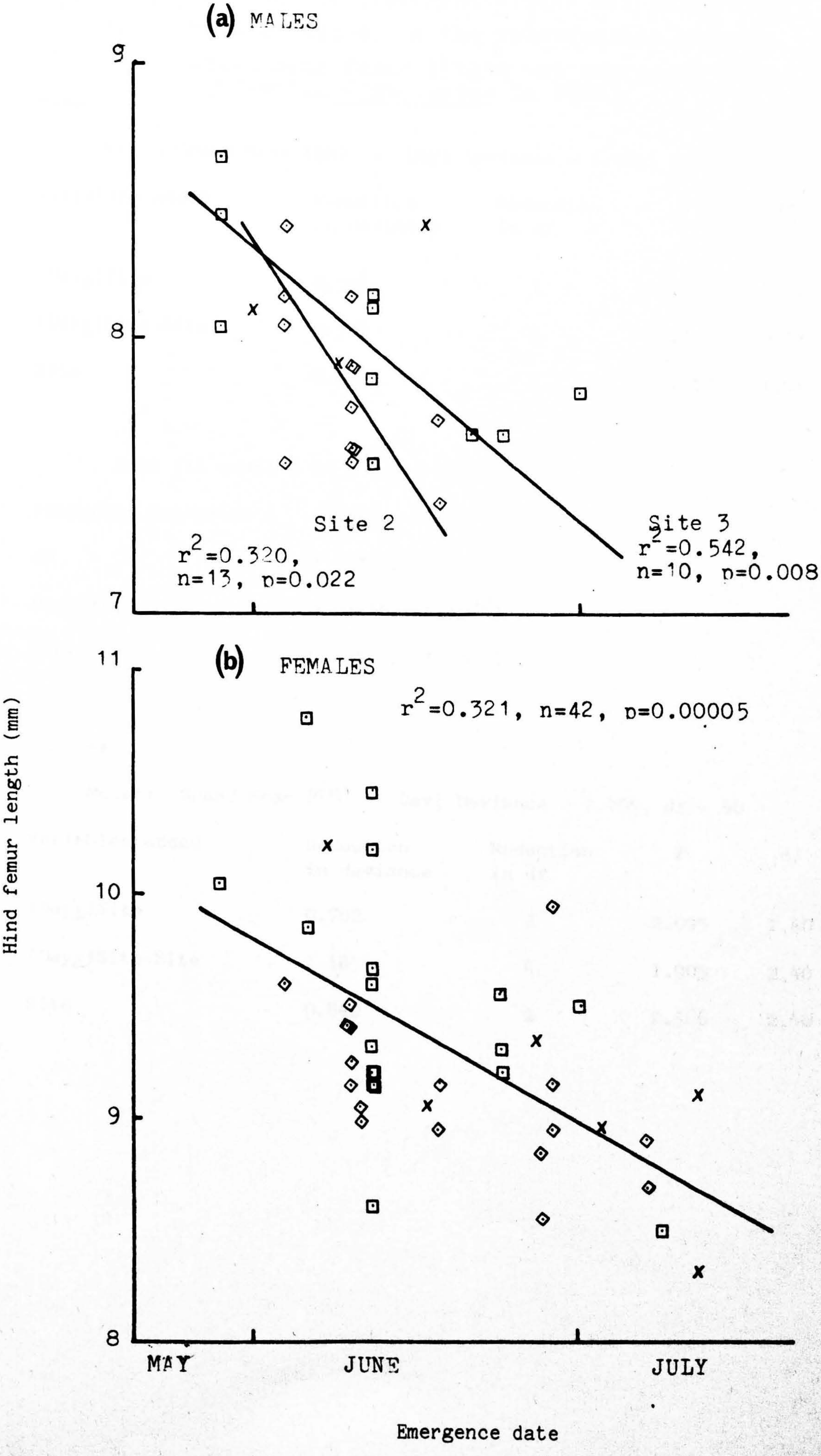
No such pattern was observed in the populations of female *C.brunneus* in 1983 (Table 4.6) since they all showed weak positive trends. The strongest trend in this species in 1983 was the negative one exhibited by males from site 3 (r = -0.516, p = 0.095). The two sexes of *C.brunneus* may therefore have different patterns of size and emergence date, since, although only a few newly-emerged males were found, all the three populations showed a negative trend and one of which was statisically significant,

FIGURE 4.3: **Relationship between *M.maculatus* adult size and emergence date, 1982**

× site 1

◈ site 2

⊡ site 3



(a) MALES
9
8
7
Site 2
r2=0.320, n=13, p=0.022
Site 3
r2=0.542, n=10, p=0.008
(b) FEMALES
r2=0.321, n=42, p=0.00005
11
10
9
8
Hind femur length (mm)
MAY
JUNE
JULY
Emergence date

TABLE 4.5: Testing for different slopes and intercepts between sites, in the relationship between adult hind femur length and emergence date ("day") in *M.maculatus* in 1982

Males

Model: Grand Mean (GM) + Day; Deviance = 1.983, df = 24

Variables added	Reduction in deviance	Reduction in df	F	df	P
(Dayx)Site	0.305	1	5.035	1,21	<0.05
(Dayx)Site+Site	0.323	2	2.705	2,21	NS
Site	0.289	1	4.712	1,21	NS

Best fit model = GM + Day x Site

Parameter Estimates (+ SE)

GM	9.785(0.479)
DayxSite 2	-0.028(0.694x10^{-2})
DayxSite 3	-0.025(0.661x10^{-2})

Females

Model: Grand Mean (GM) + Day; Deviance + 7.405, df = 40

Variables added	Reduction in deviance	Reduction in df	F	df	P
(Dayx)Site	0.702	2	2.095	2,40	NS
(Dayx)Site+Site	1.185	4	1.905	2,40	NS
Site	0.842	2	2.566	2,40	NS

TABLE 4.6: Regression coefficients of the relationships between adult hind femur length and emergence date in C.brunneus

1982:	n	r	p
Males:			
Site 1	1	-	-
2	6	-0.739	0.047
3	4	-0.216	0.392
Females:			
Site 1	3	-0.189	0.439
2	2	-	-
3	4	0.035	0.482
1983:			
Males:			
Site 1	2	-	-
2	1	-	-
3	5	-0.516	0.095
Females:			
Site 1	11	0.262	0.218
2	20	0.196	0.204
3	12	0.054	0.434

whereas all but one of the five populations of females showed very weak positive trends (Table 4.6).

The decrease in the size of M.maculatus males from site 2 with emergence date in 1982 was significantly steeper than that of males from site 3 (Fig. 4.3a; Table 4.5). There was no difference, however, among the slopes or intercepts of the graphs of female size against emergence date for the three sites (Table 4.5). This one difference in slope - that between sites 2 and 3 in Fig. 4.3a - may have been due to a real selective difference between sites or a difference in constraints on the grasshoppers (Section 4.7.4), or it may have been an anomalous result (c.f. Fig. 4.3b). A replication of the observations in another year would help to determine which alternative was most likely to be true.

To summarize these findings: there was a tendency for earlier-emerging adults to be larger than later-emergers. This correlation was found (i) among the sites and enclosures (Fig. 4.2), and (ii) between years (Fig. 4.2), in each sex of each species: it was also found among individuals within all populations of M.maculatus in 1982 (except one where only three animals were found) (Fig. 4.3) and of C.brunneus at site 2 in 1982 (Table 4.6). This correlation was not evident, however, among adults of C.brunneus in 1983 (Table 4.6).

This association between large adult size and early emergence has also been observed in field populations of damselflies (Banks and Thompson, in press), dungflies (Sigurjónsdóttir, 1980; Ward, 1983), and fruit flies (Atkinson, 1979). In the laboratory, this trend has been observed in damselflies (J. Pickup, unpublished), in C.brunneus (R. Wall, unpublished), and in fruit flies (Partridge and Farquhar, 1983;

Robertson, 1960b). Other studies which have found the opposite trend include a study of field populations of chironomids (McLachlan, 1983) and some laboratory experiments on fruit flies (Robertson, 1960a).

4.7.4. Causes of covariation between size and emergence date

4.7.4.1. The effects of other traits

It is important that a worker presenting an argument makes explicit the assumptions in his or her work so that others do not misunderstand its generality when applying it to their own work. In a review responding to some criticisms of the use of optimization theories in evolution, Maynard Smith (1978) also encourages us to state, as far as we can, our assumptions. In this spirit, I mention that a positive correlation between adult size and emergence date implies that some animals assimilated more resources than others only if other activities were not correspondingly reduced. For example, if animals consumed and assimilated the same amount of resources at the different sites but at one site the animals were under stronger selection to avoid predators, the resources might be diverted away from both growth and differentiation. Our search for differences in the sites which reduced the amount of food eaten or assimilated would therefore be fruitless. Having said this, I have no reason to believe that small late-emerging adults spent more resources avoiding predators or maintaining their somatic tissues. The idea that traits may sometimes be incompletely defined has also been discussed in Chapter 1.

4.7.4.2. Tactical covariation

Calow (1982) cites examples of organisms which slow down certain activities including growth below their maximum possible rates in an apparently adaptive way. It is conceivable, therefore, that nymphs which eventually emerge late as adults tactically slow down growth and development. However, a small adult female lays smaller egg pods (Chapter 6) and a later one will have a shorter time in which to breed repeatedly before the autumnal decline in ambient temperature and amount of sunshine (Chapter 5). Therefore, to be both smaller and later than others would appear to be maladaptive, rather than a tactical variant of being larger and earlier.

4.7.4.3. Genetic effects

Genetic differences between organisms which can produce apparently maladaptive phenotypic differences between them include the effects of lags between the time a new selection regime operates and the time the gene frequencies reach equilibrium (Maynard Smith, 1978; Dawkins, 1982). These time lags might conceivably produce the differences between sites if some sites had recently changed very rapidly, and this had lowered the mean growth and development rates for the whole population (the "lag-load"; Maynard Smith, 1976). However, this is unlikely to produce the differences found between years.

It is possible that gene flow from another site could produce a population which had some animals less well suited to the new sites than the original residents, and were therefore not able to grow and develop as quickly. However, this would be unlikely to produce the mean differences among sites and between years unless the amount of movement of aliens into the sites differed consistently from site to site and from year to year.

4.7.4.4. Environmental effects

More obvious causes of positive covariation between adult size and emergence date are environmental differences, and these would seem to apply to differences between years, sites, and among individuals within populations.

For instance, the warmer spring weather in 1982 produced an earlier hatch than in 1981, and the grasshoppers also grew and developed faster (Chapter 3).

Within each population, some grasshoppers may have been subjected to different environmental conditions since the sites were so heterogeneous (Chapter 2). A phenotypic difference caused by a slight difference in the conditions experienced by young animals might also become magnified later in life under conditions of competition (Begon, 1984). This is consistent with the results of R. Wall (unpublished) which show that earlier-emerging adults were larger than later-emergers in laboratory populations of C.brunneus reared over a range of densities in which density-dependent mortality was exhibited; but significant differences in the size at, and timing of moult between animals were not detected in the early instars. Peters and Barbosa (1977) have also described how, under conditions of high density, many laboratory-reared insects have a longer juvenile period and become adult at a smaller size.

There is some circumstantial evidence which suggests that differences in adult size resulted from responses to differences in effects of the immediate environment. First, the significant difference in adult size between years suggests that either selection caused a dramatic change in gene frequency from one year to the next, or, more likely, that the difference was due to environmental effects, such as the effect of temperature, already mentioned. Second, the enclosures were built within site 1 and therefore enclosed samples of the same population. Therefore, unless gene frequencies changed very rapidly over a few metres of apparently similar dune slope, most of the size differences between the grasshoppers from the enclosures and those from site 1 were probably caused by phenotypic plasticity.

To conclude, the most important cause of the variation in adult size observed between years, among sites, and among individuals within populations, is most likely to be the variation in the amount of resources consumed or assimilated before adulthood, rather than from any strategic alteration in the allocation of resources between growth and development. It is noteworthy that this explanation lies outside the explanatory scope of existing optimization theories of life-history evolution (see Appendix to the thesis).

4.7.5. Differences in covariation

In 1982, the rate of size decrease with date of emerging adult male M.maculatus differed significantly between sites 2 and 3, being steeper at site 2. Stearns (1983a) also mentions how the relationship betwen adult size and juvenile developmental period may differ. Two potential causes of this difference in covariation are (i) that the two traits - adult size and emergence date - are constrained to different extents at the two sites, and (ii) that there is some tactical difference in the pattern of covariation observed between the two sites.

The first of these hypotheses would be tenable if, for example, certain nutrients were required for growth or development only, and that at one site one of these specific requirements was extremely scarce so that the optimal combination of growth and developmental rates was affected by the differential effects of nutrient availability.

The second hypothesis requires that there are differences in the balance of selection pressures on adult size and emergence date.

Another example of differential effects on growth and development is described by Smith-Gill and Berven (1979) who found that in amphibians the growth rate was less affected by temperature changes than was the rate of differentiation. Invertebrates which show this phenomenon include fruit flies (Economos et al., 1982), butterflies (e.g. Gilbert, 1984) and copepods (Lock and McLaren, 1970). Smith-Gill and Berven (op. cit.) do not indicate whether they consider the different temperature sensitivities of growth and development as representing a constraint (my first hypothesis) or an adaptive response to different environmental information about future reproductive value contained in the different environmental temperature (my second hypothesis). Stearns (1982) interprets their discussion as a description of a developmental constraint. Since both growth and development rates are so clearly related to the fitness of annual organisms with size-dependent reproductive output (as discussed in Chapter 5), I shall first examine the hypothesis that there is an adaptive explanation for the change in the pattern of covariation between adult size and emergence date.

When environmental conditions deteriorate so that expectation of future survival and reproduction is diminished, and when growing larger would not improve reproductive value after moulting (post-moult reproductive value, PMRV) sufficiently to compensate for the effects of the declining environmental conditions, the grasshopper should reproduce immediately and recklessly. It is unlikely that delaying moult to grow larger could compensate for the effects of the declining environment because environmental deterioration would also reduce the potential growth rate as well as survival and reproduction. Because the rate of decrease in size with emergence date for adult male _M.maculatus_ (but not females) at site 2 was steeper than at site 3, I hypothesize that any size-independent reduction in PMRV was likely to be greater for male _M.maculatus_ at site 2 than at site 3 in 1982. Such a difference between sites might result if the food quality declined at a faster rate at site 2 than at site 3, and that this affected male PMRV more than female PMRV.

Alternative adaptive models predicting the optimal timing of life-history events by grasshoppers subject to different constraints on growth are discussed in the next chapter.

CHAPTER 5: **Optimal body size and timing of moult by arthropods subject to different constraints on growth: a general model and a particular application to grasshopper populations**

SUMMARY

1. A simple graphical model is described which predicts the nature of covariation in moulting date and body size in arthropods subject to different constraints on growth.

2. The model has three main elements: the relationships between (i) body size and time (growth), (ii) body size and fitness, and (iii) moulting date and fitness. A range of predictions is produced by varying the shapes of each of these relationships and also the constraints on the animals' growth.

3. The model predicts that: (i) animals which start off smaller or later will tend to moult subsequently at a smaller size and later than other animals; (ii) a convex (rather than a linear or concave) "size-fitness" relationship will tend to make an initially smaller animal moult even later, and a convex "time of moult-fitness" relationship makes an initially later-moulting animal moult subsequently at an even smaller size; (iii) animals with slower expected growth should moult earlier and at a smaller size than an animal with a faster expected growth rate.

4. The predictions were compared with the pattern of covariation between grasshopper adult size and emergence date described in Chapter 4. Thus, a number of reasonable hypotheses, *a priori*, could be eliminated. Some methods for further testing the different forms of the model are suggested.

5.1. INTRODUCTION

Several authors have proposed that geographic patterns of variation in body size and development time observed within insect species reflect adaptive responses to different season lengths (Harrison, 1978; Masaki, 1978; Roff, 1980). This reasoning only applies to populations which exhibit the same number of generations per season (Fairburn, 1984).

This chapter expands upon these ideas by considering not only the limitations on fitness imposed by body size and season length but also the effects of constrained growth on body size, date at moult and fitness.

Differences in constraints on growth may arise from historical (genetic) differences or from different levels of environmentally-induced stress (Chapter 1). Stearns (1983a) mentions how environmentally-induced stress can both reduce adult size and delay the time at which an organism becomes an adult. He calls a developmental path which can be altered by the immediate effects of the environment on the phenotype a plastic trajectory.

The model developed in this chapter arose from a need to explore the possible reasons why, in field populations of grasshoppers, the animals appeared to have different plastic trajectories. More specifically, larger adults emerged earlier than smaller adults - due to different immediate effects of the environment - and the slope of the relationship between adult size and emergence date differed between two populations (Chapter 4).

The rest of the chapter is set out as follows:

To provide a background to the model I first show how the trade-off between growth and development is related to that between growth and reproduction, and discuss how the effects of environmental constraints can obscure trade-offs. I then introduce the basic model, and identify the forms the relationships in the model should take when applied to the populations of grasshoppers. I then present variants of the model and summarize their predictions. This is followed by a brief discussion of two types of alternative model, and of the mechanisms which could produce adaptive combinations of growth and development. Finally, I describe how the models may be tested, and apply them to the grasshopper populations of this study.

5.2. THE TRADE-OFF BETWEEN GROWTH AND DEVELOPMENT

5.2.1. A "potential fecundity cost"

The idea that the partitioning of resources between different activities could be related to fitness was first expressed by Fisher (1930). From this was developed the concept of the cost of reproduction (Williams, 1966a,b; Calow, 1979; Bell, 1980). Bell (op. cit.) classified these costs into survival costs, actual fecundity costs (reduced future reproduction) and potential fecundity costs (reduced potential future fecundity arising from the diversion of resources away from growth - body size often correlates with fecundity - and toward current reproduction). The latter type of cost is the subject of this chapter, as I explain below.

Because potential body volume, and hence weight, of arthropods will be limited by the size of the exoskeleton, the amount of potential juvenile growth will be reduced when an animal which has a maximum potential number of developmental stadia in its life history, moults early for its size. Thus when moulting occurs resources can be considered to be directed towards reaching the reproductive stage at the expense of potential juvenile growth, and ultimately, reproductive size and fecundity. Therefore, the times at which adult emergence and moults between juvenile stadia occur should be related to the potential trade-off between growth and reproduction.

This trade-off will apply to the grasshoppers in this study, since the final moult into the adult represents the point after which resources are directed away from somatic growth and towards maturing gonads, eggs, and sperm (Richards and Waloff, 1954), though there may still be some somatic growth, as has been shown in locusts (Hill et al., 1968).

It is also likely to apply to the juvenile moults of the grasshoppers, since there would appear to be an upper limit to the number of instars in the life history. For instance, there is no evidence of any variation in the number of instars in the life history of M.maculatus, and C.brunneus also normally has four juvenile instars in Britain (Ragge, 1965), although M. Hassall (pers. comm.) has studied populations in East Anglia in which the females exhibited an extra instar following the second. Also, R. Wall (pers. comm.) has found rare occurrences of an extra juvenile instar following the fourth among females of a population of laboratory-reared C.brunneus originating from Ainsdale. It is not known whether or not there is an environmental component to this variation.

5.2.2. The trade-off obscured by environmental differences

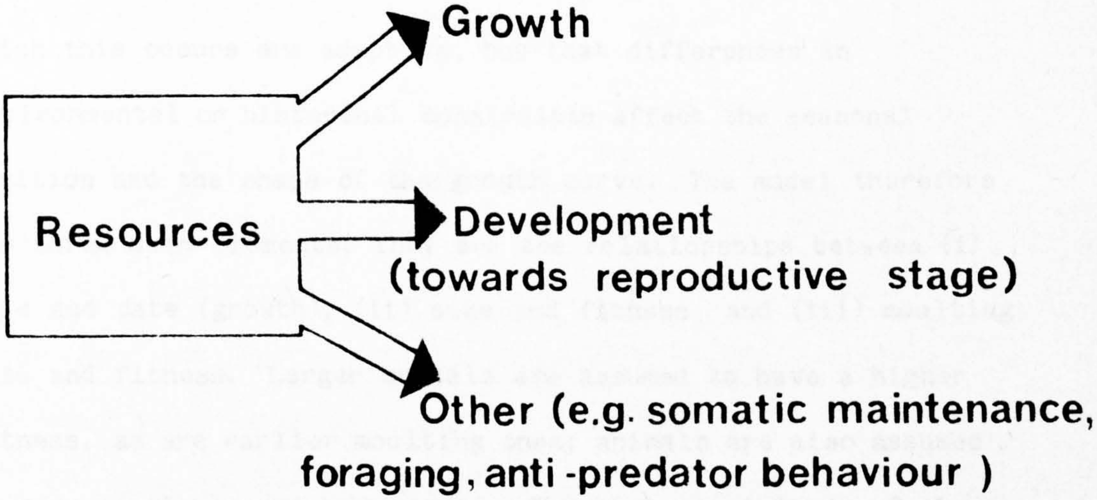
In a genetically polymorphic population a trade-off should be exhibited as a positive correlation between the date of moult and the size of the moulted animal if all animals are born at the same time and experience the same environmental conditions; that is, some animals moult early but at the expense of body size at that particular developmental stage, whereas others will moult at a larger size but at the expense of a slower rate of development towards the reproductive stage. Figure 5.1 shows how resources can be partitioned in juvenile animals, among activities which determine the form of the life history.

However, genetic trade-offs can sometimes be obscured by environmental variation as Lande (1982) has pointed out.

Robertson (1960a,b) found a negative correlation between adult size and larval developmental period between *Drosophila melanogaster* populations fed on different diets and between populations kept at different densities, but a positive correlation was found among populations which had had different selective histories and were reared under the same conditions. This is consistent with the idea of a genetic trade-off between growth and development towards reproduction, the manifestation of which may be masked by the immediate effects of the environment. In this chapter I consider how grasshoppers should partition resources between growth and development when subjected to different conflicting selection pressures on size and developmental rate, and different environmental or historical (genetic) constraints on growth. In this analysis, the amount of resources directed towards growth and development are variable but it is assumed that the amount used in feeding and body tissue maintenance (Fig. 5.1) is constant and that these latter two functions are not directly affected by growth and development. Another assumption is that there are no phylogenetic differences in the relationships between size and fitness and between time and fitness. Because the graphical method used in this model is

FIGURE 5.1.

Resource allocation in juvenile grasshoppers



flexible, all of these assumptions could be relaxed if desired, and the model developed further, as I indicate in Section 5.3.2.

5.3. THE BASIC MODEL (A)

5.3.1. The three elements of the model

The model assumes that the timing of moult and the size at which this occurs are adaptive, but that differences in environmental or historical constraints affect the seasonal position and the shape of the growth curve. The model therefore has three main elements; they are the relationships between (i) size and date (growth), (ii) size and fitness, and (iii) moulting date and fitness. Larger animals are assumed to have a higher fitness, as are earlier moulting ones; animals are also assumed to grow as the season progresses. The biological basis of these assumptions and of the forms of the relationships between body size and fitness, moulting date and fitness, and body size and time (the growth curve) are discussed in Section 5.4.

5.3.2. The production of fitness contours

In the model, I combine the size-fitness and date-fitness functions to produce lines of equal fitness, or fitness contours. I then superimpose different growth trajectories on the fitness contours in order to predict the optimal size at, and date of, moult.

The fitness contours are similar to the fitness sets of Levins (1962). The use of contours allows me to represent three dimensions (size, time, and fitness) in two dimensional form. This three-dimensional model can also be considered a "selective landscape" (Wright, 1932) but applied to phenotypes (Dobzhansky, 1937). If n traits were being considered instead of just two the selective landscape would have n+1 dimensions (n traits + fitness). Thus, the assumptions that the amount of resources used in feeding and body tissue maintenance are constant can be relaxed by increasing the number of traits examined by the model.

5.3.3. Some implicit assumptions: other costs and benefits of moulting

I try in this chapter to make explicit all of my assumptions. This should reduce the risks of overestimating the generality of particular forms of the model, and should thus discourage inappropriate experimental tests of their predictions. It is important, for instance, to recognize the full range of costs and benefits of moulting.

Moulting may be considered not only a necessary developmental event on the way to reaching the reproductive state but also a means by which an organism can continue growing without the constraints of a small exoskeleton. The converse of this benefit is the cost of a reduced growth rate which results from delaying moulting. This cost can be incorporated into the forms of the model presented here because the slope of the growth curves can be made to decline as the organisms get older.

There may be two other costs of moulting - the survival cost and the actual fecundity cost (Bell, 1980). The survival cost would affect the predictions of the model if moulting entailed a greater risk of mortality (e.g. from desiccation or predation) to one individual than it did for another, and that this mortality was independent of the size of the animals or the moulting date. This is because the expected growth rate, after moulting at a particular size or on a particular date, can be discounted by the probability of not growing at all (if the animal dies). The model can therefore incorporate the effects of size-dependent or date-dependent mortality resulting from moulting.

A smaller or later animal might utilize a greater proportion of its resources in the act of moulting and this could limit future fecundity (of adults) as well as growth (of juveniles) or survival (of both). Such a difference in the cost of moulting between different-sized animals, or animals at different times can also be incorporated into the relationships between size and fitness and moulting date and fitness used in the model, but any such difference which is independent of size or moulting date will not be represented in the forms of the model presented here. However, as I mentioned in Section 5.3.2, relationships between other traits and fitness may potentially be added to this multi-dimensional model.

5.4. BIOLOGICAL BASIS OF THE RELATIONSHIPS USED IN THE MODEL

5.4.1. "Size-fitness" relationship

a) Fitness increases with adult size

i) Evidence in support

Larger females generally have a higher fecundity at a reproductive attempt than smaller ones of the same species (e.g. Berven, 1982; Lawlor, 1976; Paris and Pitelka, 1962; Ward, 1983). Larger adult female *C.brunneus* and *M.maculatus* also laid larger egg pods (Chapter 6). Generally speaking, provided that a high fecundity is not offset by a reduction in the number of clutches per lifetime, larger females are likely to have a higher lifetime reproductive success. Indeed, Richards and Waloff (1954) found the opposite trend in laboratory-reared *C.brunneus* - larger females laid more pods. Recently, however, this relationship has been found to be dependent upon the density at which the grasshoppers are kept (R. Wall, unpublished).

Larger males also tend to have a higher mating success. For example, larger males of the dung fly, Sepsis cynipsea achieve more matings than smaller ones, and they mate more often with larger, more fecund, females (Ward, 1983). A similar positive size-assortative mating has been observed in pupfish (Kodric-Brown, 1977), in anuran amphibians (Arak, 1983; Howard, 1979), in the freshwater isopod Asellus aquaticus (Manning, 1975; Ridley and Thompson, 1979), and in the weevil Brentus anchorago (Johnson, 1982). In the laboratory, Partridge and Farquhar (1983) observed that larger males of the fruit fly Drosophila melanogaster achieved a higher lifetime mating success. Lifetime mating success in arthropods has been measured in the field in damselflies (Banks and Thompson, in press) and, in contrast to the studies cited above, was found to be size-independent. The relative mating success of large male C.brunneus and M.maculatus compared with small ones has not been documented.

Other possible benefits of being large, which should improve survival and therefore increase potential lifetime reproductive success, include better protection from predators by being too big for some predators to handle effectively (Calow, 1977; Paris and Sikora, 1965; Seed and Brown, 1978); greater mobility, which would make searching for patchily-distributed food, mates, and other resources more effective, and which would improve the ability to escape from predators and unfavourable environmental conditions; the ability to compete for food and other resources (Pianka, 1970; MacArthur, 1972); and resistance to desiccation (Nevo, 1973; Barker and Barker, 1980).

ii) Effects of food shortage

Small animals may be favoured by natural selection when food is scarce because, all else being equal, a smaller animal would have less somatic tissue to maintain and might therefore be less susceptible to the effects of starvation. The outcome of this argument will depend crucially on how much of the body size is made up of storage tissue or tissue which can be effectively autolysed to obtain energy and nutrients to help maintain the remaining somatic tissue, and how much of the tissue is essential to survival in its existing form and therefore has to be maintained. Some data which relate to this hypothesis are described by Ward _et al._ (1983) who found that on nutritionally poor hosts, aphids with many ovarioles were less likely to survive to maturity than those with fewer ovarioles, and that pre-reproductive adults with few ovarioles were more resistant to starvation than those with many. Body weight was unrelated to ovariole number, so if my hypothesis is to be corroborated by the data of Ward _et al._ (op. cit.) the relative proportion of resource-demanding tissue (c.f. storage tissue) in pre-reproductive aphids with many ovarioles must be greater than in those aphids with few ovarioles.

This counter-argument - that, on energetic grounds, the relationship between body size and fitness may sometimes be negative - is only likely to be true when feeding conditions deteriorate unpredictably after the animal has moulted. If there were no environmental deterioration or if it were predictable, the animal should moult at a smaller size.

Some animals may moult at a smaller size than others not because this gives them a higher fitness than larger animals but because either it gives them an equal fitness (e.g. if selection were frequency-dependent, Section 5.6.1) or, following a juvenile period in which conditions were less favourable for growth, it gives them a higher fitness than they would otherwise have had. In the latter case they are making "the best of a bad job" (Maynard Smith, 1982).

Therefore, because I am making the reasonable assumptions that natural selection acts on body size, that there is at least some predictability in the conditions the animals will face, and that environmental conditions for all juveniles are unlikely to be absolutely identical, the assumption used in the model - that fitness increases as body size increases - is also reasonable.

b) *Shape of the "size-fitness" relationship*

The relationship between body size and the number of eggs laid per reproductive attempt is linear in the wood frog, *Rana sylvatica* (Berven, 1982), but in the pill-bug *Armadillidium vulgare* there is a tendency towards a concave (upwards) relationship (Paris and Pitelka, 1962).

A concave relationship between size and fitness may occur if a large female lays more batches of eggs as well as larger ones. Richards and Waloff (1954) observed this phenomenon in laboratory populations of *C.brunneus*, but P. de Souza Santos jr. (unpublished) did not, and R. Wall (unpublished) only found this at very high densities.

Even if the relationship is concave over a range of male and female sizes, it is likely eventually to plateau. One reason for this is that a larger insect has a longer path between the air and the tissues, along which respiratory gases must diffuse. Tissue respiration would thereby be potentially limited.

The forms of the relationship between size and fitness I shall consider in detail, will be the two simplest realistic examples - those with positive slopes which are either linear or convex (viewed from above).

5.4.2. "Time-fitness" relationship

a) Fitness declines with date at emergence

British grasshoppers live in a seasonal environment in which the amount of solar radiation and the ambient temperature both decline in the autumn. In order to reproduce, *C.brunneus*, at least, requires a high body temperature which it can achieve by basking in the sun (Begon, 1983); in the shade reproduction is negligible. In the autumn and winter, therefore, a grasshopper would be inactive. It would have to withstand frosts and snow cover, and would probably be easy prey for homeothermic predators such as shrews and magpies. The expected fitness of an adult grasshopper will consequently drop effectively to zero in the autumn. Perhaps because of these difficulties British grasshoppers are univoltine, usually concentrating the above-ground stages of the life history between May and October (Ragge, 1965). A large number of other temperate insects will also experience similar seasonal constraints on the life history.

If, in a seasonal environment, conditions remained constant, on average, throughout the season and deteriorated sharply at one instant, after which the expected fitness was zero, the fitness of an iteroparous animal such as a grasshopper, which did not moult and grow in the adult phase and which was unlikely to benefit much from previous experience, would decline linearly. This is because only time would limit the potential number of clutches that could be laid.

b) Shape of the "time-fitness" relationship

Environmental conditions do not, however, remain constant.

As well as the seasonal change in weather, the quality and quantity of the food may change, for instance.

Because nitrogen is likely to be more limiting than energy in the diet of a herbivore (White, 1978; Mattson, 1980), food quality may affect fitness more than the amount of forage available. The amount of nitrogen in grass leaves declines after the spring flush of vegetative growth (Mattson, 1980; McNeill and Southwood, 1978; Monk, 1981) but may rise again in the autumn in some species (Monk, 1981). Herbivores tend to prefer young small, nutrient-rich plants (Mattson, 1980). This argument will apply to the grasshoppers C.brunneus and M.maculatus.

Because many animals become dormant or migrate away from temperate, seasonal environments at the onset of winter, food is therefore likely to become scarcer for resident predators as well.

The seasonal decline in mean temperature, hours of sunshine and food quality will exacerbate the rate at which expected fitness of newly-emerging adults declines throughout the season. The resulting "time-fitness" curve will, therefore, be convex (viewed from above).

If habitat quality improved with time, a concave "time-fitness" curve would result. Such conditions might occur very early in the season before the hotter summer period, but eventually time would start to run out as the end of the favourable period approached.

The grasshopper populations, to which the model will be applied, experience similar average maximum and minimum temperatures during much of the summer (June-August, inclusive; N.C.C., unpublished meteorological data, Ainsdale Sand Dunes NNR, 1969-1978). Consequently, the "time-fitness" function may be approximately linear.

The two most realistic forms of simple "time-fitness" curve, for animals which have to breed as often as they can before the end of the season, are therefore a negative linear one and a negative convex one.

5.4.3. Growth trajectory

Growth curves of animals are usually sigmoidal (Peters, 1983), or monotonically convex as Davey (1954) found for the desert locust, *Schistocerca gregaria*. In arthropods, growth trajectories for a given stadium are likely to plateau because of the limitation on growth imposed by the rigid exoskeleton.

To conclude, if the model is to represent the situation encountered by arthropods living in a seasonal environment in which the individuals benefit by reproducing as often as possible before the onset of winter, each of the three elements of the basic model should be either linear or convex relationships. In more complex forms of the model, two of the relationships (the size-fitness curve and the growth curve) may also realistically take a sigmoidal form. In Section 5.5, these simple forms of the relationships will be combined to produce fitness contours (Section 5.3.2) in order to explore the range of alternative combinations of optimal size at moult and moulting date under different constraints on growth.

5.4.4. Interactions among the elements of the model

In the formulations of the model I present, the relationship between each trait and fitness is considered as being independent of the other traits. However, any interaction between traits found in natural populations can be incorporated within the framework of modelling using selective landscapes; this framework explicitly recognizes the interactive and integrative nature of traits within organisms (Sibly and Calow, 1983).

In the particular forms of the model which take into account the end-of-season gradual decline in habitat quality, an interaction between time and size can be envisaged. As the food quality declines there may be an energetic advantage in being small because small animals will have less somatic tissue to maintain (see Sections 5.4.1 and 5.4.2). This interaction effect would add to the selection pressures on a fast-growing animal to moult early.

5.5. VARIANTS OF THE BASIC MODEL AND THEIR PREDICTIONS

5.5.1. Model **A1**: All relationships are linear functions

In the simplest form of the model each of the relationships exhibits a linear relationship (Figs. 5.2a-c). The relationships in Figs. 5.2a and 5.2b can be combined to produce fitness contours which are linear and parallel (Fig. 5.2d).

The optimal size and time for moulting.

When growth curves are superimposed on the fitness contours, the optimal combination of size and time at moult is the point at which the growth curve coincides with the highest expected fitness. Under the assumptions of the model in which all relationships are linear functions (Fig. 5.2) there is either an infinite number of optimal solutions (when the growth curve lies along a contour) or no real single optimum (when growth is always steeper or always shallower than the fitness contours) (Fig. 5.3). However, if the form of one or more of the assumptions is

FIGURE 5.2: The basic model, A1, in which all relationships are linear.

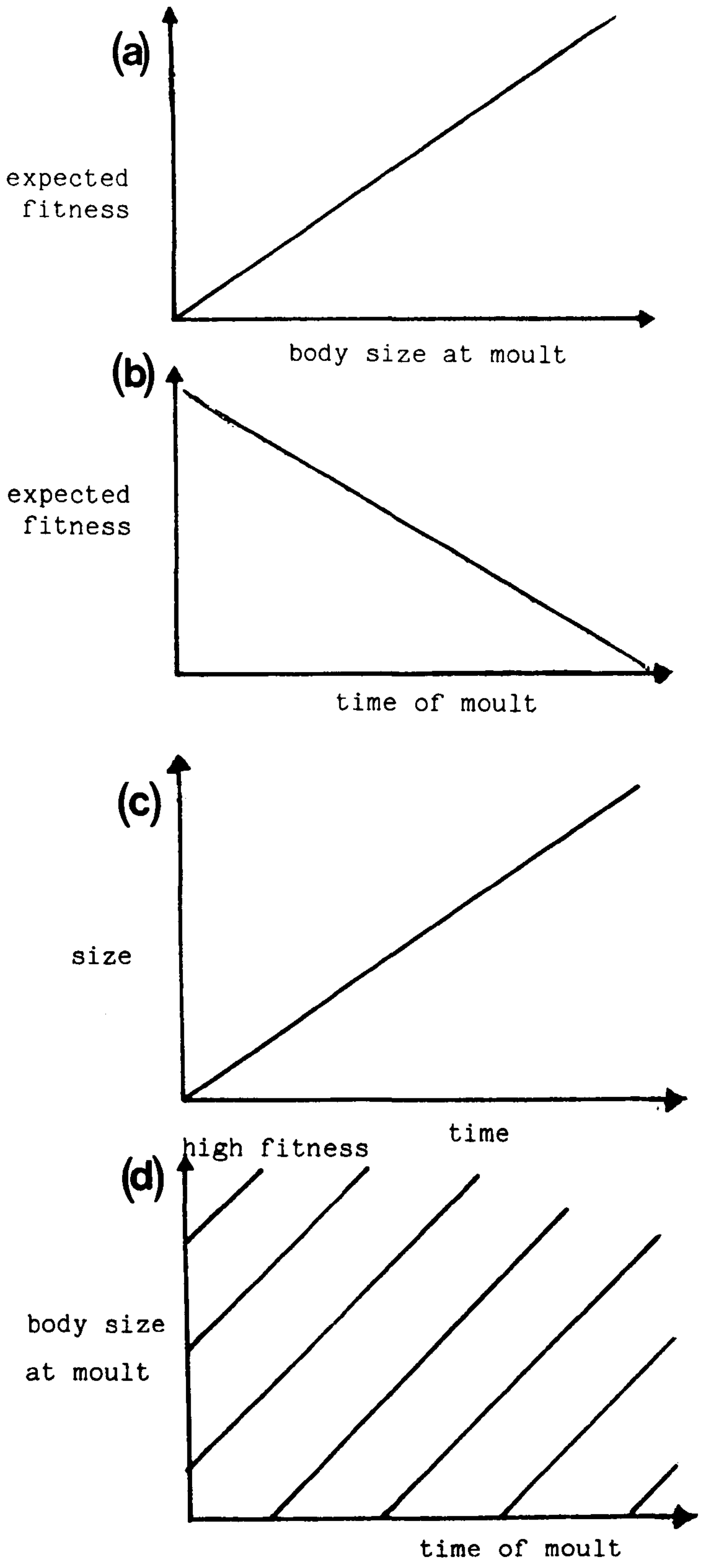
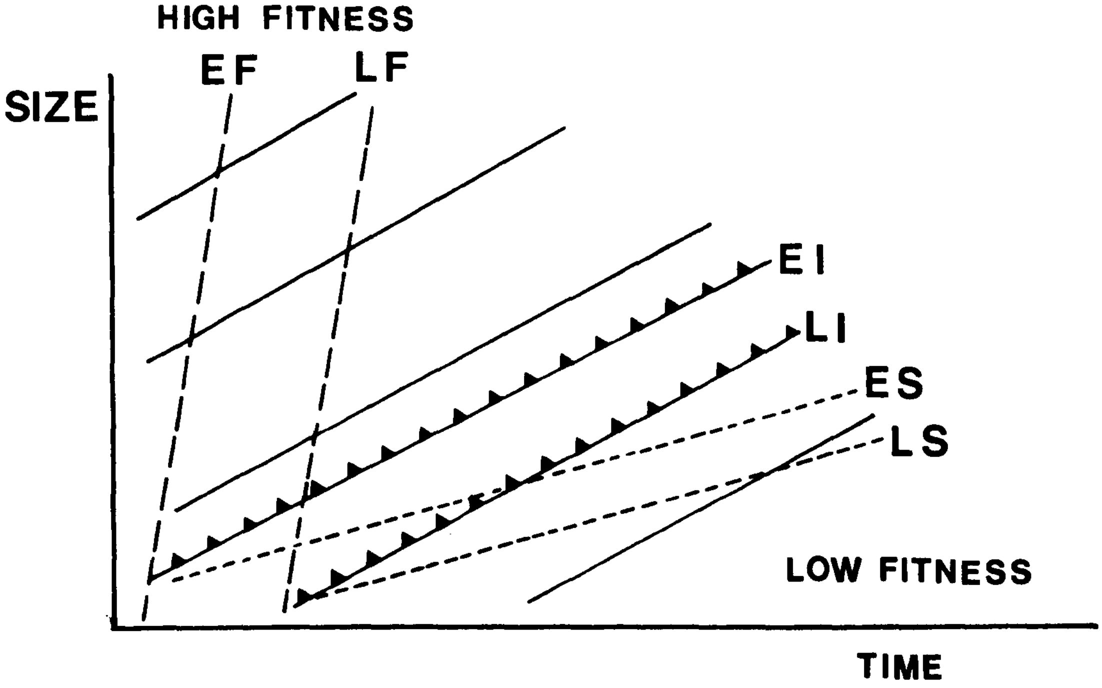


FIGURE 5.3:

Linear growth curves superimposed on linear fitness contours



EF denotes the growth trajectory of an 'early' insect with a fast growth rate

LF - 'late' and fast

EI - 'early' and intermediate

LI - 'late' and intermediate

ES - 'early' and slow

LS - 'late' and slow

monotonically curved, there can be a single optimum corresponding to the point at which the growth curve becomes tangential to a fitness contour just before expected growth starts to fall beneath that contour (Figs. 5.4 to 5.7).

Constraints on growth.

Variation in the "starting point" - the size and time at which the model is first applied to the animals - must result from variation experienced in the past. Such variation can result if one animal hatches later than another, from a smaller egg, or if it had experienced poorer growing conditions. Variation in egg weight and therefore hatchling weight in the grasshopper, *C.brunneus*, (R. Wall, unpublished) is small compared with the variation in grasshopper weight, especially the weight of older, larger animals (Chapters 4 and 6), and is therefore only likely to be important directly in affecting the timing of moult to the second instar when hatching is synchronous and growth is slow. A smaller or later starting point reduces the intercept of the expected growth curve. Because of the lack of curvature in both the contours and the growth curve they can still only coincide at an infinite number of points, or not at all, within the limits of the model's assumptions (Fig. 5.3).

Similarly, a reduction in the expected growth rate does not affect the predictions of model A1; nor does a combination of a reduction in the slope and intercept of the expected growth curve, since the growth curve and fitness contours still remain linear (Fig. 5.3).

Sections 5.5.2 to 5.5.4 explore the predictions of models in which the shape of the functions are altered.

5.5.2. Curvilinear growth trajectories (**A2**)

With a convex growth curve superimposed on the straight fitness contours of model **A1** (Fig. 5.4a, line 1) there is a single optimum size (S1) and time (D1) at which the animal should moult. An animal with a growth trajectory which is concave should moult at an infinite size (Fig. 5.4a, line 2). This latter form of growth curve is biologically unrealistic (Section 5.4.3) although growth may start off at an increasing rate before eventually starting to plateau (Fig. 5.4a, line 3). In such a case the optimum solution is straightforward - carry on growing through and beyond the exponential phase until the point on the convex section of the curve which becomes tangential to the fitness contour (D3,S3, Fig. 5.4a). This analysis will consider the monotonic form of growth curve most likely to be encountered in the latter part of an instar - a monotonic convex trajectory (Fig. 5.4a, line 1).

Constraints on growth.

a) Smaller or later starting point; expected growth rate the same.

When growth trajectories are curved, reducing the intercept on the y-axis (shifting the curve down) has a different effect on the predictions of the model from an increase in the intercept on the x-axis (shifting the curve to the right). Therefore, these two effects will be treated separately.

i) Smaller starting point; expected growth rate at a given time the same.

The slope of a convex growth curve with a lower intercept with the y-axis (compare line ES with line EL, Fig. 5.4b) is the same at a given time but is less steep for a particular size.

FIGURE 5.4: **Curvilinear growth trajectories superimposed on linear fitness contours**

(a) Trajectory 1 = a convex growth curve; optimal moulting size = **S1**, and optimal moulting time = **D1**

Trajectory 2 = a concave growth curve; this animal should continue growing

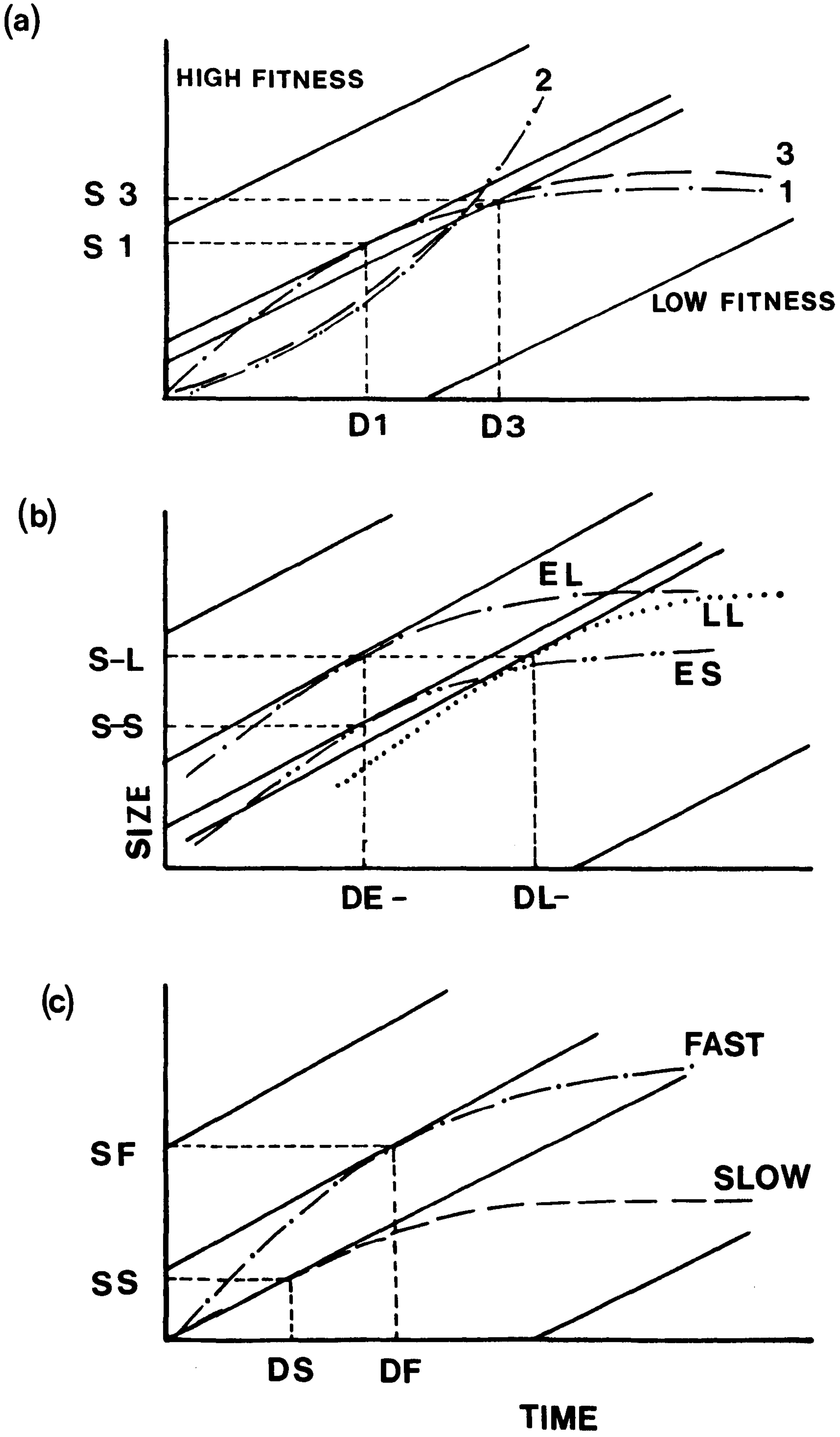
Trajectory 3 = a sigmoidal growth curve; this animal should moult at size **S3** and time **d3**.

(b) Differences in "starting point"

Growth trajectory	Optimal Size	Optimal Time
EL (initially early and large)	S_{-L}	D_{E-}
LL (initially late and large)	S_{-L}	D_{L-}
ES (initially early and small)	S_{-S}	D_{E-}

(c) Differences in slopes of growth trajectories

Animals with a slower expected growth rate should moult earlier and at a smaller size.


(a)
HIGH FITNESS
2
3
1
S 3
S 1
LOW FITNESS
D1
D3
(b)
EL
LL
S-L
ES
S-S
SIZE
DE -
DL-
(c)
FAST
SF
SLOW
SS
DS
DF
TIME

The optimum time for moulting will thus be unaltered (D_{E-}), but an animal following the lower growth trajectory should moult at a smaller size (S_{-S}), as shown in Fig. 5.4b.

ii) Later starting point; expected growth rate at a given size the same.

If the convex growth curve is shifted to the right (compare line LL with line EL, Fig. 5.4b) the slope of the trajectory is still the same for a given size but is steeper at any particular time. The optimum size will thus be unaltered, but the animal should moult later than one with a growth curve shifted to the left.

A combination of the two environmental effects (i) and (ii) can be investigated by adding the vectors. The resulting prediction is the sum of the individual predictions. For instance, if one variant of the model (i) predicts an optimal moult at the same size, and another variant (ii) predicts a moult at a smaller size, both effects would be added together to produce an optimal size at moult which would be intermediate between the sizes predicted by (i) and (ii). The same reasoning applies to the timing of moult.

b) Lower expected growth rate; starting point (intercept) the same.

An animal at the same starting size and time but with a lower expected growth rate should moult earlier and at a smaller size (Fig. 5.4c).

c) Lower slope and intercept.

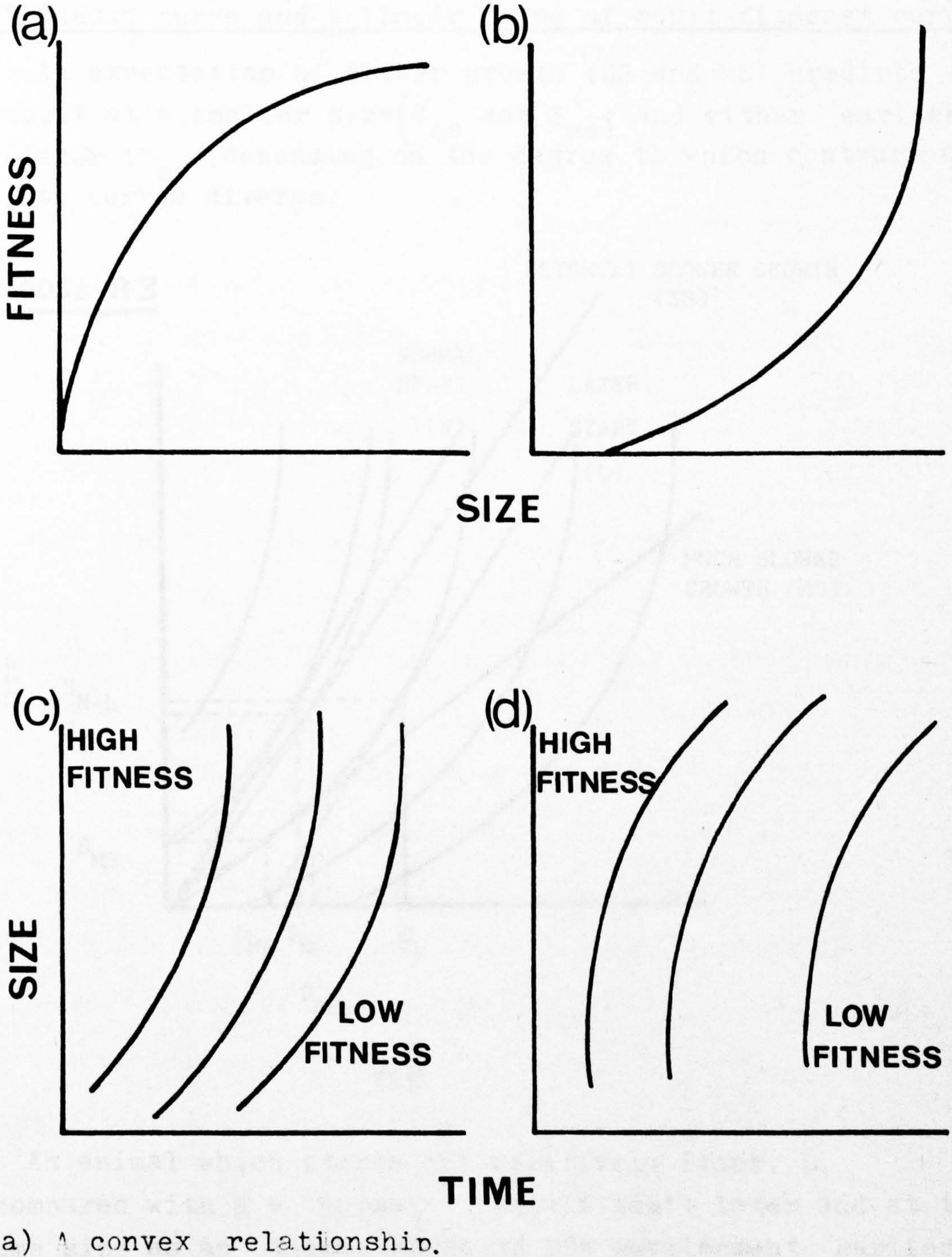
Combining the environmental effects a(i) and b, an animal starting at a smaller size and with a lower expected growth rate should moult earlier and at a smaller size (Table 5.1).

If an animal entering the analysis later also has a lower expected growth rate (effects a(ii) and b), it should moult at a smaller size but the optimum time for moulting may be earlier or later depending on how late the animal is initially and how much lower is the expected growth rate (Table 5.1).

5.5.3. Curvilinear size-fitness relationships (A3).

In some ecological circumstances, fitness may best be modelled as a non-linear function of body size, as discussed in Section 5.4.1. Fig. 5.5c shows how a convex size-fitness function (Fig. 5.5a) affects the shape of the fitness contours when the moulting date-fitness (or time-fitness) function is linear. The slope of the lower contours is shallower at a given time than contours representing higher fitness values, but the slope of all contours is the same for a given size of animal (Appendix to this chapter). A concave relationship between body size and fitness (Fig. 5.5b) is unlikely to be realistic for grasshoppers (Section 5.4.1) and will not be considered beyond its effect on the shape of the fitness contours (Fig. 5.5d) which is to produce convex lines - the opposite of the contours in Fig. 5.5c. A sigmoidal size-fitness relationship may occur in nature (Section 5.4.1); this can be produced by continuing the concave curve with a convex one. In such a case the animal should not moult until some time after it passes the size which is at the point of inflexion of the sigmoidal function; i.e. it should moult at a size which is in the convex part of the relationship.

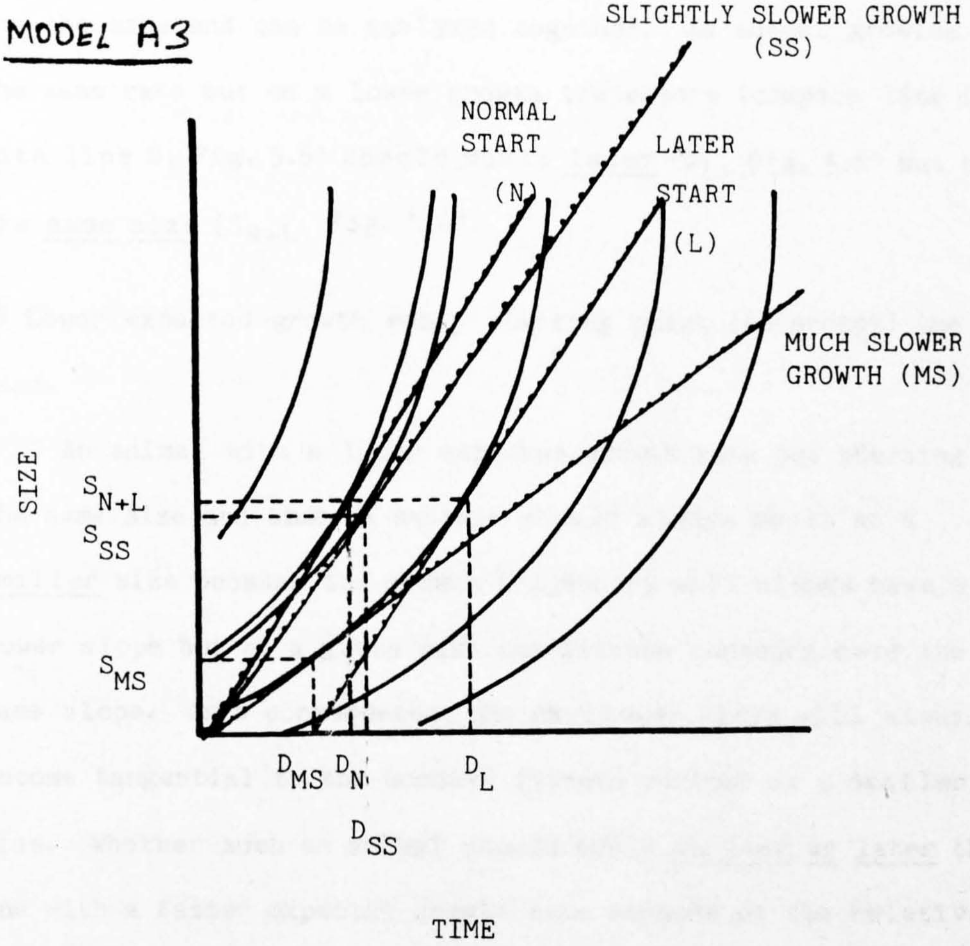
FIGURE 5.5: Curvilinear "SIZE-FITNESS" relationships



(a) A convex relationship.
(b) A concave relationship.
(c) Fitness contours produced by combining a convex "size-fitness" function with a linear "time of moult-fitness" function.
(d) Fitness contours produced by combining a concave "size-fitness" function with a linear "time of moult- fitness" function.

FIGURE 5.6: Superimposing linear growth curves on fitness contours produced from a combination of a convex "size-fitness" curve and a linear "time of moult-fitness" curve

An expectation of slower growth (SS and MS) predicts a moult at a smaller size (S_{ss} and S_{ms}) and either earlier (D_{MS}) or later (D_{SS}) depending on the degree to which contours and growth curves diverge.



An animal which starts off relatively later, L, (compared with N = "normal") should moult later and at the same size as an animal starting its development earlier.

Constraints on growth.

a) Smaller or later starting point; expected growth rate the same.

When growth trajectories are linear, shifting the intercept along the y-axis or the x-axis has no effect on the slope, so, unlike model **A2** and those derived from it (Table 5.1), the effects of being smaller at a given time and later for a given body size are the same and can be analyzed together. An animal growing at the same rate but on a lower growth trajectory (compare line L with line N, Fig. 5.6) should moult later (D_L, Fig. 5.6) but at the same size (S_{N+L}, Fig. 5.6).

b) Lower expected growth rate; starting point (intercept) the same.

An animal with a lower expected growth rate but starting at the same size and time as another should always moult at a smaller size because its growth trajectory will always have a lower slope but at a given size the fitness contours have the same slope. As a consequence, the shallower slope will always become tangential to the concave fitness contour at a smaller size. Whether such an animal should moult earlier or later than one with a faster expected growth rate depends on the relative rates at which the growth curves diverge in relation to the fitness contours (the latter being dependent, ultimately, on the degree of convexity of the size-fitness relationship).

c) Lower slope and intercept.

With both a lower intercept (resulting from a small starting size, a late start, or both) and a lower expected growth rate, an animal should moult at a smaller size, but whether it should moult earlier or later than an animal without such constraints on growth will depend on how much the intercept and slope of the growth curve are reduced and how convex is the size-fitness relationship (Fig. 5.6, Table 5.1).

5.5.4. Curvilinear time-fitness relationships (A4).

The time-fitness function likely to affect moulting arthropods in a seasonal environment in which the amount of time for reproduction was limited, is a negative and convex one (Section 5.4.2).

By combining such a function (fig. 5.7a) with a positive linear size-fitness one, concave fitness contours are produced (Fig. 5.7c). The slope of the lower contour is steeper at a given size than a contour representing a higher fitness value. However, the slope of all contours is the same at a given time (Appendix to this chapter).

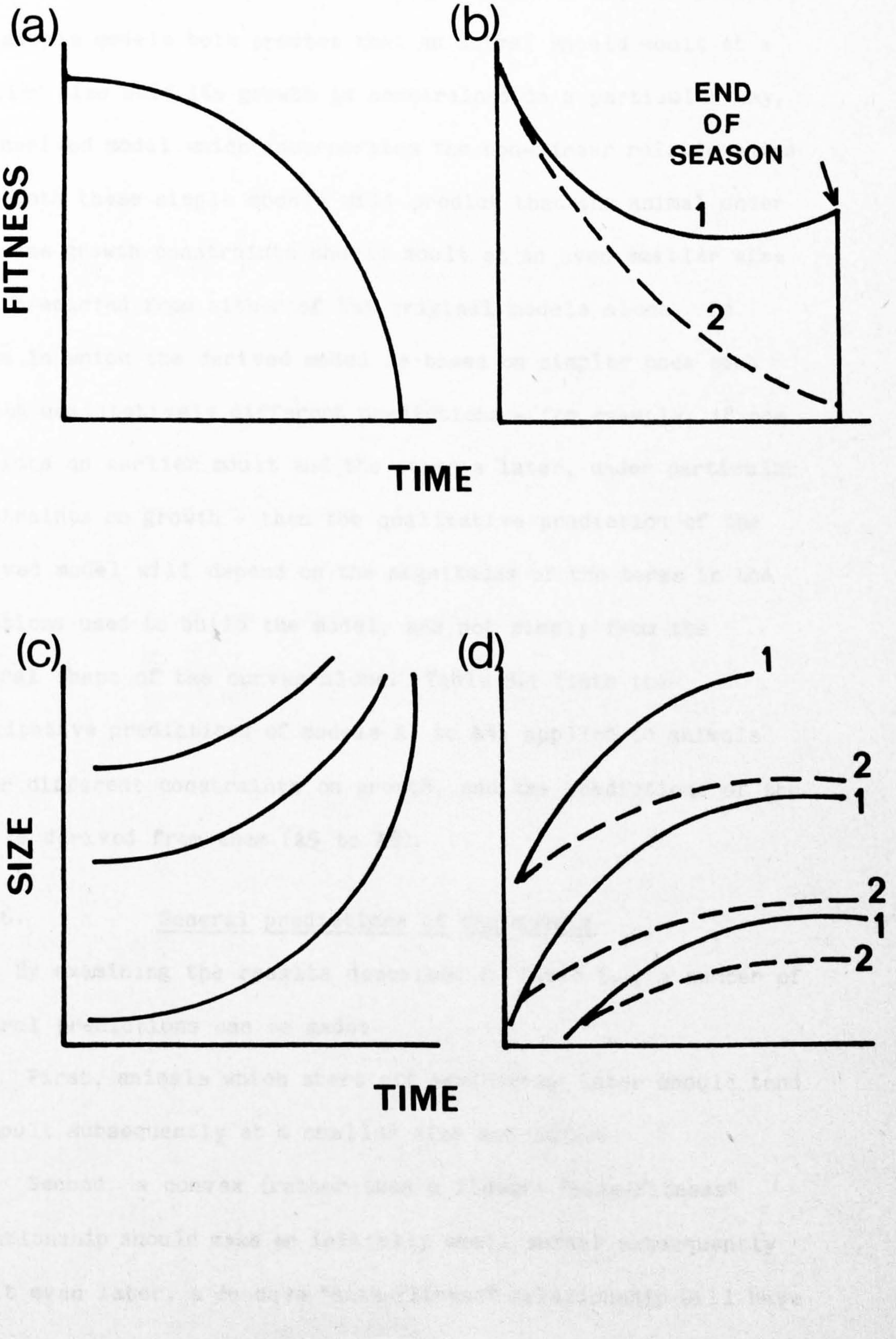
The effects of reducing the slope of the growth curve, the "starting point", or both, are summarized in Table 5.1.

[If, in the unusual circumstance of the habitat predictably improving just before predictably coming to an end, the expected time-fitness function will be concave (Fig. 5.7b) and the slope may be positive (line 1) or negative (line 2) depending on whether the increase in potential fecundity is sufficient to outweigh the effect of time running out. When they are combined with a linear size-fitness function, convex fitness contours are produced (Fig. 5.7d)].

5.5.5. Models incorporating more than one curvilinear function (A5-A8).

Qualitative predictions concerning the timing of, and size at, moult (earlier, later, or same time; smaller, larger, or same size) can be derived for models with more than one non-linear

FIGURE 5.7: Curvilinear "time of moult-fitness" relationships (a) and (b), when combined with a linear "size-fitness" function produce contours in (c) and (d) respectively.



relationship, by adding the predictions of models **A2** to **A4**. This is possible because more complex models are built from relationships taken from the simpler ones, such as **A2** to **A4**, and these relationships are combined by the addition of vectors which results in the predictions also being additive. If, for example, two simple models both predict that an animal should moult at a smaller size when its growth is constrained in a particular way, the derived model which incorporates the non-linear relationships from both these simple models will predict that the animal under the same growth constraints should moult at an even smaller size than predicted from either of the original models alone. In cases in which the derived model is based on simpler ones each giving qualitatively different predictions - for example, if one predicts an earlier moult and the other a later, under particular constraints on growth - then the qualitative prediction of the derived model will depend on the magnitudes of the terms in the equations used to build the model, and not simply from the general shape of the curves alone. Table 5.1 lists the qualitative predictions of models **A1** to **A4**, applied to animals under different constraints on growth, and the predictions of the models derived from them (**A5** to **A8**).

5.5.6. General predictions of the models

By examining the results described in Table 5.1, a number of general predictions can be made:

First, animals which start off smaller or later should tend to moult subsequently at a smaller size and later.

Second, a convex (rather than a linear) "size-fitness" relationship should make an initially small animal subsequently moult even later; a concave "size-fitness" relationship will have

TABLE 5.1: **A comparison of the models A1 to A8 and their predictions, when applied to animals starting growth and development late, from a small initial size, and/or with a slow expected future growth rate**

Key to symbols used in TABLE 5.1.

s(-),	moult at a smaller size
s(=),	moult at the same size
v(=),	same development rate
v(-),	slower development (therefore, delayed moult)
v(+),	faster development (therefore, earlier moult)
v(D),	timing of moult depends on the <u>degrees</u> of curvature of relationships used in the model.

Model	A1	A2	A3	A4	A5	A6	A7	A8
Relationships:								
Size-fitness	Linear	Linear	Convex	Linear	Convex	Convex	Linear	Convex
Time of moult - fitness	Linear	Linear	Linear	Convex	Linear	Convex	Convex	Convex
Growth	Linear	Convex	Linear	Linear	Convex	Linear	Convex	Convex
Effect on the timing of (v) and size (s) at moult of:								
a(i) Smaller start, time-specific growth the same	No finite number of real solutions	s(-) v(=)	s(=) v(-)	s(-) v(=)	s(-) v(-)	s(-) v(-)	s(-) v(=)	s(-) v(-)
a(ii) Later start, size-specific growth the same		s(=) v(-)			s(=) v(=)		s(-) v(-)	
b Slower growth		s(-) v (+)	s(-) v(D)	s(-) v(+)	s(-) v(D)	s(-) v(D)	s(-) v(+)	s(-) v(D)
c(i) = a(i) + b		s(-) v(+)	s(-) v(D)	s(-) v(+)	s(-) v(D)	s(-) v(D)	s(-) v(+)	s(-) v(D)
c(ii)= a(ii)+ b		s(-) v(D)			s(-) v(D)		s(-) v(D)	

the opposite effect - tending to make the animal moult earlier.

Third, a convex (rather than a linear) "time of moult-fitness" relationship should make an initially later-moulting animal moult subsequently at an even smaller size than an initially "earlier" animal; a concave "time of moult-fitness" relationship should have the opposite effect on the size at moult - tending to increase the relative size at moult.

Fourth, animals with a slower expected growth rate should moult earlier and at a smaller size than animals with a faster expected growth rate.

A comparison between the first and fourth predictions brings out an interesting point: if the past experience of an animal (reducing its "starting point", i.e. making it initially smaller or later than another) is relatively more important than its expectation of reduced growth in the future, then the animal should moult relatively later, rather than relatively earlier.

Before I compare the range of predictions from these variants of the basic model with the results of Chapter 4, I shall first consider briefly two alternative types of model which could predict the size and timing of moult.

5.6. ALTERNATIVE MODELS

5.6.1. Frequency-dependent selection (model B)

Rather than, or as well as, the assumption that fitness is a function of seasonal decline in habitat favourability, the temporal distribution of expected fitness may depend on the frequency distribution of competitors and limiting resources throughout the season. This idea may apply to adult male emergence - the competitors being other adult males, and the limiting resources being females (mates). It may also apply to adult female emergence; in this case the frequency-dependent timing of emergence might guarantee rapid insemination and fertilisation (P. de Souza Santos jr., pers. comm.). If this assumption of frequency-dependent selection were added to the others from the basic model - that there were differences in the effects of constraints on growth, and that large animals had a higher fitness - an alternative model would be produced which considered the timing of, and size at, moult as a competitive optimization problem or "game" (Maynard Smith 1982, Parker 1984) which incorporated the effects of constraints on phenotypic expression. In other words, a phenotype-limited evolutionarily stable strategy (G. A. Parker, 1982) would be sought.

For instance, if there were a high cost of mating in males, it would pay some males to delay emergence until after some of the other males had emerged, but the timing would depend not only on the distribution of emerging adults but also on the size distribution. After the early males had reproduced and consequently suffered a reduction in residual reproductive value (Williams, 1966b), newly-emerged males might be able to compete more successfully with them.

Bulmer (1983), Parker and Courtney (1983) and Iwasa *et al.* (1983) have produced game theoretical models predicting the timing of adult male emergence but which do not include the effects of different constraints on growth.

5.6.2. Tactical growth (model C)

So far, the animals have been assumed to be growing as fast as they can and that any variation in growth rate has been due to different feeding conditions or phylogenetic constraints.

Case (1978) suggested that growth rates may be optimized rather than maximized. That is, the rate of growth is not limited simply by environmental and genetic constraints but is fixed below the maximum possible rates by "active control" (Calow and Townsend, 1981) which is adaptive. Calow (1982) reviews the evidence for the occurrence of this phenomenon, and lists some possible selective advantages of sub-maximum feeding and growth.

In British grasshoppers, adult males emerge, on average, just before the females (Richards and Waloff, 1954; Young, 1979; Monk, 1985) but the difference between the sizes of the sexes is far greater than would be expected if males and females grew at the same rate. Males may, therefore, adaptively grow slower to achieve their optimum size and time at emergence. (The alternative hypothesis is that the growth of males is <u>constrained</u>; that is, they are less efficient at acquiring and converting resources to somatic tissue, and this reduced efficiency is not adaptive).

In some insects (see Chapter 4), larger individuals also emerge as adults earlier than smaller ones of the same sex. It is difficult, in such a case, to see how some animals of a particular sex should benefit by having a slower rate of growth <u>and</u> development if fitness increases with adult size and decreases through the season.

Tactical variation in growth can be envisaged, though, if there was also severe competition for mates among animals which moulted at about the same time (coupled with a high cost of mating, as in model B), and if the interaction effect between size and emergence date (Section 5.4.4), which gave small animals a higher fitness towards the end of the season, was also important. Thus some animals would slow down their growth, and moult into the adult stage after the large early-emerging animals had either died or suffered a reduction in the potential to achieve matings. Such a loss of competitive ability could result from high mating costs, from energetic or nutritional problems associated with their ability to maintain their large amount of somatic tissue given the seasonal decline in food quality, or from both. Slower-growing, later-emerging adults would therefore avoid some of the intense early competition, and would be at an energetic advantage over larger animals later in the season.

The three models, **A**, B and **C**, are compared in Table 5.2.

5.7. MECHANISMS

The models presented in this chapter are evolutionary ones, dealing with selection pressures on two traits - size and time of moult. They predict how the two life-history traits should covary in particular ecological circumstances but they say nothing about how the animal should achieve the optimal solution. Adaptive covariation in the size and time at moult may result from adaptive genetic variation if differences in the effects of the constraints on growth are phylogenetic, or from adaptive plastic variation if the variation in constraints is environmental. Differences in the effects of constraints on growth experienced by the grasshoppers in this study are largely environmental (Chapter 4).

Animals responding adaptively to immediate environmental variation must be able to perceive information which predicts, to some extent, future conditions and the hence the animal's potential RRV (Appendix to the thesis). In order to test the models rigorously by providing the animals with misinformation (Appendix to the thesis), it is necessary, therefore, to know the

TABLE 5.2: A comparison of the structures of models **A**, **B**, and **C**.

Model	Size-fitness relationship	Time-fitness relationship	Variation in growth rate due to:
A	Positive	Negative	Differences in constraints
B	Generally positive (but frequency-dependent)	Generally negative (but frequency-dependent)	Differences in constraints
C	Time- and frequency-dependent	Size- and frequency-dependent	Tactical differences

mechanism by which the animals regulate moult.

Although the models do not predict what sources of information are used by an animal, an optimal plastic response should utilize the most reliable predictors of RRV.

In Locusta, stimulation of stretch receptors in the wall of the pharynx during feeding brings about the release of the moulting hormone, ecdysone (Clarke and Langley, 1963a,b,c,d). Thus, moulting may be delayed if the animal is starved.

The use of photoperiod, including its rate and direction of change, by insects as a cue for the timing of events in the life history has been documented by Beck (1980). However, Beck (op. cit.) says that the "importance of photoperiodism in the seasonal development and ecological adaptations of univoltine species is little appreciated and has been investigated in very few forms. It is an aspect of ecology and physiology that merits much detailed investigation, however".

Information relating to the likely future growth rate may be based on the current physiological condition of the organism (such as the amount of reserves it has stored) in relation to the date. Such information reflecting recent feeding conditions may give a reliable indication of what the growth rate is likely to be in the near future.

In some years grasshoppers hatch earlier than in others (Richards and Waloff, 1954; Monk, 1985; Chapter 3) and this is mainly due to differences in spring temperatures (Richards and Waloff, 1954; Chapter 3). If the seasonal change in habitat favourability is not well-correlated with date, the animals should use some information which correlates better than photoperiod with the changing conditions. The animal's age might be such a cue.

If, as in models B and C, frequency-dependent selection acts on body size and the timing of moult, the juveniles should assess their developmental stage relative to others in the population. This may be difficult to achieve in practice, but juveniles could obtain some useful information if they could detect stridulation or any pheromones that adults might produce.

5.8. TESTING THE MODELS

5.8.1. General considerations

The deductive process used to test models which predict the size at, and timing of, moult, involves the elimination of models based on obviously unrealistic assumptions, comparing the predictions of the remaining models with reality, and comparing with reality the assumptions of those remaining models which make successful predictions. This latter comparison is the most powerful way, and is indeed sufficient, to distinguish between all competing hypotheses but it is often difficult to perform. To test cleanly for the effect of moulting date on fitness, for example, would involve the manipulation of moulting dates and then following the lifetime reproductive success of the animals. The testing of optimization theories by manipulating only environmental information is discussed in the Appendix to the thesis. If we observe the lifetime reproductive success of animals naturally moulting over a period of time, rather than after we had manipulated moulting date, any pattern we observe may arise from variation in other traits which correlate with date-at-moult such as age.

Obviously unrealistic assumptions such as "fitness of newly-emerged adults increases towards the end of the season", were eliminated when models **A**1 to **A**8 were formulated (Section 5.5).

Some forms of model **A** make unambiguous qualitative predictions about the timing of, and size at, moult under different growth constraints. For example, under the assumptions of model **A**4 an initially smaller animal with a lower expected growth rate should always moult earlier than an otherwise identical animal with a faster expected growth rate, and initially larger size, or both (Table 5.1). Table 5.3 lists the combinations of size and time at moult predicted by the models **A**1 to **A**8 and **C**. Model **B** would require a detailed theoretical development, not performed here, to allow a similar comparison of its range of predictions.

5.8.2. Testing the models using grasshoppers

In Chapter 4, I described how earlier-emerging adult grasshoppers were larger than later-emerging ones. Of the models and conditions presented, only the models and conditions in rows 2 and 3 of Table 5.3 can make this prediction; the others are therefore falsified.

More specifically, the adult emergence dates of the animals which moulted into adults later and at a smaller size than others were likely to be most strongly influenced by one or more of the following: (i) their past lives (producing smaller and/or later moulting penultimate instars), rather than by a future expectation of slow growth; (ii) convex (rather than concave or linear) "size-fitness" or "time of moult-fitness" relationships.

Further testing of the models might involve the application of the moulting hormone or the anti-juvenile hormone, precocene, (Bowers, 1981) to some of the grasshoppers to induce precocious moult. They would therefore have been given

TABLE 5.3: The predictions of models **A1** to **A8**, and **C**, given particular constraints on the animals.

Models and conditions in which the animals should:

1.	Always moult earlier and at a smaller size.	A2b, A2c(i), A4b, A4c, A7b.
2.	Always moult later and at a smaller size.	A5a(i), A6a, A7a(ii), A8a, C.
3.	Sometimes moult earlier and sometimes later (depending on values used in model and the magnitude of constraints on growth) but always moult at a smaller size.	A2c(ii), A3b, A3c, A5b, A5c, A6b, A6c, A7c, A8b, A8c.
4.	Always moult later but at the same size.	A2a(ii), A3a, A5a(ii).
5.	Always moult at the same time but at a smaller size	A2a(i), A4a(i), A7a(i).

misinformation about their physiological condition (Appendix to thesis), and the fitness of these animals should then be compared with that of grasshoppers which moult later or at a larger size. Another test which could eliminate some of the alternatives would involve the manipulation of the hatching date. Laboratory-reared hatchlings could be released into the field at different times, and their fitnesses compared.

In conclusion, this chapter has explored the conditions which would cause the production of larger early-moulting and smaller later-moulting grasshoppers. A number of hypotheses can predict the covariation between size and moulting date, but also a large number of apparently reasonable hypotheses, a priori, have been falsified.

APPENDIX TO CHAPTER 5

When the "size-fitness" relationship is convex and the "moulting date-fitness" relationship is negative and linear, the fitness contours have the same gradient for the same size, thus:

Let: F=fitness

S=size at moult

D=date at moult

a and c are constants.

The fitness contour can be represented as a single function of two variables - size and moulting date:

$$F= c - aD + h(S)$$

where h is a function such that $h'(S)= \frac{dh}{dS} > 0$, and $h''(S)= \frac{d^2h}{dS^2} < 0$

The equation of a line of constant fitness $F= k$, may be written

$$D= \frac{h(S) + c - k}{a}$$

Now $\frac{dD}{dS} = \frac{1}{a} h'(S) = \frac{1}{\frac{dS}{dD}}$

Therefore, the slopes of the fitness contours depend on S only, not on D (or F), and consequently will have the same slope providing that S is a constant.

To find how the slope varies with S, we differentiate with respect to S, thus

$$\frac{d}{dS}\left(\frac{dD}{dS}\right) = \frac{d^2D}{dS^2} = \frac{1}{a} h''(S)$$

Since $h''(S)$ is always negative, it can be seen that as S increases, $\frac{dD}{dS}$ will decrease, and the slope of the fitness contours, $\frac{dS}{dD}$, will increase.

Therefore, the fitness contours exhibit steeper gradients at larger sizes.

CHAPTER 6: **Ecological correlates of life-history variation in the grasshoppers *Chorthippus brunneus* (Thunb.) and *Myrmeleotettix maculatus* (Thunb.) : II. Egg size, egg pod size, and number of eggs per clutch.**

SUMMARY

1. Egg pods laid by the larger *C.brunneus* were heavier than those of *M.maculatus*, and in the latter species were significantly heavier at site 3 than at site 2. Both these results can be explained by a single positive straight-line relationship for all animals, irrespective of species, relating female mature body weight to egg pod weight. Heavier pods contained more eggs and, in *M.maculatus*, also larger eggs.

2. Variation in the number of eggs per clutch between species was explained statistically by a positive relationship between female body weight and egg number. A trade-off between egg size and number was only detected when the relationship was examined for females of a given mature weight.

3. *M.maculatus* laid heavier eggs than *C.brunneus*; and the eggs of the former (but not the latter) species showed significant differences between sites (heavier at sites 1 and 3 than at site 2) and years (heavier in 1982 than in 1981). These intraspecific differences can be explained by the fact that females with longer hind femur lengths (an index of size at adult moult) laid heavier eggs.

4. Mean egg weights correlated positively with estimates of the amount of local competition among hatchlings for grasses with thin-edged leaves, and to a lesser extent with the degree of evaporative water loss at the sites. Mean egg weights did not correlate with measures of crowding or measures of competition

for grass.

5. There is no evidence that the covariation between egg size and other traits represents a pure tactic in response to selection on both adults and hatchlings to improve size-related competitive ability or resistance to desiccation; the covariation may reflect a constraint in the design of the grasshoppers.

6. The variance in egg weights between egg pods in a given population is significantly greater than that within the pods.

6.1. INTRODUCTION

The aims of this chapter are to describe the variation in egg size, egg pod size, and the number of eggs per pod between and within the grasshopper species C.brunneus and M.maculatus co-occurring at three geographically proximate sites in a sand dunes habitat, and to investigate the potential causes of this variation using the comparative method.

In C.brunneus at least, large offspring eclose from large eggs (R. Wall, unpublished), and, according to the evidence cited by Capinera (1979), the size of insect hatchlings is likely to influence their chances of survival. This idea has been utilized in the theoretical work predicting optimal offspring size by Pianka (1970), Smith and Fretwell (1974), and Brockelman (1975).

Most of the theories which predict how adult size should vary in different ecological circumstances (see Chapter 4) can also be applied to egg size and egg pod size. The size of the egg, hatchling or egg pod may affect the amount of water they lose through evaporation and how protected they are against predators. Large hatchlings may also be better competitors.

Theories of adaptive life histories apply to traits such as offspring size and number which are often intimately correlated with others, especially body size (e.g. Blueweiss et al., 1978; Gould, 1977; Hines, 1982; Kaplan and Salthe, 1979; Leutenegger, 1979; May and Rubenstein, 1982; Peters, 1983; Stearns, 1980, 1983c, 1984) and any interpretation of natural variation which ignores these correlations is likely to be naive. Gould and Lewontin (1979) make a similar point when they claim that it may be fruitless to seek an adaptive reason for a trait which is merely an incidental consequence (an "epiphenomenon") of the relationship between two or more other traits. This criticism is taken into account in this study in which I adopt a more holistic approach to the study of life-history organisation - covariation among traits is examined as well as just the differences in a single trait (see also Chapter 1).

Egg pod size will be limited potentially by the size of the adult female, and the size of the egg may be associated with the magnitude of other traits such as maternal size (e.g. Berven, 1982) or egg number (Lack, 1954; Smith and Fretwell, 1974; Brockelman, 1975; Lawlor, 1976). Covariation between traits may result from developmental constraints, may be tactics or trade-offs, and may result from genetic or environmental differences (Chapter 1).

In this chapter I assess the relative potential importance of crowding, competition for particular resources, desiccation, indirect selection, and environmental constraints in determining egg size variation in the grasshoppers C.brunneus and M.maculatus. In order to do this the hypotheses to be tested are constructed thus: Cause x best accounts for the variation in the reproductive trait y observed among sites (or between species or between years) in the grasshoppers in this study. I will, therefore, eliminate, albeit tentatively, those hypotheses which give a poorer fit to the data.

In this chapter I first summarize the major habitat differences between the three study sites, and then describe the variation in reproductive traits and how they covary with other traits. I then correlate this variation and covariation with a series of potential causes of it, and assess the relative importance of these causes. Finally, I consider the question (referred to in Chapter 1) "Do females hedge their bets when allocating resources to their eggs?".

6.2. THE STUDY SITES

Joint populations of the two species of grasshopper were examined at three sites at Ainsdale Sand Dunes National Nature Reserve, Merseyside. The following descriptions of the sites are brief summaries from a detailed account in Chapter 2. The sites ranged from 625 m^2. (site 3) to 990 m^2. (site 1) in area, and were between 0.88km and 1.23km apart, separated by areas of dune grassland and dense coniferous woodland.

Site 1 was situated in the open dunes on an undulating but mainly SE-facing slope, was more exposed than the other sites, and had larger areas of bare sand. As a consequence, this site tended to lose more water by evaporation than the other two (see also Table 6.11).

Site 2 was furthest inland, sloped very gently, mainly towards the south-east, and had the smallest proportion of bare sand of the three sites. (Females of both species lay their egg pods in bare sand; Richards and Waloff, 1954).

Site 3 comprised mainly south-facing dune slopes, which accounted for approximately 40% of the area, and the edge of a dune slack which was flat and which occupied the rest of the site. Site 3 was sheltered by trees, and its vegetation, like that at site 1, was dominated by *Festuca* spp.; this differed from site 2 which had a greater diversity of grass species, with *Agrostis tenuis* being the most abundant.

There were, therefore, differences in habitat characteristics between these three sites in a single sand dunes area. The next question to answer is : Did the grasshoppers show any differences in reproductive characteristics between such nearby sites?

6.3. VARIATION IN REPRODUCTIVE TRAITS

6.3.1. Variation between species and sites

6.3.1.1. Egg pod collection, examination, and data analysis

Egg pods were collected from the sites in November 1982 (site 2) and January 1983 (all sites). The fresh weights of egg pods and the mean dry weights of eggs did not differ significantly between the November and January collections at site 2 (*M.maculatus*: weights of undamaged pods, n=36, t=0.36, p=0.725; mean egg dry weights, n=68, t=1.68, p=0.097; *C.brunneus*: weights of undamaged pods, n=2, therefore no test possible; mean egg dry weights, n=14, t=1.11, p=0.288). The samples were therefore combined for the data analysis. Preliminary sampling for pods revealed that pods were not laid in loose sand more than 1 metre from vegetation; this was supported by observations of the distribution of hatchlings at site 1. All sandy areas at sites 2 and 3 were small enough to be included as likely oviposition sites, and therefore randomly chosen samples of sand 6cm deep were taken in approximately equal proportions from each sandy area. At site 1, a grid was marked out on the ground using wooden pegs placed 5 metres apart. Then, using random number tables, sampling locations were chosen. If the locations were covered by vegetation or were in loose sand more than a metre from vegetation, the nearest point with bare sand less than a metre from vegetation was sampled instead. Samples of sand, 6cm deep and 280 cm^2 in area were taken from each of 60 points. All sand samples were dried at room temperature for 48 hours and then sieved to extract the egg pods. All egg pods were weighed and any damage noted before they were dissected. The number of eggs in each clutch was recorded and the eggs were then dried to constant weight (24 hours at 70deg.C. was sufficient) before they were weighed to the nearest 10ng. Dry weights were used rather than wet weights because different grasshopper eggs can take up water at different times after they are laid (Moriarty, 1969), and such differences may be related to the particular site or, as Moriarty (1970) found, to the species of grasshopper. Also, errors could be introduced if eggs from different collections lose different amounts of water between the time of collection and the time they are dissected and weighed.

Any egg pods with external damage, or which, on dissection, revealed non-turgid eggs were excluded from the analysis of egg pod weights. There were very few pods of C.brunneus without some form of damage or egg flaccidity, and this limitation precluded the statistical comparison of egg pod weights of this species among sites.

Variation in mean egg dry weight per clutch and in pod weight were analyzed using t-tests (to compare between species at a site) and Student-Newman-Keuls (SNK) multiple range tests (to compare among sites in each species). An Analysis of Variance was performed to test whether the effects of site on mean egg dry weight and on pod weight depended on the species or were the same for both species. In all tests the mean egg dry weights were weighted according to the number of eggs used to calculate the mean divided by the overall number of eggs per clutch. Variation in the number of eggs per clutch was not Normally distributed and no suitable transformation could be found. The effects of site on the number of eggs per clutch were therefore analyzed using the nonparametric Kruskal-Wallis Oneway Analysis of Variance (Conover, 1980).

6.3.1.2. The variation

Adult females of C.brunneus are not only about twice as heavy as those of M.maculatus (Richards and Waloff, 1954; Chapter 4) but they also lay egg pods which are about twice as heavy, and contain a little more than twice the number of eggs (Tables 6.1 and 6.3). Table 6.1 also includes the weights of pods with some external damage to show that the large differences between pod weights of C.brunneus and M.maculatus at the different sites were not sampling artefacts from obtaining very few complete pods of C.brunneus. However, M.maculatus laid heavier eggs, as indicated by their dry weights, although at site 2 this was not quite statistically significant (site 1, $n=132$, $t=2.37$, $p=0.019$; site 2, $n=383$, $t=1.86$, $p=0.064$; site 3, $n=265$, $t=4.86$, $p<0.01$).

M.maculatus laid significantly smaller pods at site 2 than at site 3 (Table 6.1). Also, mean egg dry weights from site 2 tended to be less than those from the other sites, but only in M.maculatus were they significantly lighter (Table 6.1). There was no significant difference in the effect of site on egg dry weight between the two species (Table 6.2), though there was some

TABLE 6.1: **Egg-pod weights, mean egg dry weights, and numbers of eggs per clutch in *C.brunneus* and *M.maculatus* at three sites**

Underlining joins together those groups of clutch sizes, and egg and egg-pod weights which do not differ significantly:

1. Student-Newman-Keuls Multiple Range Test, $p_{crit}=0.05$
2. Kruskal-Wallis Oneway Analysis of Variance

SITE	N	3		N	1		N	2	
		mean ± 95% CL weight (mg)			mean + 95% CL weight (mg)			mean + 95% CL weight (mg)	
Egg-pod weights									
C. brunneus	1	150.85 -		1	115.45 -		2	158.77 ± 2.21	
(pods with case damage only	4	124.93 ± 25.60		1	115.45 -		5	132.16 ± 22.89	
M. maculatus^{1}	28	69.64 ± 3.24		15	66.27 ± 4.84		33	62.94 ± 4.17	
(pods with case damage only)	29	69.58 3.075		17	66.194 ± 4.167		42	62.44 ± 3.38	
Egg dry weights									
C. brunneus^{1}	101	1.21 ± 0.02		28	1.23 ± 0.05		96	1.20 ± 0.02	
M. maculatus^{1}	164	1.27 ± 0.02		104	1.29 ± 0.02		287	1.22 ± 0.01	
Number of eggs per clutch	N	mean	range	N	mean	range	N	mean	range
C. brunneus^{2}	16	12.31	6-15	4	11.50	10-13	15	12.87	9-16
M. maculatus^{2}	35	5.80	5-7	27	5.30	3-6	70	5.47	3-7

TABLE 6.2: Analysis of variance table, showing the effects of species and site on mean egg dry weight.

Sources of variation	MS	df	F	P
Species	0.335	1	26.837	<0.001
Site	0.217	2	17.338	<0.001
Species x Site	0.032	2	2.554	0.078
Residual	0.013	783	-	-

tendency towards a difference (p=0.078).

Because hatchlings of both species emerge into very similar environments, I shall, in this chapter, consider the simplest type of explanation for the variation in egg size between populations, viz. that the difference between populations can best be explained by a single cause. I shall therefore examine the correlations with egg size among all the populations of grasshoppers. When mean egg size was compared among all six populations, those of M.maculatus from site 1 were significantly heavier than all others except those of M.maculatus from site 3, which themselves were significantly heavier than all others except the eggs of C.brunneus from site 1. The differences among populations can be summarized thus:

Largest eggs Smallest eggs

Mm1 Mm3 Cb1 Mm2 Cb3 Cb2

(SNK multiple range test, $p_{crit} = 0.05$)

Mm refers to M.maculatus, Cb to C.brunneus, and the number to the site from which the eggs were collected. Homogeneous subsets are joined by the same underlining.

A Kruskal-Wallis Oneway Analysis of Variance did not detect any significant differences between the number of eggs per clutch of M.maculatus (Chi-squared (corrected for ties) = 4.748, p=0.093), or of C.brunneus (Chi-squared (corrected) = 1.851, p=0.396) at the different sites. However, the trend in M.maculatus approached significance, and tended to show a decrease from site 3 to site 2 and then to site 1 (Table 6.1).

Therefore, to summarize: besides the gross differences between species - C.brunneus being about twice as heavy as M.maculatus, and producing pods about twice as big with a little more than twice as many eggs - there is also the difference in egg size to explain, not only between the species but also among the sites.

Because life-table and life-history variables are so intimately related, a model which predicts changes in population size from year to year would ultimately take into account any accompanying change in life-history characteristics. I have already shown (Chapter 4) that the adult grasshoppers are larger in some years than others, but it is not known how pod size, and egg size and number per clutch vary between years. The next section describes how reproductive traits vary between years.

6.3.2. Reproductive variation between years

6.3.2.1. Methods and data analysis

In 1981, individually-marked adult females of both species were taken on four occasions from a rectangular enclosure at site 1 (10m x 8m with a 1m high wall of polythene sheeting) into the laboratory. There, they were initially weighed and then placed in individual cages to collect egg pods from them. The nylon mesh cages were 20cm tall and 9cm in diameter with plastic petri dishes as a lid and a base, and were placed with the top of the cages level with, and 3cm from, a 60W radiant heat source. A source of radiation is essential for the reproduction of C.brunneus when the ambient air temperature is in the range 19-25 deg.C (Begon, 1983) and presumably when it is below 19 deg.C, too. Each female was given an excess amount of fresh cocksfoot grass, Dactylis glomerata, suspended in a small bottle of water plugged with cotton wool; this provided the grasshoppers with food, shelter, and basking sites. In one half of the bottom of each cage was a layer of dry sand sloping down from the wall of the cage to the base of the centrally-placed bottle of grass; this sand provided a substrate in which egg pods could be laid. After receiving eight hours of radiation on each of two consecutive days the females were reweighed and then returned to the field enclosure. Any egg pods laid were weighed and stored at -18deg.C until required for dissection. The number of eggs per pod and the dry weight of the eggs were then recorded. In 1982 the experiment was performed on 7 occasions using M.maculatus only. In 1983, the experiment was performed on eight occasions using both species.

6.3.2.2. Results

In both 1981 and 1983, M.maculatus produced eggs heavier on average than those of C.brunneus (1981, n=32, t=2.67, p=0.012; 1983, n=34, t=3.47, p=0.002). This difference occurred despite the fact that C.brunneus laid heavier pods containing more eggs (Table 6.3). The weight of the egg pods laid by either species did not differ significantly between years (C.brunneus, n=32, t=0.98, p=0.336; M.maculatus, n=49, $p<0.05$ (SNK multiple range test; Table 6.3), and neither did the mean dry weights of eggs laid by C.brunneus (n=32, t=1.1, p=0.279; Table 6.3). M.maculatus did, however, produce heavier eggs in 1982 than in 1981, though no differences were detected between 1981 and 1983, and 1982 and 1983 (Table 6.3). When the sizes of eggs from all five populations were compared, the following significant differences were found:

Largest eggs   Smallest eggs

Mm82   Mm83   Mm81   Cb83   Cb81

(SNK multiple range test, $P_{crit} = 0.05$)

The number after each species' initials refers to the year in which the eggs were collected. Homogeneous subsets are joined by

TABLE 6.3: **Egg-pod weights, mean egg dry weights per clutch, adult female hind femur lengths, and numbers of eggs per clutch in *C.brunneus* and *M.maculatus* from** a **field enclosure in three years.**

Underlining joins together those groups which, within each species, do not differ significantly:

1. t-test.
2. Student-Newman-Keuls Multiple Range Test.
3. All mean egg dry weights are weighted in the analysis according to the number of eggs used to calculate the mean.
4. Mann-Whitney U-test.
5. Kruskal-Wallis Oneway Analysis of Variance.

Year	1982			1983			1981		
Egg pod weights:	N	mean	± 95% CL	N	mean	± 95% CL	N	mean	± 95% CL
C.brunneus[1]	-			14	136.50	± 16.92	18	146.61	± 12.12
M.maculatus[2]	15	69.67	± 4.44	20	78.55	± 7.24	14	68.57	± 8.19
Mean egg[3] dry weights:									
C.brunneus[1]	-			14	1.28	± 0.06	18	1.24	± 0.05
M.maculatus[2]	15	1.47	± 0.063	20	1.41	± 0.05	14	1.36	± 0.07
Adult hind femur length:									
C.brunneus[1]	-			14	12.32	± 0.34	18	12.44	± 0.34
M.maculatus[2]	15	9.82	± 0.21	20	9.61	± 0.13	14	9.39	± 0.20
Number of eggs per clutch:	N	mean	range	N	mean	range	N	mean	range
C.brunneus[4]	-			14	11.14	4-15	18	11.67	6-15
M.maculatus[5]	15	5.35	4-6	20	5.41	2-8	14	5.43	4- 6

the same underlining.

No differences were detected between the number of eggs per clutch by females of either species in the different years (*C.brunneus*, n=32, U=112.5, p=0.603 (corrected for ties); *M.maculatus*, n=49, Chi-squared (corrected for ties)=0.288, p=0.866; Table 6.3).

Therefore, the same differences between the species were found in these data as in those analyses in the previous section. *C.brunneus* produced heavier pods with more, but smaller, eggs. Again, as in the between-site comparison (Table 6.1), mean egg dry weights did differ significantly between some groups of *M.maculatus*, but not of *C.brunneus*. Egg pod weight and egg number did not differ in either species between years in the samples collected.

Before I examine some hypotheses which predict differences in reproductive traits between species, sites, and years, I shall describe how reproductive traits correlate with each other and with adult size. This will allow me to consider a wider range of alternative causes of the reproductive variation than would be possible if the variation in a trait were considered on its own.

6.4. COVARIATION IN LIFE-HISTORY TRAITS

6.4.1. Allometry and life-history covariation

Kaplan and Salthe (1979) make the important point that when the adaptive significance of life-history variation is examined, interpretations of the results must take into account the allometric relationships between body size and other traits among the taxa used in the comparison. Historical effects can therefore have important effects on variation in a life-history trait. Differences in such phylogenetic relationships have already been reduced to a minimum in this study because populations of the same and of closely-related species are being compared. Also, the geographical proximity of the sites, and the absence of an ancient barrier separating them, suggest that the populations may have had similar evolutionary histories until after about 1914 when the first of the conifers were planted (Greenwood, 1970). Nonetheless, historical constraints cannot be ruled out altogether, since they can, in principle, be as recent as one generation old (Chapter 1).

Relationships between adult size and other traits may arise not only as historical constraints but also as (unconstrained) tactics (Chapter 1) - that is, the variation in each trait is adaptive _in itself_, and consequently, the way the traits _co_vary is adaptive. Variation in one trait may also result from differences in selection on another trait to which the first is developmentally constrained, or from differences in the amount of resources available to the organisms; both these causes can also produce a positive covariation between life-history traits (Chapter 4). In order to examine these alternative causes of reproductive variation an analysis of the covariation between reproductive traits, and of the relationships of these traits to adult size, will be necessary.

6.4.2. Measuring adult size

Hind femur length is a good index of the weight at adult emergence (Chapter 4; P. de Souza Santos jr., unpublished; R. Wall, unpublished) and, in females, at the time of pod laying (Chapter 4, P. de Souza Santos jr., unpublished). Because body lengths and weights vary considerably within the lifetime of adult female

FIGURE 6.1: **Relationship between mean egg dry weight and mean adult female hind femur lengths at different sites and in different years**

1-6: M.maculatus

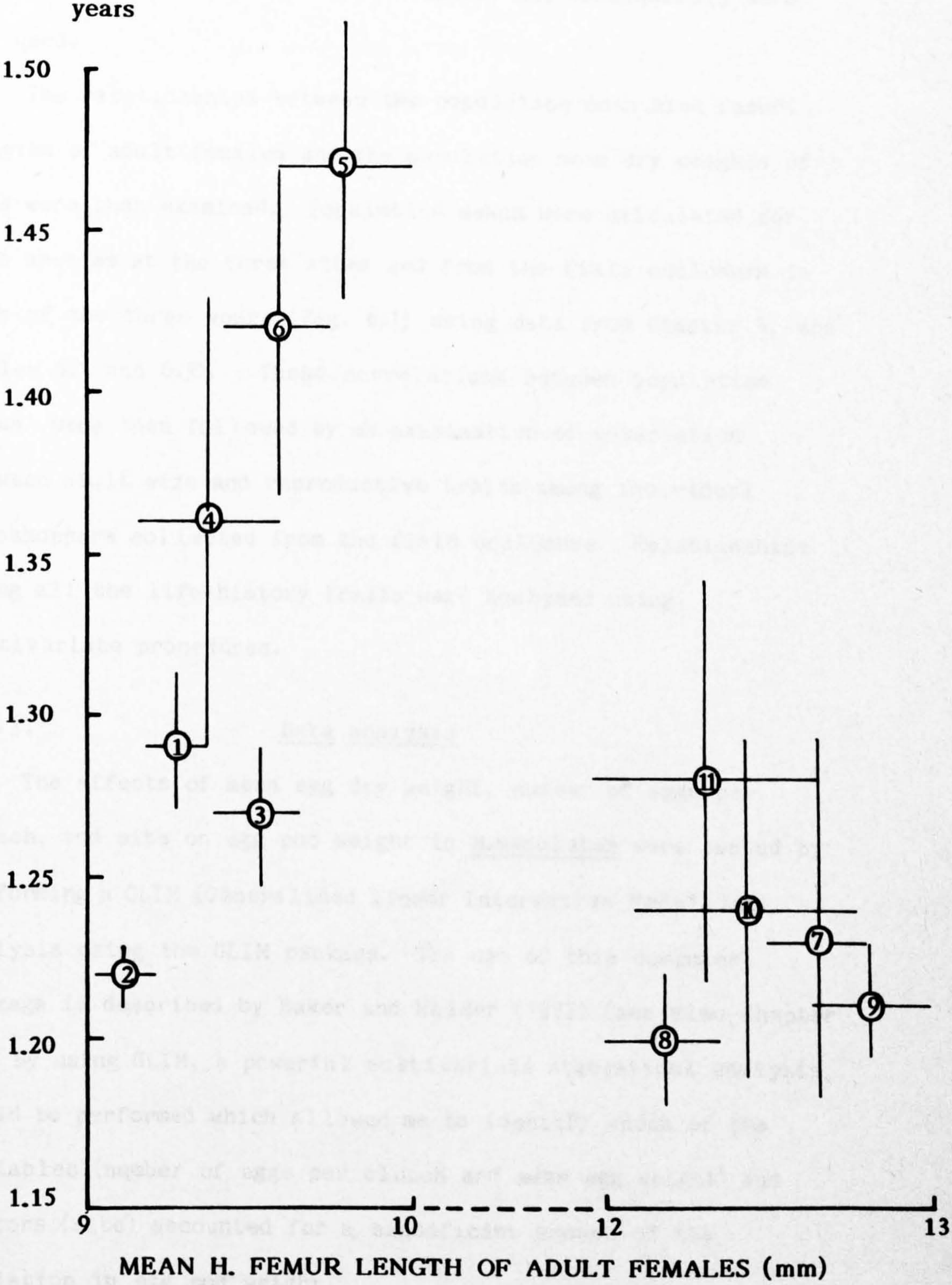
1. Site 1, 1982
2. Site 2, 1982
3. Site 3, 1982
4. Enclosure 1 (site 1), 1981
5. Enclosure 1 (site 1), 1982
6. Enclosure 1 (site 1), 1983

7-11: C.brunneus

7. Site 1, 1982
8. Site 2, 1982
9. Site 3, 1982
10. Enclosure 1 (site 1), 1981
11. Enclosure 1 (site 1), 1983

FIGURE 6.1:

Relationship between mean egg dry weight and mean adult female hind femur lengths at different sites and in different years



1-6 : M. maculatus **7-11 : C. brunneus**

Bars represent 95% confidence limits

grasshoppers, corresponding particularly to the gonotrophic cycle (Richards and Waloff, 1954; P. de Souza Santos jr., unpublished) these measurements were not suitable for distinguishing differences in adult size between sites, and consequently were not used.

The relationships between the population mean hind femur lengths of adult females and the population mean dry weights of eggs were then examined. Population means were calculated for each species at the three sites and from the field enclosure in each of the three years (Fig. 6.1; using data from Chapter 4, and Tables 6.1 and 6.3). These correlations between population means were then followed by an examination of covariation between adult size and reproductive traits among individual grasshoppers collected from the field enclosure. Relationships among all the life-history traits were analyzed using multivariate procedures.

6.4.3. Data analysis

The effects of mean egg dry weight, number of eggs per clutch, and site on egg pod weight in M.maculatus were tested by performing a GLIM (Generalised Linear Interactive Modelling) analysis using the GLIM package. The use of this computer package is described by Baker and Nelder (1977) (see also Chapter 3). By using GLIM, a powerful multivariate statistical analysis could be performed which allowed me to identify which of the variables (number of eggs per clutch and mean egg weight) and factors (site) accounted for a significant amount of the variation in egg pod weight.

Table 6.4 provides an example of the procedure adopted in the analyses. The best initial improvement in the fit of the

TABLE 6.4: **Effects of number of eggs per clutch, mean egg dry weight, and site on fresh pod weight in *M.maculatus*.**

"No. of eggs x Site" is an interaction term; if this is added to the model containing just the Grand Mean, the new model describes the effect of different relationships (slopes) between the no. of eggs per clutch and pod weights at the different sites.

Abbreviations

"Mean egg d.wt." denotes Mean egg dry weight

The best-fit models are asterisked.

Model: Grand Mean (GM); Deviance = 8488, degrees of freedom (df) = 75

Variables added	Reduction in deviance	Reduction in df	F	df	P
Number of eggs	3794	1	59.812	1,74	< 0.001*
Mean egg d.wt.	386	1	3.526	1,74	NS
Site	682	2	3.189	2,73	NS
No. of eggs x Site	4091	3	22.330	3,72	< 0.001
Mean egg d.wt. x Site	840	3	2.636	3,72	NS

Model: GM + No. of eggs; Deviance = 4694, df = 74

Variables added	Reduction in deviance	Reduction in df	F	df	P
Mean egg d.wt.	435	1	7.456	1,73	< 0.01*
Site	399	2	3.344	2,72	< 0.05
Mean egg d.wt. x Site	634	3	3.696	3,71	< 0.025

Model: GM + No. of eggs + Mean egg d.wt.; Deviance = 4259, df = 73

Variables added	Reduction in deviance	Reduction in df	F	df	P
Site	217	2	1.906	2,71	NS

Therefore, best fit model = GM + No. of eggs + Mean egg d.wt.

Parameter Estimates (+ S.E.)

GM	-6.353	(11.86)
No. of eggs	8.095	(0.997)
Mean egg d.wt.	22.560	(8.262)

model to the data was due to addition of egg number to the model with only the Grand Mean. The remaining variable (mean egg dry weight) and factor (site) were then added to the new model - the factor also being added as an interaction term. The best improvement in fit to the data was provided by the addition of mean egg dry weight. Finally, the addition of "site" to the latest model - that with the Grand Mean, egg number, and mean egg dry weight - gave no significant improvement in fit.

The analysis described so far is similar to that of a multiple regression in which variables are added in the order of decreasing importance until no significant improvement in the fit of the model to the data is found. The only difference is that factors as well as variables were also being added to the model, both singly and as interaction terms with a variable, so that, for instance, a variable (e.g. egg number) could have a different relationship to the y-variate (egg pod weight) for each level of the factor (site). This is exactly the same as testing for different intercepts (when the factor is added to the model on its own) and for different slopes (when an interaction term is added) in an analysis of covariance. Thus, a multiple regression and analysis of covariance could be performed simultaneously.

A similar analysis was performed on the same data to examine the effects of mean egg dry weight, egg number and site on egg pod weight. This second analysis was necessary in order to assess the relationships of egg pod weight to the number of eggs per clutch and site, both of which were not examined in the first analysis.

A GLIM analysis was also performed on the data collected when females were brought into the laboratory from the field enclosure to lay eggs. This analysis examined the effects of adult female hind femur length and mature body weight, number of eggs per clutch, mean egg dry weight, laying date, species, and year on egg pod weight. A similar analysis using the same variables was performed but with mean egg dry weight as the y-variate.

Correlation matrices were constructed for each species to show the interrelationships among the traits; Kendall's non-parametric correlation coefficients were calculated because the numbers of eggs per clutch were not Normally distributed (Conover, 1980).

In the matrix of Kendall's rank correlations, four measures relating to adult body size and condition were correlated with reproductive traits to help me assess the most likely cause of reproductive variation. These four measures were highly autocorrelated, so correlations between them were ignored (except for that between residual body weight and hind femur length, see below). The autocorrelation did not, however, affect the comparison of the relative strengths of their relationsips with reproductive traits. The "residual mature weight" (weight of the female before laying the pod minus the weight of the egg pod within and of the hind legs) was calculated as well as mature body weight. This allowed me to test for a trade-off between the amount of material resources put into the pod and the amount retained by the female. It also allowed me to examine the relationship between body weight and hind femur length after removing the possibility of autocorrelation caused by the effect of hind femur length on hind leg weight and therefore on total body weight. In addition to the three size measures - total mature body weight, residual mature weight, and hind femur length - the "condition" of the females before laying a pod was also calculated by dividing each female's body weight by her hind femur length. This estimate of condition was not invalidated by any disproportionate (allometric) increase in body weight as hind femur length increased, since the relationship between hind femur length and body weight was linear (i.e. isometric; Chapter 4).

Although the correlation matrix gave a more comprehensive description of the interrelationships between traits, it was not as powerful as the parametric GLIM analysis. Also, because the correlations were based on ranks, partial correlation coefficients could not be calculated to which statistical significance levels could be attached (Conover, 1980). This contrasts with the GLIM analysis which allowed me to examine the effects of individual variables after removing statistically the effects of others. Used together, therefore, the two types of multivariate analysis provided a comprehensive description of the interrelationships among the life-history traits.

6.4.4. Life-history correlates of some reproductive traits

6.4.4.1. Egg pod weight

Large eggs were associated with heavy egg pods in M.maculatus, but the number of eggs in a clutch was a more important determinant of pod weight (Table 6.4), explaining 45% of the variance. There was no difference between sites in the relationships between egg pod weight and number of eggs per clutch, and between egg pod weight and mean egg size in M.maculatus (Table 6.4).

Heavier females of both species collected from the field enclosure produced heavier egg pods (Table 6.5); this relationship was able to explain 85% of the variance in pod

TABLE 6.5: **Effects of hind femur length, mature body weight, number of eggs per clutch, mean egg dry weight, laying date, species, and year on egg pod weight.**

(2 pages)

Abbreviations

"Yr." denotes Year

"d.wt." denotes dry weight

"l'ngth" denotes length

"No." denotes number

Model: Grand Mean (GM); Deviance = 129,300, df = 80

Variables added	Reduction in deviance	Reduction in df	F	df	P
H.femur length	93,950	1	209.959	1,79	< 0.001
Mature weight	109,500	1	436.894	1,79	< 0.001*
No. of eggs	101,030	1	282.326	1,79	< 0.001
Mean egg d.wt.	26,500	1	20.365	1,79	< 0.001
Laying date	20,100	1	14.541	1,79	< 0.001
Species	92,730	1	200.319	1,79	< 0.001
Year	19,000	2	6.718	2,78	< 0.005
H.femur length x Species	96,650	2	115.447	2,78	< 0.001
Mature wt. x Species	109,840	2	220.132	2,78	< 0.001
No. of eggs x Species	104,590	2	165.075	2,78	< 0.001
Mean egg d.wt. x Species	88,990	2	86.098	2,78	< 0.001
Laying date x Species	92,610	2	98.441	2,78	< 0.001
Year x Species	94,590	4	51.778	4,76	< 0.001
H.femur length x Year	96,010	3	74.024	3,77	< 0.001
Mature wt. x Year	110,230	3	148.361	3,77	< 0.001
No. of eggs x Year	102,280	3	97.157	3,77	< 0.001
Mean egg d.wt. x Year	31,200	3	8.163	3,77	< 0.001
Laying Date x Year	29,520	3	7.594	3,77	< 0.001
H.femur lngth x Species x Year	98,250	5	47.464	5,75	< 0.001
Mature wt x Species x Yr	111,220	5	92.273	5,75	< 0.001
No. of eggs x Species x Year	106,110	5	68.635	5,75	< 0.001
Mean egg d.wt. x Species x Year	91,370	5	36.134	5,75	< 0.001
Laying date x Species x Year	93,610	5	39.343	5,75	< 0.001

Model: GM + Mature weight; Deviance = 19,800, df = 79

Variables added	Reduction in deviance	Reduction in df	F	df	P
H.femur length	0	1	0	1,78	NS
No. of eggs	1550	1	6.625	1,78	< 0.025*
Mean egg d.wt.	700	1	2.859	1,78	NS
Laying date	40	1	0.158	1,78	NS
Species	170	1	0.675	1,78	NS
Year	670	2	1.348	2,77	NS
H.femur lngth x Species	290	2	0.572	2,77	NS

cont'd.

Variables added	Reduction in deviance	Reduction in df	F	df	P
No. of eggs x Species	1570	2	3.316	2,77	< 0.05
Mean egg d.wt. x Species	750	2	1.516	2,77	NS
Laying Date x Species	420	2	0.834	2,77	NS
Year x Species	1610	4	1.660	4,75	NS
H.femur lngth x Year	670	3	0.887	3,76	NS
No. of eggs x Year	1170	3	3.118	3,76	< 0.05
Mean egg d.wt. x Year	1040	3	1.404	3,76	NS
Laying date x Year	910	3	1.220	3,76	NS
H.femur lngth x Species x Yr	1650	5	1.345	5,74	NS
No. of eggs x Species x Year	3000	5	2.643	5,74	< 0.05
Mean egg d.wt. x Species x Year	1990	5	1.654	5,74	NS
Laying date x Species x Yr	1670	5	1.363	5,74	NS

Model: GM + Mature weight + No. of eggs; Deviance = 18250, df = 78

Variables added	Reduction in deviance	Reduction in df	F	df	P
H.femur length	10	1	0.042	1,77	NS
Mean egg d.wt.	130	1	0.552	1,77	NS
Laying date	120	1	0.510	1,77	NS
Species	30	1	0.127	1,77	NS
Year	600	2	1.292	2,76	NS
H.femur lngth x Species	60	2	0.125	2,76	NS
Mean egg d.wt. x Species	190	2	0.400	2,76	NS
Laying date x Species	270	2	0.571	2,76	NS
Year x Species	1460	4	1.609	4,74	NS
H.femur lngth x Year	570	3	0.806	3,75	NS
Mean egg d.wt. x Year	580	3	0.821	3,75	NS
Laying date x Year	910	3	1.312	3,75	NS
H.femur lngth x Species x Year	1450	5	1.260	5,73	NS
Mean egg d.wt. x Species x Year	1500	5	1.307	5,73	NS
Laying date x Species x Year	1510	5	1.317	5,73	NS

Therefore, best fit model = GM + Mature weight + No. of eggs.

Parameter Estimates (+ SE)

GM	-4.809	(5.638)
Mature wt.	0.437	(0.06678)
No. of eggs	3.127	(1.213)

weight. After statistically removing the effect of female weight, heavier pods still had more eggs (Table 6.5), as was found in the pods collected from the three sites (Table 6.4). When the effects of both female weight and egg number were removed, none of the other variables or factors (femur length, mean egg dry weight, laying date, species and year) had any significant relationship with egg pod weight. Hence, although C.brunneus lays egg pods about twice the weight of those of M.maculatus (Tables 6.1 and 6.3), this difference can be explained simply as being a consequence of their different mature body sizes and the different numbers of eggs laid per pod, rather than as some differential effect of species *per se*.

The correlation matrix showed that heavier egg pods of M.maculatus were laid by heavier females, by females in the best condition, by females with longer hind femurs, by females with lower residual mature weights, and by females which contained, on average, more and larger eggs (Table 6.6). Body condition showed the strongest relationship to egg pod weight, followed very closely by mature weight (from which body condition was derived). Thus, in M.maculatus, females in better initial condition laid heavier egg pods. All the correlations with egg pod weight were consistent with the results of the GLIM analysis (Table 6.5), but there was, in addition, a negative correlation with residual mature weight. (The correlation between body condition and residual mature weight was *positive* in both species, so the effect of residual mature weight on pod weight is a real phenomenon rather than being due simply to the autocorrelation between body condition and residual mature weight.) This suggests that there was a trade-off between the amount of

TABLE 6.6: **Kendall's Rank Correlations among life-history traits**

Significance levels: * <0.05
** <0.01
*** <0.001

C.brunneus, n = 32

	H.femur Length	Mature weight	Residual body weight	Condition	Pod weight	Mean egg d.wt.	No. of eggs per clutch	Laying Date
H. femur	-	0.363	0.332	0.186	0.092	-0.099	0.209	0.087
Length		**	**	NS	NS	NS	NS	NS
Mature	0.416	-	0.418	0.832	0.570	0.170	0.552	-0.004
Weight	***		***	***	***	NS	***	NS
Residual	0.231	0.462	-	0.351	-0.020	0.283	0.342	0.004
Body Weight	*	***		**	NS	*	**	NS
Condition	0.196	0.789	0.425	-	0.615	0.197	0.519	-0.053
	*	***	***		***	NS	***	NS
Pod	0.197	0.344	-0.203	0.347	-	0.092	0.332	-0.013
Weight	*	***	*	***		NS	**	NS
Mean egg	0.388	0.356	0.146	0.259	0.241	-	0.017	-0.093
d.wt.	***	***	NS	**	**		NS	NS
No. of eggs	0.086	0.276	0.031	0.292	0.275	0.059	-	-0.017
per clutch	NS	**	NS	**	**	NS		NS
Laying	-0.150	-0.036	0.087	0.037	-0.093	-0.134	0.093	-
Date	NS	NS	NS	NS	NS	NS	NS	

M.maculatus, n=49

resources put into the pod and the amount retained by the female. Heavier egg pods were therefore produced by females in better initial condition and by those which converted a greater relative amount of their original body weight into egg pods.

C.brunneus showed a similar pattern: heavier egg pods were laid by females in better initial condition (which were also the heaviest), and contained more, but not larger, eggs (Table 6.6). (P. de Souza Santos jr. (unpublished) also found no correlation between pod weight and mean egg dry weight in *C.brunneus*). No relationship was detected, however, between egg pod weight and hind femur length or residual mature weight.

These findings - revealing the importance of mature body condition to egg pod weight - are consistent with those of P. de Souza Santos jr. (unpublished) in which heavier egg pods were laid by *C.brunneus* females which had assimilated food most rapidly.

The significant difference in the egg pod weights of *M.maculatus* between sites 2 and 3 (Table 6.1) can be explained statistically by the positive correlation described in this section between adult size and egg pod weight in *M.maculatus*. Both egg pods and adult hind femurs (body condition was not measured) were significantly smaller at site 2 than at site 3 (Table 6.1; Chapter 4).

Although the positive correlation between the measures of adult size and egg pod size can explain *statistically* the differences in pod size between species and, in *M.maculatus*, between sites, it does not provide a full *biological* explanation. It is likely that pod size is limited by the size of the adult, but the correlation cannot determine whether selection favours a particular pod size (and consequently a particular adult size) or whether the pod size is simply a consequence of more important forces affecting the size of the adult. I have not, in this chapter, specifically investigated selection pressures on pod size, but the effects on adult size have already been considered in Chapters 4 and 5.

6.4.3.2. Number of eggs per clutch

The number of eggs per clutch was not correlated with the female's hind femur length in either species, but it did correlate positively with maternal condition and mature body weight - two variables which were themselves highly correlated (Table 6.6). This suggests that the mature body weight or condition may be a more important determinant of the number of eggs laid by a female (and therefore of her pod weight; Section 6.4.3.1) than her actual skeletal body size.

A negative correlation between egg size and number would indicate that resources are allocated in some grasshoppers to fewer larger offspring, and in others to more smaller offspring. No such significant negative correlation was found in pods of *M.maculatus* from any of the sites, and in one case there was a strong but non-significant positive trend (Table 6.7). Heavier eggs were, however, associated with fewer eggs per clutch in the pods of *C.brunneus* from site 2, but no trend was evident in the pods from site 3 (Table 6,7). Therefore, in the main, a trade-off between egg size and number was not evident. However, in the GLIM analysis of data from individual females from the field enclosure, heavier eggs were associated with fewer of them per clutch when the effects of mature body weight in the two species had been statistically removed. This analysis revealed that the relationship between egg size and number was negative because the

TABLE 6.7: Kendall's Rank Correlations between mean egg dry weight, pod weight, and number of eggs per clutch

Species		M.maculatus		C.brunneus	
Site	Trait	No. of eggs	Mean egg wt.	No. of eggs	Mean egg wt.
1	Pod wt.(r)	0.537	-0.097		
	(n)	15	15	1	1
	(p)	0.006	0.310		
	No. of eggs (r)		-0.079		
	(n)	-	27	-	1
	(p)		0.308		
2	Pod wt.(r)	0.679	0.186		
	(n)	33	33	2	2
	(p)	0.001	0.066		
	No. of eggs (r)		-0.001		-0.949
	(n)	-	70	-	5
	(p)		0.495		0.011
3	Pod wt.(r)	0.307	0.137		
	(n)	28	28	2	2
	(p)	0.026	0.156		
	No. of eggs (r)		0.195		0.0
	(n)	-	35	-	4
	(p)		0.085		0.5

parameter estimate linking mean egg dry weight and egg number in the best fit model was negative (Table 6.9). The trade-off was therefore revealed amongst females *of a given mature body weight*. The relationship between mean egg dry weight and egg number was not detected from the matrix of rank correlations, and, presumably, cannot be detected without calculating partial correlation coefficients.

Lawlor (1976) found that female *Armadillidium vulgare*, a terrestrial isopod, which had higher size-specific fecundities produced smaller ova and young, and it is a well-documented phenomenon in vertebrates in which the size of young at weaning (or fledging) is inversely related to brood size (Lack, 1954). The optimum trade-off between clutch size and number has been discussed by Smith and Fretwell (1974) , Brockelman (1975), and Wilbur (1977), but like any other trade-off it may be obscured if differences in the total amount of resources available to divide between the two traits (non-genetic constraints, see Appendix to the thesis) are more important.

6.4.4.3. Mean egg dry weight

The mean egg dry weight of *M.maculatus* was not influenced by pod weight or by the number of eggs per clutch when the significant effect of site had been removed (Table 6.8).

Adult size did, however, affect egg size in *M.maculatus*. Figure 6.1 shows a clear difference between the two species in the effect of mean adult female hind femur length on each population's mean egg dry weight. Populations of *M.maculatus* with larger adult females produced larger eggs, but no relationship between mean adult hind femur length and mean egg dry weight was detected in *C.brunneus*. (The positive correlation between mean adult size and egg size in *M.maculatus* was not due

TABLE 6.8: **Effects of number of eggs per clutch, fresh pod weight and site on mean egg dry weight in *M.maculatus***

Model: Grand Mean (GM); Deviance = 0.855, df= 75

Variables added	Reduction in deviance	Reduction in df	F	df	P
No. of eggs	0.0003	1	0.026	1,74	NS
Pod weight	0.0388	1	3.520	1,74	NS
Site	0.0792	2	3.726	2,73	<0.05*
No. of egg x Site	0.0714	3	2.187	3,72	NS
Pod weight x Site	0.0882	3	2.761	3,72	0.05

Model: GM + Site; Deviance = 0.7758, df = 73

Variables added	Reduction in deviance	Reduction in df	F	df	P
No. of eggs	0.0011	1	0.102	1,72	NS
Pod weight	0.0184	1	1.749	1,72	NS
No. of egg x Site	0.0236	3	0.732	3,70	NS
Pod weight x Site	0.0319	3	1.001	3,70	NS

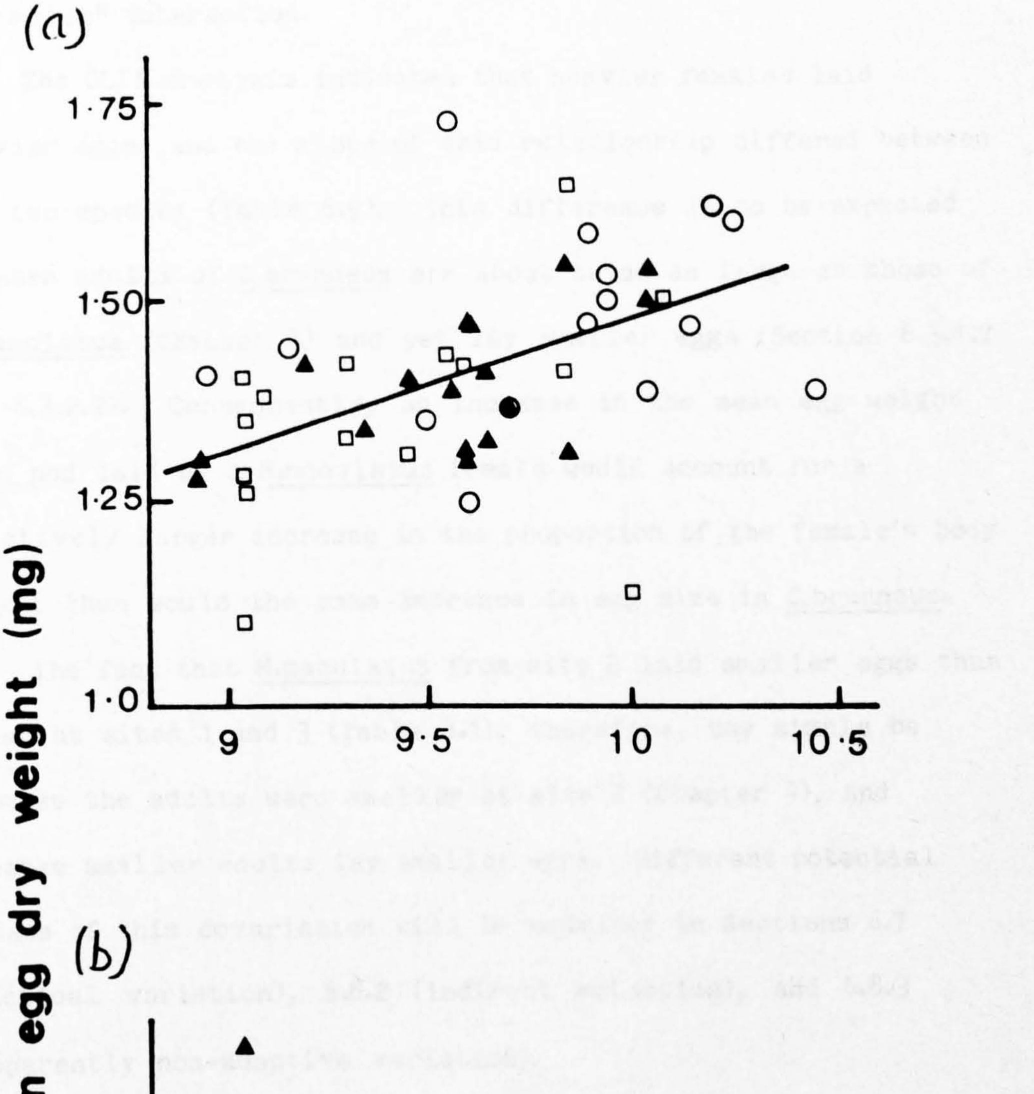
Therefore, best fit model = GM + Site

Parameter Estimates (+ SE)

GM	1.297	(0.02662)
Site 2	-0.0737	(0.0321)
Site 3	-0.01448	(0.03299)

to large eggs giving rise to large adults, because the correlation between the traits in the three consecutive years disappears if the mean weights of eggs are correlated with the size of adult females from the generation which hatched from them (rather than from the generation which laid them)). This difference between species showed up also in the rank correlations among individual grasshoppers (Table 6.6, Fig. 6.2). *M.maculatus* mean egg dry weights correlated best with hind femur length followed by other measures of body size - mature body weight and body condition - and then pod weight; conversely, the only correlation with mean egg dry weight in *C.brunneus* was the positive one with residual mature weight, the biological meaning of which is difficult to interpret. (P. de Souza Santos jr. (unpublished) also found no correlation between maternal hind femur length and mean egg dry weight in *C.brunneus* reared in the laboratory). The conclusion that the effects of size at adult emergence on *M.maculatus* mean egg dry weight were stronger than the effects of mature body weight or body condition contrasts with the relative effects of these measures on egg pod weight - body condition and mature weight were more important than hind femur length (Table 6.6). The relationship between mean egg dry weight and maternal hind femur length in *M.maculatus* did not emerge from the GLIM analysis because hind femur length and mature body weight were themselves highly correlated in the two species, and although hind femur length showed a slightly stronger correlation with mean egg dry weight in *M.maculatus*, *C.brunneus* showed a tendency (though not a significant one) for heavier adults to produce larger eggs (whereas there was no such trend between *C.brunneus* hind femur length and mean egg dry

FIGURE 6.2: Relationship between adult female hind femur length and mean egg dry weight in (a) M.maculatus and (b) C.brunneus.



weight; Table 6.6): the addition of the interaction term "mature weight x species" therefore accounted for more of the total variation in mean egg dry weight than did the "hind femur length x species" interaction.

The GLIM analysis indicated that heavier females laid heavier eggs, and the slope of this relationship differed between the two species (Table 6.9). This difference is to be expected because adults of C.brunneus are about twice as large as those of M.maculatus (Chapter 4) and yet lay smaller eggs (Section 6.3.1.2 and 6.3.2.2). Consequently, an increase in the mean egg weight of a pod laid by a M.maculatus female would account for a relatively larger increase in the proportion of the female's body weight than would the same increase in egg size in C.brunneus.

The fact that M.maculatus from site 2 laid smaller eggs than those at sites 1 and 3 (Table 6.1), therefore, may simply be because the adults were smaller at site 2 (Chapter 4), and because smaller adults lay smaller eggs. Different potential causes of this covariation will be examined in Sections 6.7 (tactical variation), 6.8.2 (indirect selection), and 6.8.3 (apparently non-adaptive variation).

The observation that, within a species, large adults lay larger eggs has also been described for wood frogs (Berven, 1982).

When the effects of mature body weight, species, and number of eggs per clutch (i.e the trade-off, Section 6.4.3.2) had been accounted for, heavier eggs were associated with heavier egg pods, but the relationship between them was different in the two species and in the three years (Table 6.9). The difference between species is to be expected because the eggs of M.maculatus were larger than those of C.brunneus, but the latter species laid much heavier pods: the ratio of egg dry weight to pod weight was

TABLE 6.9: **Effects of adult hind femur length, mature body weight, number of eggs per clutch, egg pod weight, laying date, species, and year on mean egg dry weight (per pod)**

(3 pages)

Model: Grand Mean (GM); Deviance = 1.666, df = 80

Variables added	Reduction in deviance	Reduction in df	F	df	P
H.femur length	0.376	1	23.026	1,79	< 0.001
Mature weight	0.292	1	16.789	1,79	< 0.001
No. of eggs	0.481	1	32.067	1,79	< 0.001
Pod weight	0.341	1	20.331	1,79	<0.001
Laying date	0.271	1	15.347	1,79	<0.001
Species	0.490	1	32.917	1,79	<0.001
Year	0.348	2	10.297	2,78	<0.001
H.femur length x Species	0.544	2	18.909	2,78	<0.001
Mature weight x Species	0.617	2	22.939	2,78	<0.001*
No. of eggs x Species	0.510	2	17.206	2,78	<0.001
Pod weight x Species	0.579	2	20.774	2,78	<0.001
Laying date x Species	0.509	2	17.157	2,78	<0.001
Year x Species	0.606	4	10.862	4,76	<0.001
H.femur length x Year	0.552	3	12.718	3,77	<0.001
Mature weight x Year	0.464	3	9.908	3,77	<0.001
No. of eggs x Year	0.577	3	13.599	3,77	<0.001
Pod weight x Year	0.488	3	10.633	3,77	<0.001
Laying date x Year	0.387	3	7.766	3,77	<0.001
H.femur length x Species x Yr.	0.631	5	9.145	5,75	<0.001
Mature weight x Species x Yr.	0.6977	5	10.808	5,75	<0.001
No. of eggs x Species x Yr.	0.595	5	8.333	5,75	<0.001
Pod weight x Species x Yr.	0.6727	5	10.159	5,75	<0.001
Laying date x Species x Yr.	0.582	5	8.054	5,75	<0.001

Model: GM + (Mature weight x Species); Deviance = 1.049, df = 78

Variables added	Reduction in deviance	Reduction in df	F	df	P
H.femur length	0	1	0	1,77	NS
No. of eggs	0.1149	1	9.471	1,77	<0.005*
Pod weight	0.022	1	1.649	1,77	NS
Laying date	0.022	1	1.649	1,77	NS
Species	0.024	2	1.803	2,76	NS
Year	0.0903	3	3.579	3,75	<0.025
H.femur length x Species	0.001	2	0.036	2,76	NS

continued

Variables added	Reduction in deviance	Reduction in df	F	df	P
No. of eggs x Species	0.1257	2	5.173	2,76	<0.01
Pod weight x Species	0.0985	2	3.938	2,76	<0.025
Laying date x Species	0.0647	2	2.498	2,76	NS
Year x Species	0.1098	4	2.163	4,74	NS
H.femur length x Year	0.090	3	2.346	3,75	NS
No. of eggs x Year	0.1653	3	4.676	3,75	<0.01
Pod weight x Year	0.0867	3	2.252	3,75	NS
Laying date x Year	0.0815	3	2.106	3,75	NS
H.femur lgth x Species x Year	0.0984	5	1.511	5,73	NS
No. of eggs x Species x Year	0.1848	5	3.122	5,73	<0.025
Pod weight x Species x Year	0.1745	5	2.913	5,73	<0.025
Laying date x Species x Year	0.1184	5	1.858	5,73	NS

Model: GM + (Mature weight x Species) + No. of eggs; Deviance = 09341, df = 77

Variables added	Reduction in deviance	Reduction in df	F	df	P
H.femur length	0.0008	1	0.065	1,76	NS
Pod weight	0.0039	1	0.319	1,76	NS
Laying date	0.0207	1	1.722	1,76	NS
Species	0.0094	1	0.773	1,76	NS
Year	0.0838	2	3.696	2,75	<0.05
H.femur length x Species	0.0008	2	0.032	2,75	NS
Pod weight x Species	0.0797	2	3.498	2,75	<0.05
Laying date x Species	0.0423	2	1.779	2,75	NS
Year x Species	0.0908	4	1.965	4,73	NS
H.femur length x Year	0.0902	3	2.836	3,74	NS
Pod weight x Year	0.073	3	2.091	3,74	NS
Laying date x Year	0.0748	3	2.147	3,74	NS
H.femur lgth x Species x Yr.	0.0948	5	1.626	5,72	NS
Pod weight x Species x Year	0.1611	5	3.001	5,72	<0.025*
Laying date x Species x Yr.	0.0919	5	1.571	5,72	NS

Model: GM + (Mature weight x Species) + No. of eggs + (Pod wt. x Species x Year)

Deviance = 0.773, df = 72

Variables added	Reduction in deviance	Reduction in df	F	df	P
H.femur length	0.0129	1	1.205	1,71	NS
Laying date	0.0014	1	0.129	1,71	NS
Species	0.0087	1	0.808	1,71	NS
Year	0.0367	2	1.745	2,70	NS
H.femur length x Species	0.0155	2	0.716	2,70	NS
Laying date x Species	0.0188	2	0.872	2,70	NS
Year x Species	0.0479	4	1.123	4,68	NS
H.femur length x Year	0.0417	3	1.312	3,69	NS
Laying date x Year	0.0641	3	2.080	3,69	NS
H.femur lgth x Species x Year	0.0462	5	0.852	5,67	NS
Laying date x Species x Year	0.0692	5	1.318	5,67	NS

Therefore, best fit model = GM + (Mature weight x Species) + No. of eggs
+ (Pod weight x Species x Year)

Parameter Estimates (+ SE)

GM	1.113 (0.08951)
No. of eggs	-0.02738 (0.008904)
M.maculatus mature weight	0.001811 (0.0008753)
C.brunneus mature weight	0.002952 (0.0007089)
M.maculatus pod weight 1981	0.002224 (0.00137)
" " " 1982	0.00362 (0.001426)
" " " 1983	0.002466 (0.001204)
C.brunneus " " 1981	-0.002126 (0.0009974)
" " " 1983	-0.00194 (0.001033)

therefore different between the species. Also, the difference between years in the relationship between mean egg dry weight and pod weight is to be expected, in M.maculatus at least, because the dry weights of the eggs differed significantly between years: again, therefore, the ratio between egg and pod weight would have changed between years. The correlation matrix showed that when the effects of other variables were not taken into account, heavier eggs of M.maculatus were associated with heavier egg pods. No such correlation was found among the pods of C.brunneus. This positive correlation between egg and pod weights among the pods of individual grasshoppers from the field enclosure is consistent with the finding that both eggs and pods of M.maculatus from site 2 were significantly smaller than those from site 3. Although eggs from site 1 were larger, on average, than those from site 3, (whereas pods from site 3 were larger than those from site 1), the differences between these sites were not significant in either case (Table 6.1). Different potential causes of this covariation between egg and egg pod size in M.maculatus will be discussed in Sections 6.7 and 6.8.2.

The benefits of examining, among individuals or populations of the same species, the effects of adult body size on reproductive traits are evident from this study in which the trade-off between egg size and number was revealed only after removing statistically the effects of maternal body weight. Also, because larger pods (containing more eggs) were produced by heavier females, whereas larger eggs were produced by females, of M.maculatus, which had longer hind femurs (rather than by those in better condition), it is clearly important to distinguish between different aspects of adult body size when examining covariation with life-history traits. In particular, the current body condition (reflecting recent adult storage of resources) should be distinguished from the skeletal body size (reflecting the result of juvenile growth and development; Chapters 4 and 5; R. Wall, unpublished). Such a division is likely to be useful because the magnitude of some traits may be fixed by the skeletal allometric relationships whereas others may be more dependent on the amount of resources available at the time the phenotypic reponse is being made.

The correlations between adult hind femur length and mean egg dry weight, described here for M.maculatus, correspond to the significant differences in mean egg dry weight found among the sites and years (Tables 6.1 and 6.3). These correlations suggest a number of alternative explanations for the variation in egg size which would not normally have been considered if only the variation in egg size had been described. The main objective of the rest of this chapter is to examine this range of alternative potential causes of egg size variation and covariation among the different populations. I start by examining two groups of hypotheses which predict the adaptive responses of egg (and hatchling) size to selection for competitive ability (Section 6.5), and to selection for resistance to desiccation stress (Section 6.6), respectively.

6.5. EFFECTS OF CROWDING AND COMPETITION ON EGG SIZE

6.5.1. Introduction

It is, of course, impossible to perform a direct correlation between egg dry weight and hatchling weight. However, it has been shown that the dry weight of the egg correlates positively with the wet weight of the egg (P. de Souza

Santos jr., unpublished) and the egg wet weight correlates positively with hatchling weight (R. Wall, unpublished data). A number of hypotheses predicting how hatchling size should differ in different environments will therefore be tested against the data on egg size variation. The first of these hypotheses is the effect of crowding amongst young grasshoppers. It assumes that large hatchlings are better competitors than smaller ones and that in crowded environments large hatchlings are selected for. These assumptions form part of the theory which predicts the effects of r- and K-selection on life-histories (Pianka, 1970).

The relative densities of first instars of each species at the three sites were similar over the three years, and differences in the spatial distribution of potential oviposition areas were also consistent over the three years (Chapter 3 and pers. obs.). Therefore the hypothesis that differences in egg size among populations could be attributed, in part at least, to consistent differences in the degree of selection for competitive ability between the sites was not immediately invalidated.

In this section I present indices of competition with different assumptions and degrees of sophistication to show how potentially misleading the use of crude indices can be, and what, if selection for competitive ability is an important determinant of egg size variation between these populations, is most likely to be the nature of the competition.

Population census data collected in 1982 using randomly-located 1 m^2 sampling units, as described in Chapter 3, were used to calculate each of the indices (described below) expressing the crowding or competition experienced by first instars on the visit when their densities were at a maximum.

6.5.2. Crowding

1. The simplest measure of crowding is the mean density of first instars in the population. This index, which I have labelled **A1**, is the sum of the number of first instars of species **s** in each sample unit $(\sum \mathbf{x(i)_s})$ divided by the total number of sample units (**n**).

$$\text{Index } \mathbf{A1} = \sum_{j=1}^{j=n} \frac{(\mathbf{x(i)_s})_j}{\mathbf{n}} = \frac{\text{total no. of first instars of sp. } \mathbf{s}}{\text{total no. of sample units}}$$

The total density can be regarded as an index of the competition for space, since the measurement incorporates the total number of competitors divided by the amount of space from which they were collected.

2. However, the actual crowding experienced by the first instars is also dependent on their spatial distribution. Hatchlings are usually highly aggregated (Bradley, 1975; Davis and Wadley, 1949; Putnam and Shklov, 1956; pers. obs.) because eggs are laid in clutches rather than singly and because potential oviposition areas (e.g. patches of sand) are not uniformally distributed in space (Davis and Wadley, 1949; Chapter 2). Because of this aggregation, the number of competitors likely to be encountered by a hatchling is best measured using a sample unit which is the same size as, or smaller than, the range over which the hatchlings move. The number of competitors encountered, on average, by a first instar per square metre of ground is therefore more likely to reflect the intensity of competition than is the average number of first instars for the whole site. An index of such local crowding (**A2**) can therefore be calculated as the number of first instar conspecifics experienced in a m^2 sample unit on average by a first instar, thus:

$$A2 = \sum_{j=1}^{j=n_{is}} \left(\frac{x(i)_s^{2}}{x(i)_s}\right)_j = \frac{\text{total no. of first instar conspecifics encountered by each first instar of sp. s.}}{\text{total no. of first instars of sp s}}$$

where $x(i)_s$ = no. of first instars of species s in a 1 m^2 sample unit

n_{is} = no. of sample units containing first instars of species s.

The added realism gained by producing an index of local crowding rather than a measure of total density will depend on how free the hatchlings are to avoid the crowded areas. If they are highly motile and capable of rapidly finding suitable areas of ground - with the appropriate microhabitat characters, and where competition is less severe - the advantages of calculating an index of local crowding will be negligible.

3. Because of the similarity in egg (and therefore hatchling) size and microhabitat of first instars of the two species (Tables 6.1 and 6.3; Richards and Waloff, 1954) the competition may be strongly inter- as well as intra-specific. A third index of crowding (A3) was therefore calculated:

$$A3 = \sum_{j=1}^{j=n_{is}} \left(\frac{x(i)_s \; x(i)}{x(i)_s}\right)_j$$

where $x(i)$ = the number of first instars (of both species) in a 1 m^2 sample unit.

4. Since grasshoppers of later instars also tend to feed on the food that first instars eat (Bernays and Chapman, 1970b) and since both species can be reared on the same grasses (pers. obs.), a fourth index of crowding was calculated which treats all grasshoppers irrespective of species or instar as potential competitors with a first instar of a species s, thus,

$$\mathbf{A4} = \sum_{j=1} \left(\frac{x(i)_s - x}{x(i)_s} \right)_j$$

where x = the number of grasshoppers (of all instars and both species) in a 1 m^2 sample unit.

None of the indices of crowding **A1-4** show any effect of overall density (**A1**) or local crowding (**A2-4**) on egg size (Fig. 6.3, Table 6.10).

6.5.3. Limitation by food availability - grass

Competition should not be dismissed as an ineffectual cause of life-history variation among populations just because there appears to be no correlation between a trait and population density. The density should be measured per unit of limiting resource. Food is the most obvious resource which is likely to be in short supply for the hatchlings.

Mulkern *et al.* (1964), Bernays and Chapman (1970b) and Monk (1981) found that grasshoppers eat a wide variety of grasses but rarely forbs (non-graminaceous herbs). The sites had different amounts of grass (Chapter 2) and therefore indices of competition should take this into account (see also Chapters 3 and 4). The percentage cover of leaves of all grass species at each site, estimated in June 1983 using the point-intercept method (Chapter 2; Mueller-Dombois and Ellenburg, 1974) was used as a measure of the abundance of grass since leaves of a grass species were rarely touched more than once by the pin in a particular location. These measures of abundance were summed for grass blades of all species. Each of the crowding indices **A1-4** for each population was divided by the measure of total grass abundance (grass percentage cover expressed as a fraction of 1) of the respective site and labelled **B1-4**.

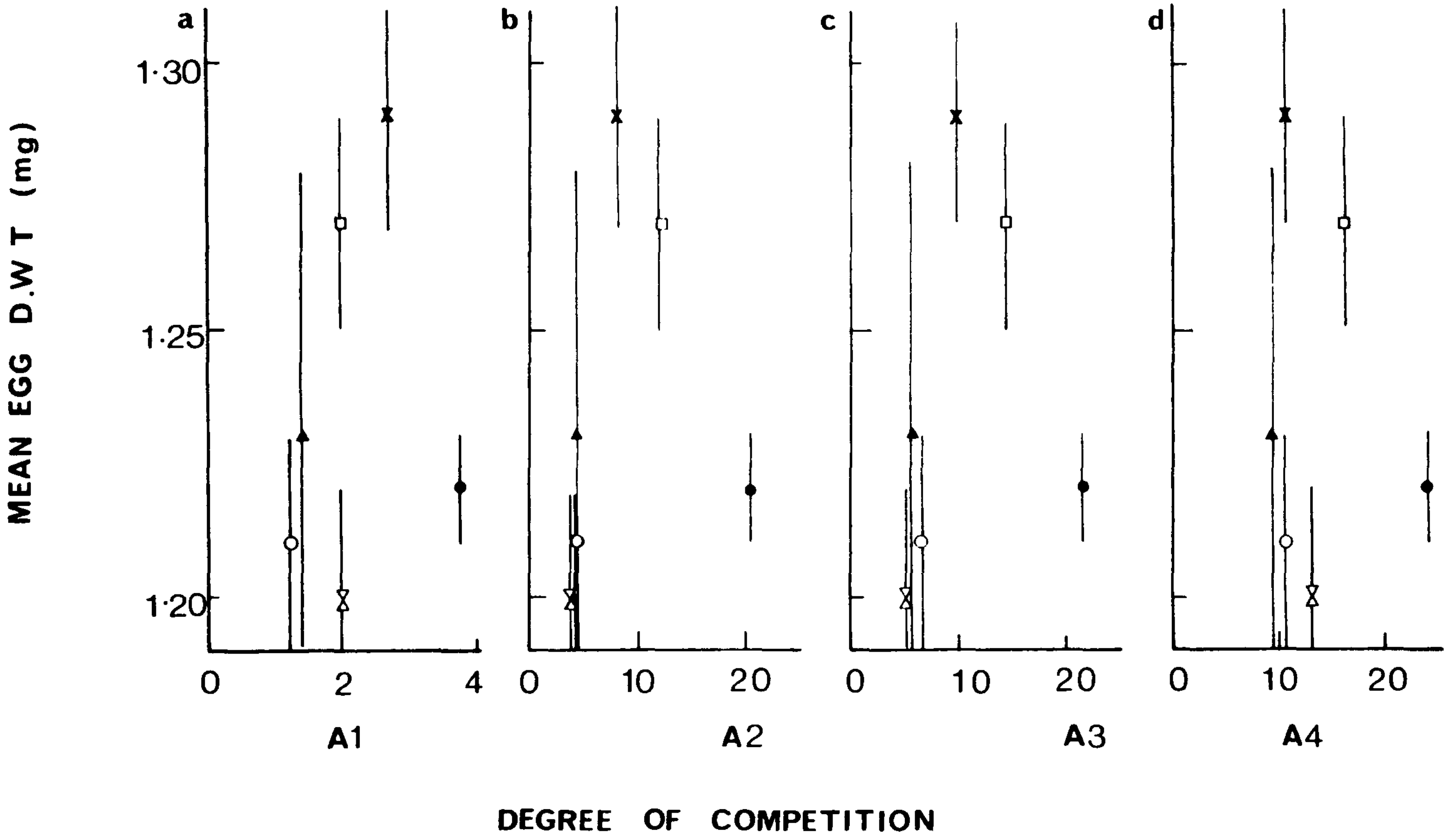
TABLE 6.10: **Twelve competition indices and their rank correlations with mean egg dry weight**

Competitors	Local/Overall Density?	Resources	Competition Index	r	p
All first instars	Overall	Space	A1	0.200	0.287
First instar conspecifics	Local	Space	A2	0.200	0.287
All first instars	Local	Space	A3	0.333	0.174
All grasshoppers	Local	Space	A4	-0.067	0.425
All first instars	Overall	Grass	B1	0.333	0.174
First instar conspecifics	Local	Grass	B2	0.467	0.094
All first instars	Local	Grass	B3	0.467	0.094
All grasshoppers	Local	Grass	B4	0.200	0.287
All first instars	Overall	Non-*Festuca* grass	C1	0.733	0.019
First instar conspecifics	Local	Non-*Festuca* grass	C2	0.867	0.007
All first instars	Local	Non-*Festuca* grass	C3	0.867	0.007
All grasshoppers	Local	Non-*Festuca* grass	C4	0.867	0.007

FIGURE 6.3: **Relationships between four measures of crowding and mean egg size**

See text for description of crowding indices **A1** to **A4**.

Bars represent 95% confidence limits


a
b
c
d
MEAN EGG D.W T (mg)
1·30
1·25
1·20
0
2
4
0
10
20
0
10
20
0
10
20
A1
A2
A3
A4
DEGREE OF COMPETITION

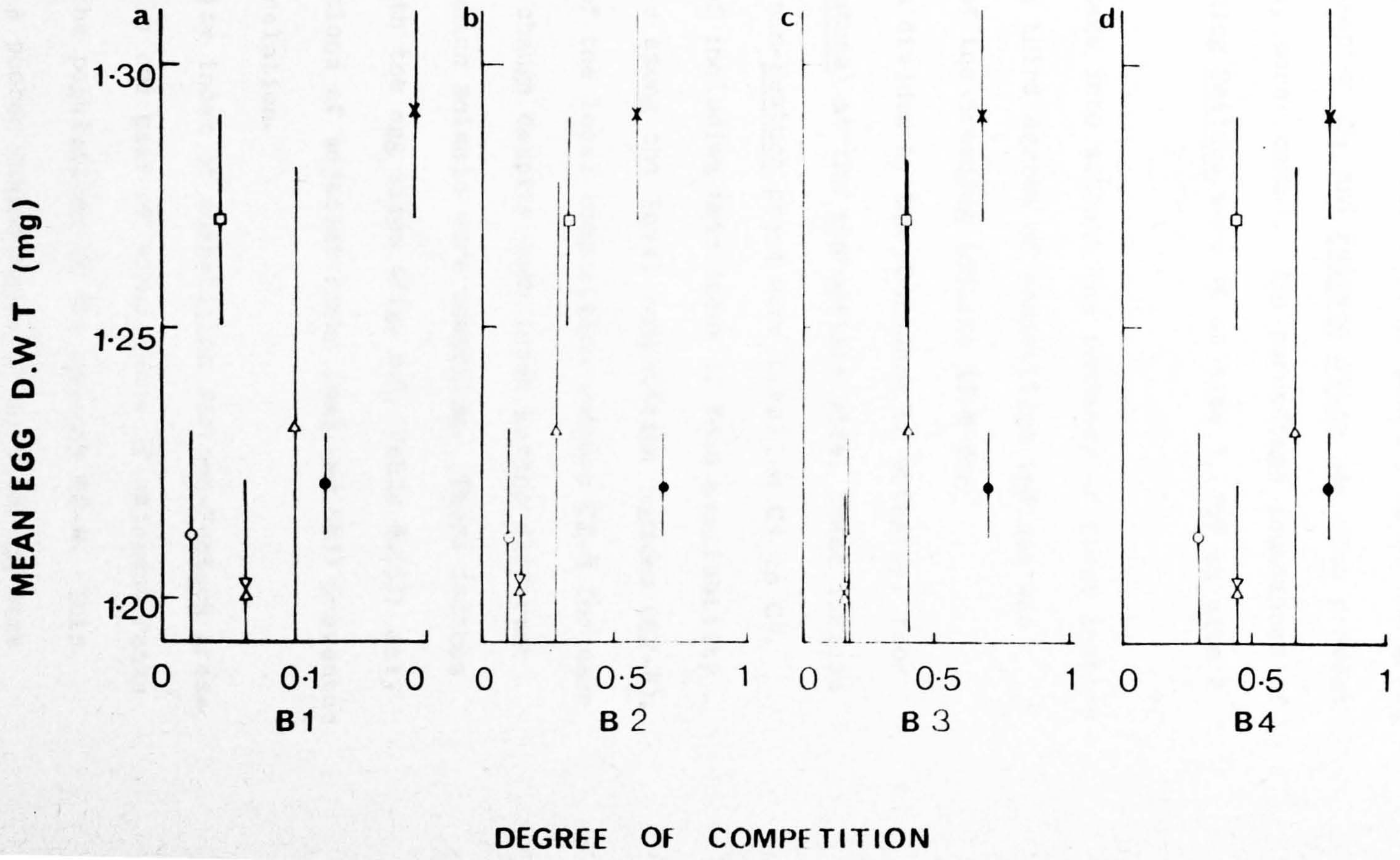
By considering the amount of grass leaves at each site (B1-4), populations at site 1 rose through the ranks (Fig. 6.4) because there was less grass there (14%; c.f. 30% at site 2, and 37% at site 3; Chapter 2). The rest of the sites were bare, or were covered in moss, grass flowers and leaf sheaths, and forbs (Chapter 2). However, none of these indices gave a significant rank correlation with egg size (Fig. 6.4, Table 6.10). Therefore, differences in the strength of selection for the ability to compete for space or grass do not seem to be a major cause of differences in egg sizes between sites (assuming that large offspring are better competitors).

6.5.4. The effect of natural diet restriction.

At first consideration, food would not appear to be limiting since the grass was not all eaten by the grasshoppers. Richards and Waloff (1954) also make this point. However, not all grass may be of equal value to feeding grasshoppers, as the study of the diet of first instar C.parallelus by Bernays and Chapman (1970a) showed. They found that first instars tended to avoid Festuca rubra which has rolled leaves and therefore does not present a leaf edge thin enough for the small first instars to bite into. They found that F.rubra was not rejected by the young hoppers when the leaves were unrolled. Monk (1981) and Young (1979) also found that C.brunneus tended to feed less on Festuca than would be expected if the grashopper were unselective. Therefore, a measure of food abundance should take into account the diet restrictions imposed on the animals. A similar point was made by Dempster and Pollard (1981) in a different context. They said that density-dependent resource limitation of insect numbers may go undetected unless the

FIGURE 6.4:
(See text for description of competition indices) Bars represent 95 perc. confidence limits

RELATIONSHIPS BETWEEN FOUR MEASURES OF COMPETITION FOR GRASS AND MEAN EGG SIZE



resource is identified and measured. White (1978) commented that ecologists frequently underestimate the variation in food quality and the inability of animals to exploit the food supply efficiently.

Festuca rubra accounted for a large proportion of the grass at sites 1 and 3 (Chapter 2), and Festuca ovina was also present at site 3 (K. Payne, pers. comm.). The percentage abundances of grass blades excluding Festuca were 4% at site 1, 25% at site 2 and 14% at site 3.

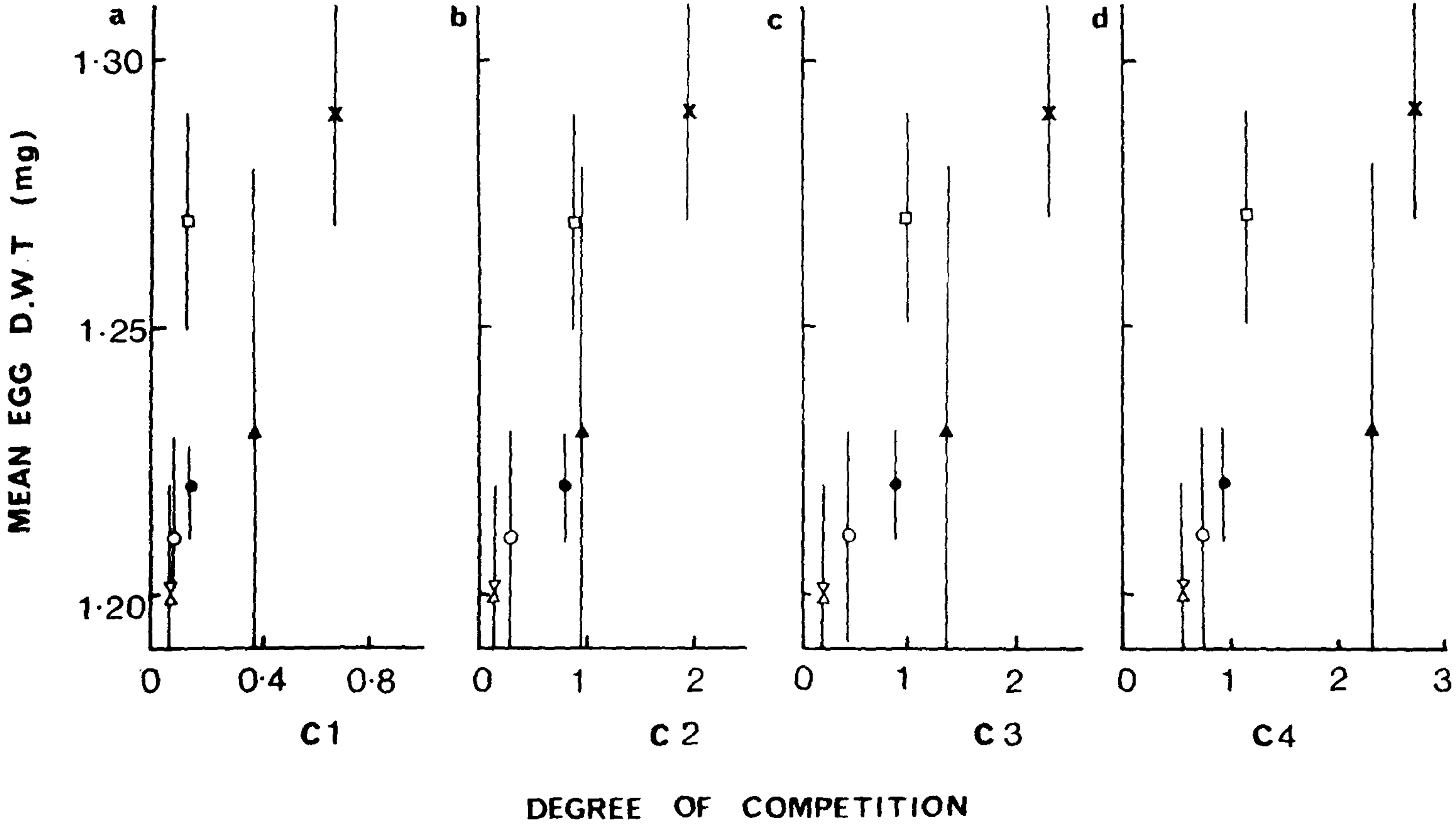
In order to take into account the tendency of first instars to avoid Festuca, a third series of competition indices was calculated. Each of the crowding indices **A1-4** for each population was divided by the abundance of potential food (grass leaves - Festuca) at the appropriate site. These indices of competition for non-Festuca grass were labelled **C1** to **C4**.

The effect of including this index of food availability was to fix the ranks among the local competition indices (**C2-4**). That is, the rank of the local competition indices **C2-4** for each population did not change despite each index having different assumptions about which animals were competing. These indices correlated well with the egg sizes (Fig. 6.5, Table 6.10): only one pair of populations of adjacent ranks (Mm3 and Cb1) prevented a perfect rank correlation.

The simple density index of competition for non-Festuca grass (**C1**) differed by only one pair of populations of adjacent ranks from the ranks of the populations in the indices **C2-4**. This difference gave **C1** a poorer ranked correlation with egg size (Table 6.10). Therefore, if differences in selection for size-related competitive ability are operating on the hatchlings among the six populations, the competition is better expressed on a

FIGURE 6.5: (See text for description of competition indices) Bars represent 95 perc. confidence limits.

RELATIONSHIPS BETWEEN FOUR MEASURES OF COMPETITION FOR NON - <u>FESTUCA</u> GRASS AND MEAN EGG SIZE



local scale than a general one, and the limiting resource is more likely to be non-Festuca grass than total grass or space.

6.5.5. Why should large hatchlings be better competitors?

Capinera (1979) states that insects from large eggs are generally more mobile, suffer less mortality early in life, develop faster, and have fewer instars. This, he says, is especially true for the western tent caterpillar (Malacosoma californicum pluviale), the gypsy moth (Lymantria dispar), and the migratory locust (Locusta migratoria) which have been most studied in this regard.

If there is strong competition for thin-edged grass leaves, large hatchlings may not be selected solely for their ability to compete directly for this grass but may also result from selection for the ability to eat some of the thicker-edged, rolled leaves. Implicit in this reasoning is that large hatchlings can eat larger food items. Patterson (1983) mentions the close correlations between grasshopper body size and mandible size.

Larger hatchlings may be better competitors not only because of an ability to disturb the feeding of others whilst being less affected by the presence of smaller competitors, but also, if they are more motile, because they will be better able to find the food first. Therefore, the proximity of food to the hatching site may also be an important determinant of hatchling size, as well as the overall amount of thin-edged grass leaves at a site. Ideally, therefore, more complex indices of competition than those calculated in this study should be produced which incorporate the spatial distribution not only of competitors but also of the food in relation to the competitors.

Because site 1 had the largest areas of bare sand (Chapter 2), oviposition sites were more likely to be further away from food, or from clumps of vegetation providing a wide range of microclimates from which the grasshoppers could choose (Ruscoe, 1970). If larger hatchlings were more motile, these patches of vegetation might be found sooner. There may (as I discuss in Chapter 4) be no differences in selection for competitive ability if the animals are sufficiently motile to be able to find underexploited patches of resources.

Also, larger hatchlings may be heavier because they have more energy reserves from the yolk and therefore are better able to withstand the effects of food shortage. However, Blackith and Howden (1961) found that although the fat content of hatchlings of Locusta varied from 0 to 14.14%, individuals which were almost without any fat on eclosion survived as well as those with high fat content, though fat was undoubtedly depleted during starvation. Larger eggs of the western tent caterpillar and the gypsy moth contain more yolk, and the amount of which can be modified environmentally (Wellington and Maelzer, 1967; Capinera et al., 1977). The period of food shortage will be longer when suitable food is difficult to find. Thus, there are several mechanisms by which larger hatchlings are potentially better able to survive under conditions of food shortage or when food is further away from the hatching site. To distinguish between the potential advantages of being a large hatchling, a number of manipulations of resource abundance and distribution could be performed, and the fate of different-sized hatchlings followed.

6.5.6. The nature of phenotypic reponses to density in other arthropods

The idea that insects produce larger offspring when their juveniles experience more severe competition is supported by the comparison between Blaesoxipha fletcheri and other sarcophagid flies in Forsyth and Robertson's (1975) study. The larvae of B.fletcheri, which are larger than those of the eleven other sarcophagid species they examined, experienced very intense density-dependent mortality compared to the others. Heavier hatchlings are also produced by each of three species of locust when they are reared under conditions of high density (Uvarov, 1966). This non-genetic effect of crowding on hatchling size can be thought of as being "strategic," rather than as a direct effect of a shortage of resources, because the hatchlings are larger when the amount of resources the parent is likely to be receiving is reduced. Therefore, the information the locusts use to regulate hatchling size overrides any constraints on it imposed by a shortage of resources (see Appendix to thesis).

For phenotypic plasticity in egg size to be adaptive, the environmental conditions experienced in one season by female grasshoppers would have had to have provided some indication of the relationship between egg or hatchling size and fitness over the winter period or in the next breeding season (or both), and the females would have had to have been able to perceive and respond to the appropriate information (Appendix to thesis).

The African migratory locust, Locusta migratoria migratorioides exhibits adaptive plastic phenotypic responses which are transmitted from parent to offspring over three generations (Albrecht, 1973). This insect often experiences four generations per year, two under increasing photoperiod and two under decreasing photoperiod. Each generation experiences different conditions of temperature and humidity, and photoperiod acts as a stimulus, adjusting the physiology of the insect in advance to the seasonal changes. British grasshoppers, with one generation per year, do not experience a succession of conditions which are highly predictable from previous generations, and therefore adaptive phenotypic plasticity is less likely to be an important determinant of egg size variation than in the African migratory locust.

The terrestrial isopod, Armadillidium vulgare, produces larger offspring when the female is provided with less food (Brody and Lawlor, 1984). Because it is viviparous - giving birth, rather than laying eggs which hatch some time after the mother has died, as the British grasshoppers do - the variations in the environment into which the offspring are born will be more predictable to the adult A.vulgare than the conditions that the grasshopper hatchlings encounter will be to their mother. Thus, adaptive phenotypic plasticity in offspring size is more likely to be found in A.vulgare than in C.brunneus or M.maculatus.

The significant changes in mean egg dry weight between 1981 and 1982 in M.maculatus from the field enclosure (Table 6.3), and the correlation in this species between adult female hind femur length and mean egg dry weight (Fig. 6.1, Table 6.6) suggest that egg size variation in M.maculatus has a strong environmental component. Circumstantial evidence supported the idea that the variation in adult female hind femur length had a large environmental component (Chapter 4), and the evidence for an environmental effect on egg size is also circumstantial. It is conceivable, for example, that significant changes in egg size between years could have resulted from a change in gene frequency over one generation, rather than from an immediate effect of the environment on the phenotype. A reciprocal transplantation experiment would be necessary to quantify the environmental and genetic components of mean egg dry weight.

6.5.7. Keeping and discarding hypotheses

So far, the variation in mean egg dry weight between species and among sites has been found to correlate significantly with the potential for selection on the ability of hatchlings to compete for thin-edged grass leaves (assuming that the severity of competition depends on the degree of aggregation of first instars; indices **C2-4**). The hypotheses represented by indices **C2** to **C4** should not therefore be eliminated.

However, we can, at this stage, tentatively discard those hypotheses stating that selection for hatchling competitive ability is the main determinant of differences in mean egg dry weight, if they assume that competition is unaffected by the degree of aggregation of first instars, or if the limiting resources are space or all grass species at a site (i.e. hypotheses represented by competition indices **A1-4**, **B1-4**, and **C1**).

Other selection pressures may also affect egg or hatchling size. The relationship between egg size and the degree of desiccation at the sites will next be examined.

6.6. EFFECTS OF A DESICCATING ENVIRONMENT ON EGG SIZE

6.6.1. Why should large eggs be better protected?

Large bodies have smaller surface area-to-volume ratios than smaller bodies of the same shape, because an increase in length is associated with only a quadratic increase in area but the corresponding increase in volume is cubic. Consequently, a large body size should be favoured in dry and desiccating conditions because of the relatively smaller surface area through which water can be lost.

6.6.2. Measuring the relative risks of desiccation

During two series of experiments in May and June 1983, daily rates of water loss were measured directly from evaporation tanks randomly positioned at the three sites (Chapter 2). The mean daily evaporation rates at the three sites, weighted according to the distribution of first instars (see below, and the Appendix to this chapter), were compared using Wilcoxon Matched-Pairs, Signed-Ranks Tests.

The unweighted measures provided a comparison of the relative amounts of desiccation stress likely to be experienced by organisms on the ground distributed randomly in space at the three sites. However, it is evident that first instars are in fact highly aggregated, being associated particularly with sparse vegetation (Lensink,1963). Also, young hoppers of the two species are distributed differently in space; those of C.brunneus tend to be relatively more abundant (than those of M.maculatus) in taller vegetation (Appendix to this chapter, and pers. obs.) which is a less desiccating microenvironment (Ruscoe, 1970). Therefore, the hatchlings of the two species are likely to have experienced different microclimatic conditions, and conditions which were not simply site averages but were those associated with particular vegetation types. By taking into account the different distributions of first-instar grasshoppers of the two species, therefore, a comparison of the relative desiccation risks experienced by the two species can be made at each site. This would also make the comparison between desiccation risks experienced by young nymphs of the same species at the different sites more realistic. Information on the distribution of first instars in the different vegetation types was collected as I describe below.

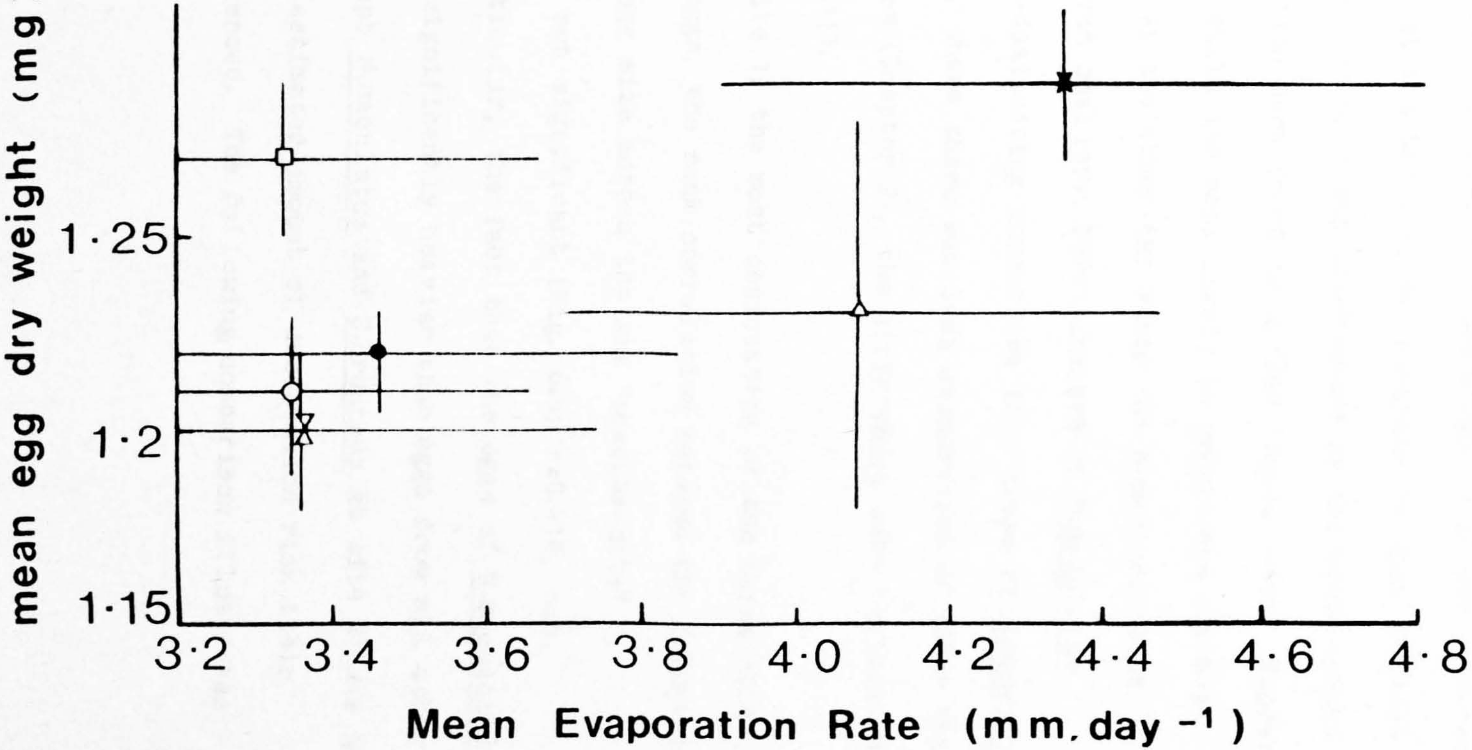
In 1981 and 1982, stage-frequency data were collected from each of the three sites using counts from randomly-located 1 m^2 sample units (Chapter 3). At the same time, the structure of the vegetation or "vegetation type", (sensu Lensink, 1963; see also Chapter 2) in each sample unit was noted. Thus the numbers of each instar of each species associated with each of the vegetation types from **I** (very sparse) to **VI** (tall, dense vegetation) were obtained. Data from the visits in which the peak number of first instars of each species was observed were used to describe their relative associations with different vegetation types. The data from both years were pooled and used to weight the evaporation rate measures according to the vegetation type in which each tank was located (Appendix to this chapter). The relative risks of desiccation to first instars in each population was then compared with the mean egg sizes of these populations (Fig. 6.6).

6.6.3. Differences in microclimate experienced by first instars

Evaporation rates were greater at site 1 than at site 2 which was more desiccating (but not significantly) than site 3 (Chapter 2). Evaporation is less amongst thick grass swards than over bare ground (Ruscoe, 1970). First-instar grasshoppers of

FIGURE 6.6: Relationships between mean evaporation rate and mean egg dry weight.

Kendall's rank correl. $r = 0{\cdot}414$
$n = 6$
$p = 0{\cdot}126$



both species, but especially M.maculatus (Appendix to this chapter) were more abundant in sparse vegetation than in dense vegetation at the three sites. Having taken into account the relative abundance of first-instar grasshoppers in the different vegetation types at the three sites (Appendix to this chapter) the relative desiccation risks experienced by the young nymphs from each population were found to differ (Table 6.11). Hoppers from site 1 were still the most likely to experience the most desiccation, but at the other two sites the non-significant difference was even smaller. First instars of M.maculatus experienced more-desiccating conditions than those of C.brunneus, though at site 3, where there was less evaporation of water than at the other sites (Chapter 2), the differences were reversed but slight (Table 6.11).

Although site 1, the most desiccating of the three sites, had the largest eggs, the rank correlation between the degree of desiccation and egg size across the six "species-site" combinations was not significant (Fig. 6.6; r=0.414, n=6, p=0.126). In particular, the fact that the eggs of M.maculatus from site 3 were significantly heavier than eggs from all other populations (except M.maculatus and C.brunneus at site 1) was not explained by the estimated amount of desiccation risk their hatchlings experienced. The following comparison illustrates this point:

TABLE 6.11: **Estimated mean evaporation rates from evaporation tanks in vegetation types where first instars of (a) M.maculatus and (b) C.brunneus were found at their peak densities**

Means were weighted by the relative abundance of the respective species in each vegetation type.

(a) M. maculatus

	Site 1			Site 2			Site 3		
Date	mean	range	n	mean	range	n	mean	range	n
29.5.83	4.10	2.94-6.38	5	2.15	1.61-2.76	8	1.78	1.20-2.51	8
2.6.83.	2.17	0.69-3.14	5	2.36	1.83-2.53	5	2.46	1.60-2.58	8
5.6.83.	3.38	2.22-3.93	6	2.75	2.16-3.22	7	2.76	1.95-2.95	8
6.6.83	7.51	4.72-8.60	6	5.91	4.80-6.94	8	5.93	3.48-6.06	8
8.6.83.	4.35	2.86-5.38	6	3.22	2.72-3.55	8	3.46	2.20-3.69	8
9.6.83.	2.96	2.30-3.46	6	1.49	1.08-1.84	8	2.95	2.11-3.27	8
16.6.83.	1.88	1.17-2.65	6	1.01	0.80-1.22	3	1.01	0.21-1.61	8
18.6.83.	4.61	3.20-5.98	6	3.55	2.62-3.73	4	3.14	2.30-4.57	7
19.6.83.	5.56	4.26-6.10	6	4.72	4.20-4.98	7	4.79	2.88-5.54	8
20.6.83.	6.61	5.00-7.62	6	5.92	4.84-6.84	7	5.14	3.60-6.80	8
	GM	± 95% CL	n	GM	± 95% CL	n	GM	± 95% CL	n
	4.35	0.45	58	3.46	0.39	65	3.34	0.33	79

(b) C.brunneus

Date	Site 1			Site 2			Site 3		
	mean	range	n	mean	range	n	mean	range	n
29.5.83.	3.72	1.62-6.38	7	2.15	1.61-2.76	8	1.79	1.20-2.51	8
2.6.83.	1.95	0.69-3.14	7	2.17	1.83-2.53	5	2.45	1.60-2.58	8
5.6.83.	3.00	1.84-3.93	8	2.62	2.16-3.22	7	2.73	1.95-2.95	8
6.6.83.	6.76	4.52-8.60	8	5.54	4.80-6.94	8	5.90	3.48-6.06	8
8.6.83.	4.04	2.70-5.38	8	3.17	2.72-3.55	8	3.41	2.20-3.69	8
9.6.83.	2.86	2.30-3.46	8	1.39	1.08-1.84	8	2.90	2.11-3.27	8
16.6.83.	1.77	1.17-2.65	7	1.02	0.80-1.22	3	1.08	0.21-1.61	8
18.6.83.	4.54	3.20-5.98	7	3.54	2.62-3.73	4	3.29	2.30-4.57	7
19.6.83.	5.41	4.54-6.10	7	4.72	4.20-4.98	7	4.83	2.88-5.54	8
20.6.83.	6.65	5.54-7.62	7	5.86	4.84-6.84	7	5.09	3.60-6.80	8
	GM	± 95% CL	n	GM	± 95% CL	n	GM	± 95% CL	n
	4.08	0.39	74	3.36	0.39	65	3.35	0.31	79

Egg size (This comparison, described in Section 6.3.1.2, is repeated here for ease of comparison)

Largest Smallest

Mm1 Mm3 Cb1 Mm2 Cb3 Cb2

Estimated desiccation risk

Highest Lowest

Mm1 Cb1 Mm2 Cb2 Cb3 Mm3

A common underlining joins together populations which do not show significant differences (SNK multiple range test, $p_{crit} = 0.05$, for egg size; Wilcoxon Matched-Pairs, Signed-Ranks tests, $p_{crit} = 0.01$, for degree of desiccation).

Although site 1 lost more water per day due to evaporation and had the largest eggs of each species, the rank correlation between mean egg size and mean evaporation rate was poorer than that obtained for competition for non-*Festuca* grass. This indicates that differences in strengths of selection for competitive ability accounted better for the egg size variation observed among all six populations, though it cannot be ruled out that selection for the ability to withstand evaporative water loss might be particularly important in explaining why eggs from the more desiccating habitat of site 1 were larger than those from the other sites.

The two hypotheses may, however, be closely linked if, as Ranwell (1972) noted, rolled leaves, as found in marram, *Ammophila arenaria*, (and also in *Festuca*) tend to be relatively more abundant in more xeric conditions. Water loss is reduced by having rolled leaves because the area of exposed leaf surface area is reduced, and, in *Ammophila* at least, the stomata are mainly on the inside of the tubular leaf. Thus the larger eggs laid by both species at site 1 may not be due to any direct selection pressure on offspring size by desiccation stress but may be a consequence of the effects of desiccation stress on grass structure or species-composition resulting in more severe competition for thin-edged grass leaves.

A recent study by Monk (1985) describes significant differences in hatchling size among populations of <u>C.brunneus</u> and <u>C.parallelus</u>. She suggests that the larger eggs were produced where conditions for embryonic development were harsher. This too would be a density-independent cause of a typical "K-selected" character.

Egg (or hatchling) size is only one of the traits which may be altered by a particular selective regime. Some environmental differences, such as those described by the theory of r- and K-selection (MacArthur and Wilson, 1967; Pianka, 1970), are expected to produce phenotypic variation in a number of traits which together are co-adapted to solve particular ecological problems. That is, tactical variation would be expected (Stearns, 1976). This idea is considered in the next section.

6.7. IS THE VARIATION IN EACH COVARYING TRAIT INDEPENDENTLY ADAPTIVE ?

This hypothesis considers not only the adaptive variation in egg size, but also whether it covaries with another trait which itself shows adaptive variation. Three covariates of egg size will be considered - maternal body size, egg pod size, and the number of eggs per clutch.

6.7.1. <u>Maternal size</u>

6.7.1.1. <u>K-selection</u>

Larger <u>M.maculatus</u> (but not <u>C.brunneus</u>) adult females laid heavier eggs (Table 6.6, Figs. 6.1 and 6.2), so it is conceivable that this covariation represents a tactic adopted by M.maculatus.

The theory of r- and K-selection predicts a suite of life-history traits including a positive correlation between adult size and offspring size (Pianka, 1970). Pianka predicted that K-selection would favour larger adults and offspring, since larger organisms should, he assumed, be better competitors.

However, although egg size correlated with indices of hatchling competition (Table 6.10), adult size did not correlate with estimates of adult competition (Chapter 4). The theory of r- and K-selection is not able, therefore, to explain the covariation in M.maculatus. This conclusion brings out the assumption, which is implicit in the r-K scheme, that the theory only applies to organisms which experience differences in competition that are consistent for both the adult and the juvenile stages of the life history.

6.7.1.2. Desiccation risk

Under conditions of high desiccation risk, large hatchlings and adults should both be favoured by natural selection. Site 1 had the most desiccating conditions (Chapter 2, Table 6.11) and the largest eggs of M.maculatus (Table 6.1) but not the largest adults (Fig. 6.1, Chapter 4). Also, the eggs and adults at site 2 were significantly smaller than at site 3 but were, if anything, subject to higher desiccation risks (Section 6.6.2, Chapter 4).

The covariation between maternal size and egg size in M.maculatus is unlikely, therefore, to be a tactical response to K-selection or desiccation stress.

6.7.2. Egg pod size

The association of heavier eggs of M.maculatus (but not of C.brunneus) with heavier egg pods (Table 6.6) may also, in principle, represent adaptive variation in each trait. This possibility exists, despite the fact that there is clearly some autocorrelation contained in the relationship between the two traits, because it is still logically possible that the adult could vary only the amount of matrix or the number of eggs in a pod when a different-sized pod is produced.

The relationship observed in M.maculatus was probably a consequence of larger females laying larger eggs and pods, because the effect of egg size on pod size disappeared when the more important effect of adult mature weight was removed (Table 6.5). If both covariates were adaptive (and responded to the pressures examined in this study), the relatively lower estimated levels of competition for food (non-Festuca grass) experienced by hatchlings at site 2 (Fig. 6.5) - the site from which both eggs and egg pods of M.maculatus were significantly smaller than at site 3 (Table 6.1) - would also be associated with conditions favouring small egg pods. The latter might be selected for if risks of size-dependent physical damage to egg pods were low.

6.7.2.1. Physical damage

Physical disturbance was likely to be relatively high at site 1, which had large areas of loose sand (Chapter 2). The sandy areas at sites 2 and 3 were small and no obvious difference in the likely disturbance to the oviposition sites was noticed between them.

Pod damage by physical causes may be reduced if a thicker layer of pod matrix surrounded the eggs. Perron and Corpuz (1982) found that large egg capsules of the neogastropod, Conus pennaceus were both thicker and stronger than small ones. However, as capsules become larger their surface area to volume ratios decline. These authors therefore suggested that because of this reduction in relative surface area and because thicker membranes are less permeable to gases (Giese, 1973) net gas transport (O_2 and CO_2) per unit of capsule contents would be reduced in larger capsules. The influence of the thickness of the grasshoppers' egg pod matrix on the survival of eggs has not, to my knowledge, been studied.

Small egg pods might also be selected for if the laying of many pods per lifetime, rather than a few, was favoured by natural selection (increased iteroparity).

6.7.2.1. Selection for iteroparity

This hypothesis will only be valid if time and material resources are limited and if the material resources must be partitioned between present and future reproduction. In other words, the highly iteroparous organism puts relatively less material resources into each egg pod, and in so doing incurs a lower cost (in terms of reduced RRV), thus allowing the production of more pods per lifetime of limited duration.

It is noteworthy that if more resources are available to animals living in a time-limited or seasonal habitat which experience selection favouring increased iteroparity, they might be able to produce not only egg pods at a faster rate but also larger ones. In such a case, environmental stress would override the genetic trade-off - a phenomenon also discussed in Chapter 5.

Smaller pods will be produced under conditions in which resources are limiting and in which increasing iteroparity is favoured only if the habitat is seasonal (time-limited). If there were no time-limitation, iteroparous animals could reproduce at the same rate as more semelparous ones and therefore produce the same-sized pods, but they would do so at the expense of extending their period of reproduction. Thus, the hypothesis that selection for iteroparity leads to the production of smaller pods could be nullified if there were differences in the amount of material resources or in the time available for reproduction.

One possible cause of iteroparity, which is relevant to the grasshoppers in this study, is that an increased probability of total reproductive failure per attempt will select for iteroparity. This explanation can only apply if the reproductive failure is independent of pod size.

Parasitoids may destroy whole clutches of eggs (Richards and Waloff, 1954), but whether they are important causes of total failure of egg survival in a pod at the three sites, and whether their effect would be dependent on pod size, are not known.

6.7.3. Number of eggs per clutch

The only significant correlation between egg size and number was a negative one in the pods of C.brunneus from site 2 (Table 6.8). The site which had the largest eggs of C.brunneus (site 1) had the smallest number of eggs per clutch and the site with the smallest eggs (site 2) had the largest numbers per clutch, but the differences in both egg size and number among sites were not significant. Other negative relationships were revealed, however, when the effects of mature body weight were removed (Table 6.9). A negative relationship probably represents a trade-off rather than a case of the variation in each trait being adaptive independently of the other. This is because it is difficult to imagine why a grasshopper should freely lay fewer eggs without this resulting from a compromise.

To conclude the discussion on independently-adaptive variation in each of a pair of covarying traits; there is no evidence to indicate that most of the variation in egg size among populations of M.maculatus is freely co-adapted with maternal size or egg pod size. (i.e. Egg size and its covariate - maternal size or egg pod size - do not each show adaptive variation independently of the variation in other traits). Nor is there evidence for independently adaptive variation when the covariation is between egg size and number per clutch in C.brunneus.

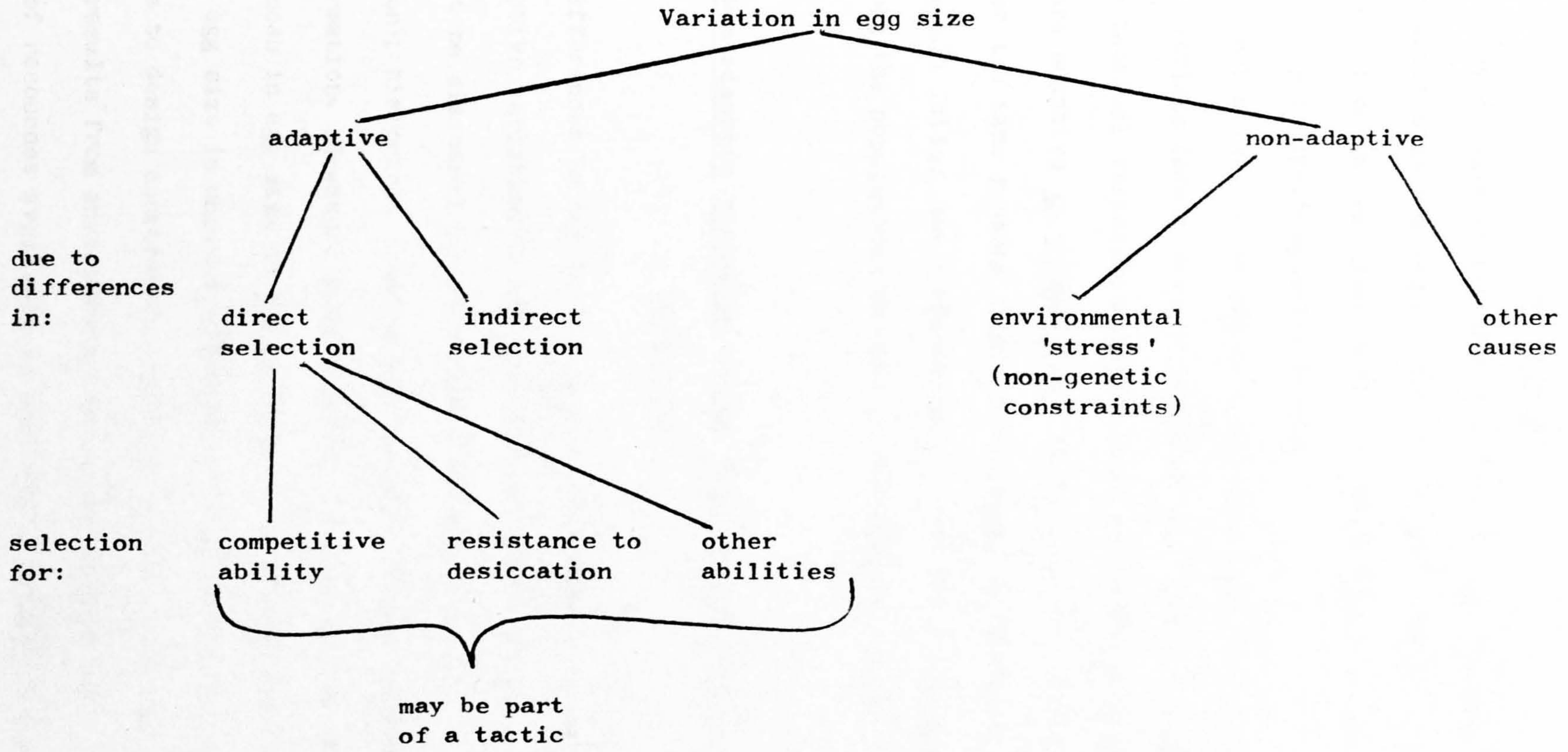
6.8. ALTERNATIVE HYPOTHESES

6.8.1. The range of alternatives

Scientific knowledge grows by the elimination of hypotheses which are incorrect (Popper, 1959; Peters, 1983). It is therefore useful to discuss the merits of, and eliminate, as many existing alternative explanations for a particular relationship as possible. Figure 6.7 shows the types of alternative hypothesis that could predict phenotypic differences in egg size.

Some potential influences on variation in egg size have not been considered in this study and therefore cannot yet be eliminated from the list of possible causes. These include most causes of phenotypic variation which appears to be non-adaptive (Chapter 1), and differences in selection pressures besides those for the ability of hatchlings to compete or withstand the effects of a desiccating environment. In this section I briefly examine the possibilities that differences in egg size results from differences in the strength of selection on some other trait

FIGURE 6.7: Variation in egg size: partitioned into the components examined in this chapter.



(indirect selection, Chapter 1), or from differences in constraints imposed by the environment (or by development) on the mothers.

6.8.2. Indirect selection

This hypothesis states that the covariation between egg size and adult size and egg pod size is largely the result of direct selection on the other traits to which egg size is unavoidably and physiologically linked.

Indirect selection on egg size requires that the variation in the covariate (adult size or egg pod size) is adaptive *in itself* (whereas tactical variation requires that differences in *both* traits are adaptive *in themselves*). The hypothesis therefore fails for the same reasons that the "tactical hypothesis" (Section 6.7) fails: the differences in adult size and egg pod size among the populations do not, in themselves, appear to be adaptive.

6.8.3. Non-adaptive variation in egg size: a conflicting hypothesis

Differences in the following potential causes of apparently non-adaptive variation in egg size have not been studied, and will not be discussed further: random effects (neutral variation); historical constraints; genetic disequilibrium; misinformation. However, there remains the possibility that differences in egg size in *M.maculatus* are produced simply because egg size is unavoidably associated with maternal body size due to design constraints, and that variation in the latter mainly results from environmentally-induced differences in the amount of resources available to the female (Chapters 4 and 5).

The background to this hypothesis is as follows:

Larger adult M.maculatus emerged earlier in the season than smaller ones (Chapter 4), as had been found in laboratory-reared C.brunneus in which good competitors emerged both earlier and at a larger size than poor competitors (R. Wall, unpublished). Also, since adult size did not correlate positively with the estimated degree of competition or with desiccation stress (Chapter 4) and because there was some evidence that the variation was probably largely due to environmental causes, I concluded that the most likely cause of the variation in adult size (of the ones I investigated) was the differences in the amount of resources available to the growing nymphs (external non-genetic constraints, Appendix to the thesis). Egg size, if it is unavoidably associated with body size due to design constraints, may vary, therefore, because different grasshoppers had assimilated different amounts of resources during their juvenile life.

The results of this chapter and of Chapter 4, therefore, suggest two conflicting hypotheses which can explain the covariation in M.maculatus between adult size and egg size among sites and years. The first is that direct selection for hatchling competitive ability (or possibly for resistance to desiccation) produced most of the variation in egg size, and this is unavoidably associated with adult size due to design constraints, so that adult size can be said to be selected for indirectly. That is, the only way a grasshopper can produce large eggs is by becoming a large adult. The second hypothesis states that differences in adult size among the populations are caused mainly by differences in the effects of constraints imposed by the environment (Chapters 4 and 5), and that egg size varies simply because it is unavoidably associated with maternal body size due to design constraints. Further work to quantify the relative sizes of the genetic and environmental components of the variation in egg size and adult size would be useful in order to start distinguishing between the hypotheses.

6.9. DO FEMALES HEDGE THEIR BETS?

So far, I have considered the variation in egg size among individual grasshoppers or between populations or species, but have ignored the variation in egg size produced by individual females. Intragenotypic variation can also have adaptive significance (Bradshaw, 1965; Capinera, 1979; Crump, 1981; Caswell, 1983; Kaplan and Cooper,1984), so in this final section I shall consider the variation in egg size within egg pods.

In variable environments in which the organisms are unable to predict future conditions and in which different phenotypes are favoured in different conditions, bet-hedging (Chapter 1) would be favoured by natural selection. That is, an organism should spread the risk by producing offspring with a range of phenotypes, thereby minimizing the variance in pay-off and the chances of extinction. This type of reasoning underlies a number of so-called bet-hedging or variance models of life-history evolution (e.g. Lacey _et al._ 1983, Rubenstein 1982).

If a female produces a wide range of egg sizes within a clutch as Crump (1981) found in tree frogs, this would indicate that insufficient egg material was available for a proportion of the eggs (a constraint), or that the female was hedging her bets by producing eggs with a range of phenotypes (an adaptation to unpredictiable environmental conditions), or both. Constraints

TABLE 6.12: A comparison of the relative amounts of within-clutch and between-clutch variation in egg dry weight using the Kruskal-Wallis Oneway ANOVA.

Species	Site	Number of eggs	Significance of between-clutch variation:	
			Chi^2	p
M.maculatus	1	104	79.20	< 0.001
	2	294	247.25	< 0.001
	3	165	117.31	< 0.001
C.brunneus	1	29	9.52	0.049
	2	96	69.35	< 0.001
	3	101	79.85	< 0.001

on the size of a proportion of the eggs could have a genetic basis if there were some inherited, non-adaptive asymmetry in the size of functional ovarioles or in the partitioning of yolk between them, for example, and non-genetic constraints on egg size would result from limitiation in the amount of resources used to produce the eggs. There is no evidence to support the former suggestion, and the latter cause of increased size variation, if egg size constancy were important, should only reduce the size of one egg. Therefore, it is likely that a large variance in egg sizes within a clutch indicates that the female is bet-hedging. However, in iteroparous organisms the converse - that a small variance in egg size within a clutch indicates that the female is not hedging her bets with respect to egg size - is not necessarily true because an iteroparous female potentially has the opportunity to vary egg size between clutches as well as within them (Kaplan and Cooper, 1984).

The egg size variation among clutches of unknown parentage of each species at each site was significantly greater than that observed within clutches (Table 6.12). However, in the laboratory, P. de Souza Santos jr. (unpublished) has found greater variation among the clutches of individual C.brunneus females than within clutches, and not significantly less variation than between different females. The grasshoppers may still, therefore, hedge their bets in response to unpredictable conditions experienced by eggs and hatchlings but by spreading the risk between clutches rather than among the eggs of a single clutch.

APPENDIX TO CHAPTER 6

The distribution of first-instar grasshoppers and evaporation tanks in relation to vegetation types

The numbers of first-instar grasshoppers in each vegetation type, counted on the days when the peak number of first instars of each respective species was recorded, were used in this analysis. Data from 1981 and 1982 have been pooled to provide a large sample size.

Evaporation tanks were randomly distributed at each site in each of two series of experiments and the vegetation type in which they were placed was noted.

Because the evaporation rates of water from different vegetation types differ - they tend to be greater in sparse vegetation such as vegetation type I (Lensink, 1963) - and because the two species of grasshopper were found in different proportions in the different vegetation types, the relative degrees of desiccation risk experienced by hatchlings of the two species could be estimated.

The evaporation rate datum for each evaporation tank could therefore be weighted for each species by the percentage of first instars found in the same vegetation type divided by the number of tanks placed in that vegetation type.

TABLE: The association between the abundance of first instars and vegetation type, and its use in the weighting of evaporation tank data.

* The weighting attached to each evaporation tank datum was adjusted according to the number of operational evaporation

tanks on any one day (on some days fewer tanks were operational due to disturbance by vandals), and all weightings were converted to whole numbers by multiplying by 12. Also, in order to avoid bias caused by the absence of evaporation tanks in vegetation types in which grasshoppers were abundant, the weighting was adjusted by equalizing the density of grasshoppers among adjacent vegetation types. For example, at site 1, 28% of first instars of M.maculatus occurred in vegetation type II but no evaporation tanks had been placed in this vegetation type for the first series of readings. The 28% was therefore divided equally among, and added to, the weightings for the adjacent vegetation types, I and III. The calculations for all weightings are shown in the table.

M.maculatus: SITE 1

Vegetation type	I	II	III	IV	V	VI
No. first instars	76	33	7	0	0	0
Percentage	66	28	6	0	0	0
Max. no. evaporation tanks (Series I)	4	0	2	2	0	0
*** Weighting to evap. tank. (I)**	30/4	-	20/2	0	-	-
Maximum no. evap. tanks (Series II)	4	2	0	1	1	0
*** Weighting to evap. tank. (II)**	66/4	31/2	-	6/2	0	0

SITE 2

No. first instars	62	96	64	3	0	0
Percentage	28	43	28	1	0	0
Maximum no. evap. tanks (Series I)	1	4	1	2	0	0
*** Weighting to evap. tank. (I)**	28/1	43/3	28/1	1/2	-	-

continued...

Maximum no. evap. tanks (Series II)	0	0	4	3	0	0
* Weighting to evap. tank. (II)	-	-	99/4	1/3	-	-
SITE 3						
No. first instars	63	19	37	12	5	3
Percentage	45	14	27	9	4	2
Maximum no. evap. tanks (Series I)	0	0	2	1	4	1
* Weighting to evap. tank. (I)	-	-	86/2	9/1	4/4	2/1
Maximum no. evap. tanks (Series II)	0	1	1	2	3	1
* Weighting to evap. tank. (II)	-	59/1	27/1	9/2	4/3	2/1
<u>C.brunneus</u>: SITE 1						
Vegetation type	I	II	III	IV	V	VI
No. first instars	25	22	16	6	0	0
Percentage	36	32	23	9	0	0
Maximum no. evap. tanks (Series I)	4	0	2	2	0	0
* Weighting to evap. tank. (I)	52/4	-	39/2	9/2	-	-
Maximum no. evap. tanks (Series II)	4	2	0	1	1	0
* Weighting to evap. tank. (II)	36/4	43/2	-	20/1	0	-
SITE 2						
No. first instars	2	65	33	11	1	0
Percentage	2	58	30	10	1	0
Maximum no. evap. tanks (Series I)	1	4	1	2	0	0
* Weighting to evap. tank. (I)	2/1	58/4	30/1	11/2	-	-

continued...

Maximum no. evap. tanks (Series II)	0	0	4	3	0	0
*** Weighting to evap. tank (II)**	-	-	90/4	11/3	-	-
No. first instars	15	19	36	20	9	1
Percentage	15	19	36	20	9	1
Maximum no. evap. tanks (Series I)	0	0	2	1	4	1
*** Weighting to evap. tank. (I)**	-	-	70/2	20/1	9/4	1
Maximum no. evap. tanks (Series II)	0	1	1	2	3	1
*** Weighting to evap. tank. (II)**	-	34/1	36/1	20/2	9/3	1/1

CHAPTER 7: **Conclusions and Prospects**

This study has found significant differences in life-history characteristics between populations which were less than 1.3km apart. By using the comparative method, the general aims of the project - to assess the relative importance of a wide range of potential causes of life-history variation, so that a number of hitherto reasonable explanations can be eliminated - have been fulfilled.

However, because a large number of correlates of life-history variation have been examined, and the number of populations studied was small, there are still a few likely explanations which remain, and which will have to be tested further using direct manipulative experiments. For example, egg size correlates with: (i) adult female size in M.maculatus (Chapter 6), which is probably influenced more by the immediate effects of hatching date and/or juvenile growth conditions than by differences in selection pressure on size-related competitive ability of the adults or their ability to resist desiccation (Chapters 4 and 5); (ii) conditions favouring an ability of hatchlings to compete for grasses with thin-edged leaves (Chapter 6); and (iii) to a lesser extent, conditions favouring the ability to resist desiccation (Chapter 6).

The correlation of egg size with adult size emphasizes the point made in Chapter 1, that we should be careful we do not incompletely or inappropriately define a trait when we are looking for its adaptive significance.

A start is being made on the testing of some of the remaining alternative explanations for variation in egg size. For instance, the relationship between relative humidity and hatchling mortality in different-sized hatchlings is currently being examined experimentally by A.J. Cherrill. Experimental manipulations of density and the amount of non-Festuca grass should also be performed in field enclosures to assess the effects of competition for non-Festuca grass on the fitness of hatchlings of different sizes.

A comparison of the results of Chapters 4 and 6 suggests that the theory of r- and K-selection may not apply to the grasshoppers in this study, since differences in selection (e. g. for competitive ability (density-dependent) or for the ability to resist desiccation (density-independent)) could explain the variation in hatchling, and therefore egg size, but not the variation in adult size. This difference between adults and eggs probably occurs for at least two reasons. First, the adults are more motile, and better able to move away from conditions of severe crowding or desiccation risk, whereas the hatchlings are initially less motile, are initially highly aggregated, and hatch in areas of bare sand with high risks of desiccation. Second, the relative selective effect of, say, desiccation risk on adults, (c.f. other selection pressures) is likely to be less than on hatchlings simply because they have smaller surface areas in relation to their volumes: this does not eliminate the possibility that differences in the risks of desiccation are important selective differences between populations, but they are likely to become relatively less important compared to some other selective differences. Similarly, competition for grasses which have thin-edged leaves may be negligible, since adults will have larger gapes than hatchlings so that a wider range of foodstuffs will be available to them.

A cause which could override the difference in adaptive responses was found best to correlate with adult size (Chapter 4). This result led to the theoretical explorations of Chapter 5 which examined adaptive responses under different constraints on growth. Models of this sort may be of more value in predicting life-history variation than the traditional optimization models (Stearns, 1976; Horn and Rubenstein, 1984), which consider the effects of differences in selection pressures but do not consider the effects of differences in constraints on organisms. An exception to these models is provided by the work on phenotype-limited strategies (G. A. Parker, 1982).

Thus, life histories can vary due to influences of many kinds, and some of these may override adaptive responses. If we are to be able to predict how life histories will differ between particular habitats, we will have to be able to decide which of the different types of cause (e.g. density-dependent, frequency-dependent, age-dependent, size-dependent, time-dependent selection pressures; gene flow; historical constraints; environmental constraints) are likely to be the most important in particular habitats, in order to know which of the theories are most likely to apply. We should sometimes also check our judgement by performing rigorous tests to discriminate between the different types of cause of life-history variation (e.g. see Appendix to the thesis).

Another complementary area of study would be of the physiological mechanisms which effect life-history responses to environmental conditions. Such studies should (i) enable us to define more completely and appropriately those traits of particular organisms which will show a clear relationship to particular environmental conditions; and (ii) provide knowledge which can be used to design tests of the adaptive significance of particular patterns of resource allocation (i.e. suggest ways of manipulating the life history to produce "strategic alternatives" (Appendix to the thesis)).

If studies of the types indicated above - which aim to identify the relative importance of a wider range of different causes and which examine more closely the relationships between the functioning of the organism and its environment - are performed as part of a balanced approach to studying life histories, a better-predicting theoretical framework should emerge.

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APPENDIX TO THE THESIS: **INFORMATION, NON-GENETIC CONSTRAINTS, AND THE TESTING OF THEORIES OF LIFE-HISTORY VARIATION***

(Suggested running head-line: NON-GENETIC EFFECTS ON LIFE HISTORIES)

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ABSTRACT

I present a simple classification of non-genetic variation in life histories which makes explicit those non-genetic effects on the phenotype which can, and those which cannot, be interpreted by using existing life-history theory.

Theories predicting optimal life-histories can be tested directly by providing organisms with misinformation about their external environment or physiological state. Adaptive phenotypic differences may also be detected when the effect of <u>information</u> on a trait runs counter to, and overrides, the effect on the trait of differences in <u>non-genetic</u> <u>constraints</u>.

Methods of manipulating life histories, other than by altering information only, may not allow the rigorous testing of the theories.

INTRODUCTION

Theories of life-history evolution predict what sorts of life history should evolve in specified ecological circumstances (Stearns 1976). The technique used (optimization modelling) predicts optimal phenotypes (Maynard Smith 1978) and therefore can be used to predict the phenotypic effects of both genetic and environmental (phenotypic plasticity) adaptive responses to environmental conditions (Caswell 1983). In this paper I consider only that component of life-history variation which is non-genetic.

THE PROBLEM

Some recent studies in which the life histories of different organisms have been compared have shown how differences in the immediate environment can conceal the life-history patterns predicted by current theory (Atkinson, 1985; Berven, 1982). These studies highlight the importance of considering all the important influences on life-history variation and not just those explicitly described by life-history theory. The problem is how to interpret life-history variation caused by non-genetic differences.

To solve at least part of the problem I produce a simple dichotomous classification which partitions non-genetic phenotypic variation and which makes explicit those causes which are within, and those which are outside, the explanatory scope of existing theory. I use this classification to show how differences in the effects of constraints, under different environmental and physiological conditions, can limit the explanatory power of existing theory, and also how optimization theories of life-history evolution can be tested directly.

CAUSES OF NON-GENETIC VARIATION (PHENOTYPIC PLASTICITY)

Non-genetic causes of phenotypic variation - whether they are measured as differences in the organism's habitat (i.e. 'external' causes) or as non-genetic differences in the organism's physiological state ('internal' causes) - may act as items of *information* which initiate or modify a phenotypic response (change in resource allocation). They may also act as *non-genetic constraints* which do not provide information but which limit the allocation of resources to some activity such as growth or reproduction. A particular environmental factor can *both* provide information and can act as a constraint, but their different effects may sometimes be difficult to separate.

That component of variation in a trait which is affected by differences in information can be described as free; it may be adaptive, neutral, or (sometimes, when selection pressures have changed in the recent past) even maladaptive.

Non-genetic constraints may arise from non-genetic differences in physiological condition (physiological constraints), stage of development (developmental constraints), and constraints on the availability of resources imposed by the external environment (external environmental constraints). Food shortage and low temperature are examples of environmental factors which can act as external environmental constraints. (Food shortage may also provide *information* about feeding conditions at some time in the future when a particular phenotypic response becomes effective (Brody and Lawlor 1984; Calow and Woollhead 1977)). In contrast to all of these, differences in phylogenetic constraints are *genetic*.

The dichotomous classification presented here, which partitions non-genetic variation in life histories can be summarized thus:

Non-genetic phenotypic variation

Free (due to differences in information)		Constrained (due to differences in the following non-genetic constraints)	
Internal	External	Internal	External
(may be adaptive, neutral, or maladaptive)		Developmental	Physiological

Only adaptive variation is predictable using existing life-history theory.

TESTING OPTIMIZATION THEORIES OF LIFE-HISTORY VARIATION

In order to test whether a life history is optimal or not it should be manipulated to produce 'strategic alternatives' to that found occurring naturally. Strategic alternatives are those life histories that can be achieved by an organism with the same amount of resources and the same physiological and developmental constraints. If the naturally-occurring life history is optimal all strategic alternatives should have a lower fitness than the unmanipulated life history. The life-history should be manipulated by providing the organism with misinformation about either its own physiological state or the external environment. At the same time, the overall effects (on the rate at which resources are allocated to particular activities) of differences in genotypes and non-genetic constraints should be controlled.

The most direct way of manipulating life histories by providing misinformation is by hormonal or pheromonal treatment. For example, the application of pheromones from a mature male induces young rodents to grow faster (cited in Batt 1980), and induces oestrus, blocks pregnancy, and accelerates the maturation of female rodents (Bronson 1971). Crowded female rats and humans synchronize their oestrous (menstrual) cycles; in the rats this is known to be caused by an airborne chemical (cited by Dunbar, this symposium). The application of gibberellins stimulates flowering in a number of plants (Pharis and Morf 1969; Watson, Carrier, and Cook 1982). The manipulation of insect reproductive behaviour and hence of their population sizes by the use of pheromones (Tette 1974) is a well-established technique which may potentially be used to test optimization theories of life-history variation.

However, if precautions are taken to ensure that the constraints are the same, other techniques may be used, and may even be preferable because hormones can have a number of effects on a phenotype besides the desired one. By temporarily removing males, for example, egg production can be delayed or reduced in crickets (Woodring, Clifford, and Beckman 1979). To use this technique, the effects of male presence on the females' feeding rate and on any resources which may be acquired from the males' semen should be controlled. A female dunnock which copulates with two different males rather than with the same male will lay a larger clutch (Davies 1985). Because both the males which copulate with the female will help to feed the young (Davies 1985), a larger brood can be reared successfully. If this effect on clutch size is not due directly to genetic differences between the females which copulate with different numbers of males, then the enlarged clutch might result from differences only in information. Differences in non-genetic constraints due to differences in the amount of nutrients from the males' semen will be negligible (Davies 1983), although the ability of the female to attract more than one mate might also conceivably be related to her age or condition (physiological constraints and information). The breeding system in the dunnock should permit the first rigorous testing of the hypothesis that females producing the normal clutch sizes have a higher fitness than those producing larger-than-normal clutches: when females lay an extra egg after copulating with two different males, one of the males should then be removed so that there is only one male parent to feed the young. If the naturally-occurring clutch size is optimal, the fitness of the female which is given the misinformation (in this case, 'that there will be two males to share in the feeding of the young') will be lower than females which had not been given misinformation but which laid the number of eggs appropriate to the number of different mates they'd had.

We need not be limited to the use of hormones or the carefully controlled use of a narrow range of environmental manipulations to show that a difference in life-history is caused mainly by a difference in information. The effect of the information contained in an environmental cue will be discernible if it affects a trait in the opposite way from, and overrides, the constraint contained in the environmental factor. For example, Brody and Lawlor (1984) found that the size of newborn offspring of the terrestrial isopod, *Armadillidium vulgare* increased when maternal food supply was reduced. Thus the information contained in the food limitation (about conditions the offspring would face when they became independent) more than countered the direct effect of a reduction in the amount of food. For this to happen, of course, some other activity must have been reduced even more than would be expected from the direct effects of food limitation alone. Another example of a phenotypic response running counter to the direct effect of resource limitation is the stimulatory effect of a decrease of nutrients on flowering in the water hyacinth (Richards 1982).

Other forms of environmental manipulation of life histories can give ambiguous results. For example, if birds whose clutch sizes are artificially increased have a higher fitness than birds laying the normal number of eggs, the result could be interpreted as meaning that the birds normally 'hedge their bets' (Stearns 1976) and lay a small clutch because feeding conditions during the period the chicks are fed by the parents are unpredictable and that in some years, when feeding conditions during this period turns out to be good, the actual clutch size appears smaller than the optimum for that year. However, if the female had invested additional resources into producing extra eggs as well as into feeding additonal chicks, a life history with a larger-than-normal clutch might be found to have a lower fitness in any given year than one with a clutch of normal size. The manipulated life history is not strictly a strategic alternative to the unmanipulated one because the experimental birds had been provided with extra resources in the form of additional eggs (i.e. the non-genetic constraints had been altered).

The general methodological rule is this: in order to detect those non-genetic differences in life histories which are adaptive, the effects of differences in information on the rate at which resources are allocated to different activities should be separated from the effects of differences in non-genetic constraints. These effects can be separated either when the organism is provided with misinformation about its environment or its physiological state, or when environmental or physiological information affects a trait in the opposite way from, and overrides, the effect of constraints on the trait. The traditional way of testing the adaptive significance of clutch size (by adding or removing eggs from the nest) does not produce rigorous tests because strict strategic alternatives are not produced.

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