

6 : DISCUSSIONI. FAUNISTIC STUDY

a. Terrestrial fern species and associated entomofauna :

India is endowed with a great diversity of climate, varied flora and its dependent fauna. The Himalayan ranges and their foothill areas of the Indian subcontinent are one of the important centres of plant and animal diversity and richness. The present study highlights the aspects of diversity of the fern flora and its associated entomofauna delimited to the Darjeeling plains, also known as Terai of Eastern Himalaya.

In India the first comprehensive account of ecology and distribution of pteridophytes of Darjeeling and Sikkim Himalayas was furnished by Mehra and Bir (1964). Subsequently Bir (1987) also provided a list of fern species of Eastern Himalayas that include endemic as well as exotic elements. However, no ready account was available from the plain of Darjeeling. The present study reveals not only a floristic account of the terrestrial ferns for the first time, but also a frequency of the species occurring in the patches that are found sparsed in the area of study. The frequent occurrence of D. esculentum and C. crinipes indicated

a special adaptability of these ferns in this agroclimatic region.

Insect-host plant relationships in a geographic range is dependent on the growth form and apparency of the plants besides many other factors. Insufficient information is available to quantify the relationship of ferns and their dependent entomofauna especially from India. Ottosson and Anderson (1983 b) demonstrated that ferns are attacked by about half the number of insects attacking other angiosperms of comparable apparency. A subsequent report indicated that about 25 native fern species of Iceland had no insect herbivores. Such a study implies that ferns despite all the contributory characters can not be rich in insect herbivore species as compared to other plants of similar apparency (Lawton, 1976). This view is upheld by Ottosson and Anderson (1983 b) in analysing the British fern entomofauna, who reiterated that ferns are difficult group of plants for insects to exploit.

In the present survey work the species frequency of the ferns occurring in mixed patches across the Terai region by far showed dominance of Diplazium esculentum, followed by Christella crinipes while species like Microlepia spesuncae, Lindsea ensifolia and Dicranopteris linearis occurred in reasonably reduced proportions. Of the eighteen terrestrial species

of fern recorded from Terai, the above mentioned five species were, therefore, regularly surveyed to find out their associated insects. As most of the insects could be recorded on D. esculentum followed by C. crinipes and only a few could be recorded on M. speluncaae and L. ensifolia and none on D. linearis, it seems that plant apparency reflected through the frequency of occurrence of the fern species may have a bearing on the association of the insect herbivores. Although plant size play a major role in determining its apparency, but it is doubtful if only size difference can account for the variation in the phytophagous insect species (Ottosson and Anderson, 1983a). Thus other contributory factors like dietary, non nutritional, toxic and physical parameters than simply distribution and growth-form should be explored.

The study on seasonal occurrence of the fern insects indicates their presence throughout the year. Although the fern species under study are perennial, they are expected to have changes in the physical and biochemical profile along with the change in the season as has been observed for British ferns by Ottosson and Anderson (1983 a). These seasonal changes of the host plants can be a decisive factor in getting utilized by the insects of different guilds. Ferns in the winter

months are mostly having old and senescent fronds which could hardly be utilized by the mandibulate herbivores, whereas the haustellate herbivores, which principally feed on the plant sap are mostly the winter representatives. A few other specialized feeders like the mining microlepidopterans, a couple of coleopteran species and the sawfly showed their partial occurrence in the winter months which may be the result of special adaptation. With the onset of spring and sprouting of fresh fronds, as would be expected, there is a greater occurrence of the plant-tissue chewers with only a few hemipteran species. In a similar observation on British fern feeders, after Lawton (1976) and Ottosson and Anderson 1983 b, only 19.5% of the frond feeding species are reported at the onset of the season i.e. spring, while the majority i.e. 63.4% of the fern feeders represented by hymenopteran, lepidopteran, some dipteran, two coleopteran and a few homopteran species have been reported to occur from June onward. i.e. the summer and the rainy season.

Examination of the British fern-feeding insects (Ottosson and Anderson, 1983 b) and comparison with a more elaborate list by Hendrix (1980) revealed that the present list of the fern associated insects of Darjeeling plains was having most of the orders in common excepting

Collembola and the phytophagous Diptera. The finding the thysanopteran representatives from the fern fauna of Nilgiri and Annamalai hills by Mohan Daniel and Chandrasekar (1986 b) was corroborated by the present observation from this part of India, when the association of thrips were also recorded with the sporophylls of Diplazium esculentum . However, most of the representative species of the insect-fauna of ferns observed in the present survey seem to be restricted to the Oriental region as they had little in common with the comprehensive list comprising the elements from other parts of the world (Hendrix, 1980).

Insects that do utilize ferns are not a representative sample of all phytophagous insects in general. Little specialization on fern by phytophagous insects has occurred at the family level and only in a few genera there are five or more congeneric fern-feeding species. So these results should be subject to both evolutionary and ecological interpretations (Hendrix, 1980). Evolutionarily, the ferns are an old group. The comparison of fern and insect fossil record suggests that despite broad overlaps between the two groups, the adaptive radiation of fern have been minor. If adaptive radiations have occurred, it would be expected that groups of insects well represented on fern would be closely related and would tend to be monophagous on ferns. Only the Hymenoptera show this trend and a large

number of tenthredinidae representing one subfamily tend to be monophagous. Fern feeding aphididae also show a high degree of monophagy (Eastop, 1973). Our present study showed that there were hardly congeners amongst the different orders and families studied. Although species of tenthredinidae and aphididae have been recorded in the present study, the families are represented by a few species each. As such the question of adaptive radiation could not be observed. This may be due to the small size of the available sample from a relatively restricted area surveyed. However, monophagy of the sawfly species corroborates Eastop's observation (1973).

Strong et al (1977) and Strong (1979) suggested that host-plant switching rather than autochthonous evolutionary proliferation of plant-insect associations account for the majority of the insects utilizing a plant species. This appears to be the case with insect fauna of ferns. Hendrix (1980) also reiterated the same hypothesis, that host plant switching rather than slow evolution of fern feeders from non-phytophagous ancestors account for the present insect fauna of ferns. Geographical range of the fern hosts can also be a decisive factor for the characteristic number of insects associated with them (Lawton and Schroder, 1977). Further, Strong and Levin (1979) suggested that the greater morphological

complexity of a host plant may offer greater diversity for potential **pest niches** and that this partially accounts for the decreasing number of pest species associated with different less complex growth forms. Whatever may be the requirement for occurrence of the number of more/ less number of species on a plant, the host-plant switching from angiosperms to ferns by insects utilizing vegetative plant parts should not be a great evolutionary or ecological hurdle. Sites for foliage feeders are as diverse and abundant in most ferns as in the herbaceous angiosperms which suggest that these guild of insects should not be under represented on fern. The list prepared in the present study for the insects that has the potential to switch over from fern to angiosperm and back, bears out the above hypothesis.

b. Insect-fern-crop interaction:

Insect-host interaction occurring in cropping system can be influenced by presence of associated weeds. Interestingly enough, phytophagous insects can mediate the interaction between crops and weeds (Altieri, 1986). The oligophagous and the polyphagous species create potential for frequent host shifts (Strong, 1977). The ability of weeds to harbour insects is well-known and

alternative host plants are particularly important where the cropping season is short and followed by cold or dry season of fallow or total replacement of different cropping systems (Van Emden, 1981). In the present study, a number of insects specially vegetative part feeders have been observed or reported to use fern (= weed) as well as one or more economic plants as alternate or alternative hosts. (Table No. V.). Out of these insects, a few were chosen to substantiate the fact that fern can be, at least in this region of Darjeeling plain, a supporting vegetation to be utilized by these crop pests.

Many instances can be cited with regard to natural enemies with free living stages that feed on wild plants and with predatory / parasitic stages that feed on prey or hosts on wild plants (Ananthakrishnan, 1992). In the early stages of crop growth, the presence of specific weed may act as a reinforcement for natural enemies of crop pests and thus sustain the population of predators prior to the onset of pest and later these control-agents tend to migrate from the weedy areas of the crop (Perrin, 1975). In the present study a few predators and parasites recorded on insect herbivores of fern may be of some importance. Specially, the hymenopteran species of braconid

and chalcid infesting the larvae and eggs respectively of the arctiid moths are expected to be of some significance in this context. Further, the larval-pupal parasite of family Tachinidae, with definite identification can act as a good natural control agent for the arctiid moths. However, its chances of proving a oozy fly of silk moths need to be ruled out before encouraging its natural occurrence on its hosts subsisting on fern. Therefore, weed hosts not only favour the herbivores by acting as reservoirs but also provide a sort of refuge to natural enemy population to have their continued interaction with pest population.

II. BIOECOLOGICAL STUDIES

a. Host-plant preference :

Laboratory feeding trials tend to produce more positive responses than is representative of the wild animal. This is because the animal is deprived of its normal such behaviour and further more it has a restricted choice. The relevant data arising out of such laboratory experiments are the differences in the apparent palatability among the plants tested. A more generalist feeder should discriminate less strongly in favour of any particular species, but would still be expected to discriminate strongly against very unpalatable species (Rowell et al. 1983). Keeping in view the above possibility and also from the observations of the natural occurrence of the species considered under host-preference experiment, a wide choice of the more apparent terrestrial fern plants occurring mostly in composite patches had been furnished. Further, for a better understanding of the nature of preference between the most preferred fern species and a reported or a potential angiospermic host plant, a second set of experiment was set up. Such a study was intended to give an idea of fern-angiosperm palatability by selected generalist species.

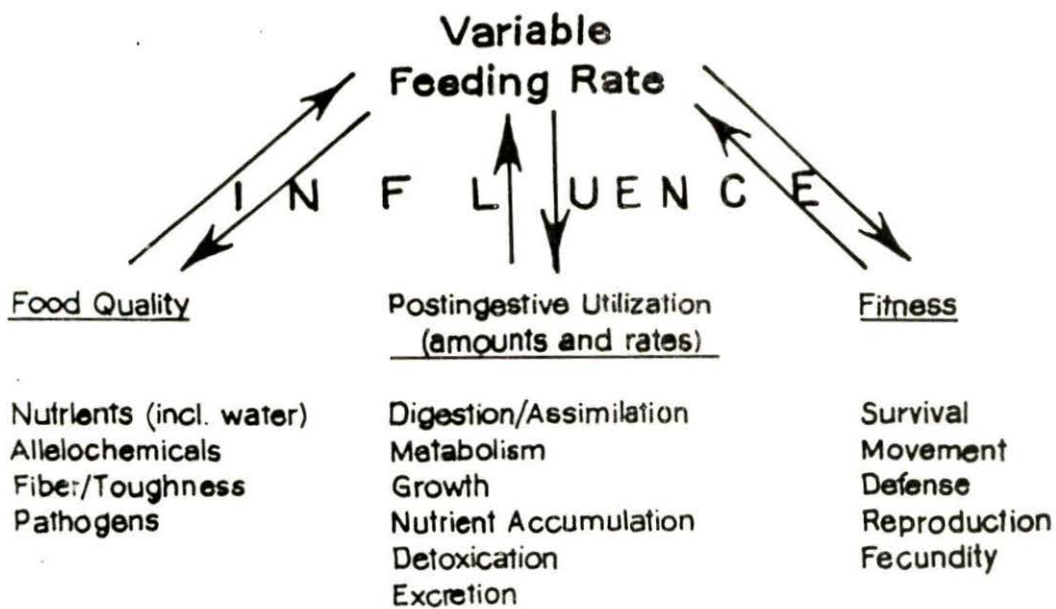


Fig.37. Interactions between feeding rate and food quality. (Scheme adopted from Slansky, 1993)

The feeding behaviour of many insect species is flexible being modified by environmental inputs and thus other undoubtedly interrelated decisions, like when, how often, and at what rate to feed. One decision made by an insect regarding feeding involves what to eat. Inputs include many features of the food (i.e. colour, size, shape, texture, toughness, and presence of conspecific individuals, etc.) but probably in the majority of the species the primary ones are of a chemical nature (i.e. odour and taste). (Slansky and Rodriguez, 1987). (Fig.37)

The preference among the fern species by the three generalists, two lepidopteran congeners S. obliqua and S. casigneta for D. esculentum, and the acridid species A. crenulata for D. esculentum and C. crinipes, speak of a restricted preference for only a few species of ferns out of five apparent species found in Darjeeling plain. A shot-gun analysis of the chemical parameters of the concerned ferns revealed that some of the chemical factors may be responsible for nonpreference of rest of the ferns, or in other words the acceptance of D. esculentum by the arctiid larvae and D. esculentum and C. crinipes by the acridid species may be due to tolerable level of these factors.

Feeny (1976) emphasized that a high quantity of tannin may act as a good chemical defence against herbivores. Plant tissues high in tannin, in fact are largely

avoided by most feeders because of the astringic taste they impart. One of the major function of tannins in plant is to act as a barrier to herbivory. The condensed tannins occur almost universally in ferns (Harborne, 1984) and the soluble tannins, which give an idea of the relative astringency and therefore, defence against herbivory (Suresh, 1988) have also been found in a host of fern plants that have been considered for the palatability study of grasshoppers by Rowell et al. (1983). The higher values of both relative astringency (TAE) and condensed tannin in three fern species (L. ensifolia, M. speluncae and D. linearis) over two other fern species and the angio-sperms may partly explain the unpalatability of the three aforesaid fern species by both the arctiid larvae and the acridid nymphs. Further, tannin has the property of forming indigestible complexes with protein (Goldstein and Swain, 1965) and starch (Feeny, 1970). Therefore, a high protein-tannin and starch-tannin ratio seem to be imperative for ensuring the supply of a rich amount of basic nutrients from the host to the herbivore. In the present situation, in spite of a fair amount of protein and carbohydrate being present in the three aforesaid fern hosts, the high amount of associated tannin may be responsible for making the hosts nutritionally poor. Marginal preference of C. crinipes over D. esculentum by the acridid species

A. crenulata cannot be readily explained by the existing biochemical profile of the two fern species. Possibly, it is due to the fact that species of acridoid do respond to particular phagostimulants found in their specific host plants (Bernays and Chapman, 1978) and maintenance of feeding.

The preference and maintenance of feeding exercised by A. crenulata for C. crinipes over the angiosperm C. capsularis, may be to some extent influenced by a low carbohydrate-protein ratio, higher lipid, lower phenol and reduced condensed tannin in the fern species. Further, the role high fibre content in the leaves of C. capsularis may have defensive function and hence reduce palatibility which has also been found during the study of velvetbean caterpillars by Slansky and Wheeler (1991).

The palatibility of C. capsularis by the early instars of S. obliqua and non-palatibility for the fern D. esculentum may be an adaptive strategy of the polyphagous species for exploiting the angiosperm during its early stages. The choice of a food plant by the immature insect, is specially based on visual and chemical (nutritional and allelochemical) cues. At one extreme, a caterpillar may not consume a plant leaf because of the lack of feeding stimulants (these can be nutrients and allelochemicals) or presence of repellents or deterrents

(Slansky, 1993). In light of the biochemical profile of the host plants considered in the study, it would be difficult to interpret that any one factor is favouring palatability of C. capsularis by the early larvae over D. esculentum. The fact that the advanced instars of S. obliqua accept both the fern and the angiosperm as their food, speaks for their nutritional requirement and taste that may change as a function of age. A caterpillars nutritional needs may vary depending on age, sex, previous diet and other factors (Slansky and Scriber, 1985). Thus feeding by caterpillars involves in large part, their attempt to obtain appropriate nutrients at an adequate rate in the face of qualitatively and quantitatively variable supplies and changing requirements, while experiencing various costs and risks. As a consequence, their feeding behaviour exhibits various degree of flexibility which is likely related to the extent of variation in food quality they typically experience to life style differences and to other factors (Slansky, 1993).

In contrast to the nature of preference exhibited by S. obliqua, its congener S. casigneta showed a uniform predelection both in the early and advanced instars for the fern plant (D. esculentum) when compared to the angiosperm (M. indica). This, however, is better under-

standable in light of the nutritionally rich fern plant having a less amount of deterrent factors. Although M. indica happens to be an ideal host plant for the silk moth and is also reported to be exploited by S. obliqua (FAO manual, 1987) yet it does not prove to be biochemically adequate to offer a fair palatability, and therefore, adequate acceptance by S. casigneta. A higher preference for ferns as compared to angiosperms is available from a quantified study by Balick et al. (1978) in which damage to three Mexican ferns was found greater than damage to seven angiosperms.

b. Survivorship study :

Effect of variation of values of diets can be measured in terms of growth, development, reproductive performance, mortality, longevity and morphological abnormalities . Life survivorship tables are a convenient format for describing mortality schedule of a population . These tables are the age specific summaries of the mortality rates operating on a population (Krebs, 1978). Host plant significantly influence vital features such as rate of development, survival . reproductive potential of insects which ultimately

determine the rate of population build up (Painter, 1951). Since in the lepidopterans and partially in orthopterans the larval / nymphal stages are the active feeding forms, it is expected that host plants influence is also maximum on these trophic stages. The survivorship or otherwise the rate of mortality throughout these development stages is an index of how well the species has adapted itself to the host plant. So, the survivorship tables of the immature forms have been useful in comparing the performance of both the arctiid and the acridid species on economic and fern hosts in the present study.

According to Pearl (1928), when there is very little loss of population in most of the life span and then a high loss in the older forms it is described as Type I curve. Diagonal survivorship curve Type II implies a constant rate of mortality independent of age and Type III curve indicate high loss in early life followed by a period of much lower and relatively constant losses. (Fig. 5a). The survivorship curve of S. obliqua on jute resemble Type I curve. On Diplazium it resembles an intermediate between Type I and II, therefore supporting the idea that most larval stages of S. obliqua are able to survive on the alternative host i.e. D. esculentum.

Survivorship curve of S. casigneta stands between Type I and Type II curves on both the hosts. Since the survivorship curve on D. esculentum shows a closer similarity to Type I and the survivorship curve on mulberry shows a closer similarity to Type II, it can be understood that the species is more adaptive to the fern species, and therefore surviving better on D. esculentum than on M. indica.

A comparison of survivorship curves of the nymphs of A. crenulata on the economic and the fern hosts shows a closer similarity to Type II curve. Hence, it may be interpreted that there is a constant rate of mortality independent of age and development stage. In a slight modification of the generalization it may be pointed out that in the last instar there is an increased mortality on both the host plants, possibly suggesting that both the host are not ideal at least for the advanced nymphs. It may be assumed that in nature these nymphs get an opportunity to feed on other alternative host because of their high polyphagous nature (Gangwere et al. 1989), to have a better survival. So by and large all the survivorship curves studied fall between Type I, and Type II as has been suggested to be ideal for a large number of species by Krebs (1978). Further the same

author has indicated that man in developed nations tend to have Type I survivorship curve which may be analogised with the survivorship of a herbivore insect on an ideal and nutritionally rich host. On D. esculentum the longer developmental period of S. obliqua as compared to that on C. capsularis may be due to an additional instar of the caterpillar. This additional instar possibly makes up for the nutritional shortfall to enter pupation. This is more apparent from the study of the dry mass-budget of the species. Apparently C. capsularis seem to be a more suitable host, since on this, species survival is better with a shorter development period. Moreover, the eggs laid after successful completion of the development on C. capsularis, showed 98.89 % survival. It appears that the fern plant, D. esculentum, can nevertheless be used as an alternative host and support at least in part the life cycle of the arctiid species.

Performance of S. casigneta on the hosts

D. esculentum and M. indica establishes the former as a more acceptable host than the latter. The poor survival of the species with enhanced casualty at larval, pre-pupal and pupal stages on M. indica when compared to that on D. esculentum indicates the former to be an

unrelated host that can be exploited only to a limited extent. Although S. casigneta is a well established pest of a number of angiospermic plants (Banerjee and Haque, 1983 b; Chatterjee and Chaudhuri, 1989), yet it can utilize the food resource of the fern as an alternative host. On the fern host, the high hatchability and notable viability of the developmental stages and their completion within a reasonable period, beyond doubt establishes D. esculentum as a suitable related host. The said information further establishes the fact that unlike S. obliqua which is reported to be a mulberry pest (FOA manual 1987) S. casigneta lacks the ability to utilize M. indica as a true host. The additional larval instar recorded on mulberry is possibly due to their inability to acquire adequate nutrients from the host and to attain certain weight for entering pupation (Slansky, 1982).

Comparable performance of A. crenulata on C. crinipes and the economic host C. capsularis signifies that both the hosts can be used. C. capsularis being a cash crop is grown during the rainy season and may act as a good food resource to the acridid species. In absence of C. capsularis the fern species C. crinipes has certainly the potentiality to support a fair population as indicated

by their higher survival values and shorter development period.

The additional instar for the females of the species on both the hosts possibly indicate a common requirement of the females to acquire, allocate and utilize some additional nutrient for their future reproductive programmes (Slansky, 1993).

c. Development and performance :

i. Incubation period and hatchability:

Variable nutrient allocation to eggs can result from food quality differences among female caterpillars of the parental generation and can also occur between the early and later laid eggs, with subsequent effects on the caterpillar's performance i.e. dispersal, development rates, weight gain and survival (Capinera and Barbora, 1976, 1977; Capinera, 1979; Wagner and Leonard, 1979). Further, Banerjee and Haque (1985) observed longer embryonic development period with a higher hatchability for D. casignetum (= S. casigneta) on a more nutritionally rich host i.e. sunflower, than on hempweed that had a higher phenolic content.

In the present study, S. obliqua seemed to utilize C. capsularis better than D. esculentum, which was reflected through a reasonable incubation period and a fair hatchability of the eggs. The few eggs laid on D. esculentum with no maturation and hatchability is difficult to explain through the nutritional qualities analysed for the host. Expectedly, some factors other than the ones studied for the fern species may be interfering with the reproductive programme and embryonic development of this arctiid moth.

A reverse phenomenon was observed in S. casigneta where a high egg hatchability and a reasonable incubation period indicate the suitability of the fern host over M. indica where no egg laying was observed. The nutritionally rich D. esculentum seemed to support the reproductive and the embryonic development activity well in this arctiid species.

Although no significant difference was noted in the embryonic development period (incubation) for A. crenulata eggs, the higher hatchability on C. crinipes over C. capsularis indicate a better suitability of the fern host. Such a performance is not unusual in view of richer basic nutrients and lower allelochemicals of C. crinipes as compared to that of C. capsularis.

Slow growth and lengthened development frequently occur for caterpillars feeding on sub-optimal foods. However, because the disadvantages to fitness can be substantial, slowed growth and extended development are probably more common consequences of inability to adequately compensate for reduced food quality (Slansky, 1993).

C. capsularis proves to be a more suitable host than D. esculentum as far as larval period and survival of S. obliqua are concerned. Although the dietary parameters do not indicate a better nutritional value for S. obliqua, yet the larval performance undoubtedly speaks in favour of a better supporting capacity of C. capsularis.

The high survival of S. casigneta larvae on D. esculentum establishes the fern species as a more optimal host than the angiosperms M. indica. However, the non variability of the larval period possibly imply that some sort of a compensatory mechanism operates in the larvae to make up for the reduced food quality of the angiosperm host.

Nymphal performance of A. crenulata with a shorter post embryonic development and a better survival on C. crinipes establishes the fern host to be more adequate and supportive than the angiosperm host, C. capsularis. Dietary parameters also portray C. crinipes to be nutritionally richer than C. capsularis having a reasonably reduced non-basic nutrients and secondary components. The overall observation on the above insect herbivores indicate that the plant species which are favourable for larval / nymphal survival are also suited for their rapid development-- an observation also reported for D. obliqua by Kabir and Miah, (1987).

ii. Additional instar and minimal weight

The ultimate goal of the larval and nymphal stages is to produce an adult whose quality matches its

genetically determined potential. The species in the same and in different guilds differ in the development and growth subcomponents of their life history strategies and in their tactics by which they attempt to achieve this goal (Slansky and Rodriguez, 1987). In some species the number of instars may vary depending on the environmental condition generally having more instars under unfavourable conditions (Sehnal, 1985).

That insects are not operating at their maximal feeding rate, it is indicated by the increase in food consumption frequently observed in response to a deterioration in food quality. The degree to which different species exhibit this compensatory response may be related to their life style (Slansky, 1982). Greater consumption can result from prolongation of larval development time which may include extra larval instars (Slansky, 1993). The decision to pupate or moult to adult often depends on attainment of some minimal body weight. Above this minimal body weight, the larva may make a choice that balances the potential costs of prolonged development and those of producing an adult whose size and performance are somewhat reduced. The percentage of optimal weight at which the minimal weight is evolutionarily adjusted varies between species and is probably related to their particular life style (Slansky 1982).

In the present study, the additional instar (VII) of S. obliqua reared on D. esculentum when compared to six instars on C. capsularis, once again emphasises the suitability of C. capsularis. Similarly the lesser number of instars of S. casigneta on D. esculentum establishes this fern host as more suitable than the angiosperm, M. indica. Under less ideal conditions, the decision to moult probably involves integrated inputs including the nature of the unfavourable conditions, like poor quality of food (Slansky and Rodriguez, 1987). Since no sex bias was observed for the additional instar and all the larvae on the said food plant had undergone the additional moults, it seems that the nutritional qualities of the host plant might have forced the arctiid species to take such a decision. The situation arising in case of A. crenulata, where only the females underwent an additional moult, can be understood in light of the additional nutritive requirements of the female sex. Adult females, associated with their great resource output in reproduction than males are frequently larger and heavier than males and this is often accomplished by longer developmental times in female larvae which may also go through an additional instar (Slansky and Scriber 1985). The same authors

also reported that in addition to selection for longer development time for females to accumulate sufficient nutrients for egg production, there can be selection for early male emergence (protandry), which can facilitate access of emerging females for mating. The present finding in which only the females of A. crenulata undergo an additional moult may also stand as an example of the above fact.

There is likely an adaptive component to the magnitude of prolonged development both because its ecological consequences may differ among species, and because its underlying cause i.e. the need to obtain a species specific minimum body size or mass prior to pupation, is likely an evolved trait (Slansky, 1993). Fitness associated performance criteria of insects are often positively correlated with body size (Yamada and Umeya, 1972; Barbosa et al. 1981; Wickman and Karlson, 1989; Banno, 1990). Caterpillars could pupate at body sizes below their genetic potential in order to avoid prolonging their duration of development. However, various degree of prolonged development do occur because probably in large parts all insects must achieve some minimum body size or mass before pupation (Nijhout, 1975). Poor food quality or inadequate food utilization (because of allelochemicals) result into unfavourable conditions leading to extra instars (Sehnal, 1985).

A greater number of such instars may provide an increase in the body weight so that an optimal body weight is attained and the larvae may take decision to pupate (Slansky, 1982). In light of the above proposition, the occurrence of the additional instar (VII) of S. obliqua on D. esculentum and of S. casigneta on M. indica is possibly meant to compensate and attain the minimal weight to enter pupation. Since on C. capsularis for S. obliqua, and on D. esculentum for S. casigneta, the optimal weights (> minimal weight) have already been attained by the VI instar larvae, they have taken a decision to pupate (and not to enter into any further instars).

For most such species, prolonged development to achieve their maximal body size or weight may not be a viable strategy in nature with depleted or deteriorated larval food supplies because it leads to death without reproducing. Under such circumstances, a substandard sized adult might experience a reduced reproductive contribution compared to a full-sized adult, but it would nonetheless have greater fitness than if it attempted to achieve its maximum body mass through prolonged development (Slansky 1993). The caterpillars fail to achieve their genetic potential in body size, mass, nutrient storage and development time despite

compensatory changes in the consumption and utilization of food indicate that these responses are not always effective at fully mitigating the impact of food in variable environment to their performance (Slansky, 1993). The present study in which S. obliqua failed to have fertile eggs on D. esculentum as well as failure of S. casigneta to reproduce on M. indica may stand as an example of the above conjecture.

According to Angello and Slansky (1984) and Banno (1990), even though lepidopteran species span the range in minimum size for pupation, the significance of these values to lifestyle differences has not been rigorously investigated. Further Slansky (1993) emphasized that there is a lack of sufficient information for most insect species and specially species with phytophagous larvae to adequately assess the precise fitness tradeoffs between prolonged development and reduced body size or mass.

iii. Pupal period, pupal survival and pupal weight :

Feeding can have biologically significant costs. This is most likely to occur for those species in which energystored by a caterpillar is critical for pupal

survival and /or adult performance (Slansky 1993). The arctiid species studied fall in the category where the adults are non feeding and the only source of nutrition and energy is through the feeding activity of the larvae. The greater pupal survival and higher pupal weight of S. obliqua on C. capsularis and S. casigneta on D. esculentum once again establish the angiosperm to be a more suitable host for the former moth as compared to a better suitability of the fern plant for the latter. In a similar finding for D. casignetum , Banerjee and Haque (1985) reported heavier pupae with better survival on sunflower, the more suited host than on hempweed. While reporting the performance of D. obliqua on a number of hosts Kabir and Miah (1987) documented that more suitable the host is, greater is the survival and higher is the weight of pupae and adults. Irrespective of the host plant used for rearing, no significant difference occurred in the duration of the pupal stage, a fact also observed by Banerjee and Haque(1985) for D. casignetum. Further, in support of the observations made by the above authors in both the species i.e. S. obliqua and S. casignetum, the female pupae were found to be constantly heavier than males. As would be expected and also reported , Banerjee and Haque (1985) and Kabir and Miah (1987) for two of the arctiids, the adult weights on a suitable host always exceeded that on a

less suitable one. This observation was also found to be true for the two arctiid species studied here. In a slight departure from the above fact the body weight of males of the acridid, A. crenulata did not show a great difference on two of its hosts. However, the females showed a higher body weight on the more suitable host i.e. C. crinipes in line with the information available for the lepidopteran species.

iv. Adult weight and longevity

Influence of a more suitable host on the longevity of both the sexes of A. crenulata was apparent but a variation in longevity between sexes was observed in case of the arctiid moths. While a longer adult life in males indicated a positive influence of the suitable host, this was not so in females of S. obliqua. In a partially supportive finding Banerjee and Haque (1985) showed a higher longevity for both sexes of D. casignetum on a more suitable and nutritionally rich host.

v. Fecundity :

The effect of foods on egg production results

from balance between a multiplicity of factors, such as species specific requirements, temperature, metabolism, food constituents and quality. Both the quantity and quality of food influence the total egg production and egg laying (Engelmann, 1970). The high fecundity recorded for A. crenulata on C. crinipes, and S. casigneta on D. esculentum are quite understandable in view of the nutritional richness and suitability of the hosts. However, the markedly increased fecundity of S. obliqua on C. capsularis cannot be readily supported by the nutritional parameters of its hosts considered here for comparison. A couple of nutritional attributes that make C. capsularis more distinct from D. esculentum is its comparatively high nutritive carbohydrate and fibre content. It has been emphasized by Engelmann (1970) that carbohydrates are possibly necessary for utilization of dietary protein reserves in both autogenous and anautogenous species. Apparently only a combination diet of sugars and protein allows maturation, and also qualitatively different sugars may have in some cases different effectiveness in promoting egg maturation. Different proteins may also be more or less-nutritious. In the present situation, the high fecundity of S. obliqua on

C. capsularis possibly may be explained through further analyses of the different qualities of dietary proteins and carbohydrates. An unpublished data show that the quantam of albumin and globulin as compared to glutelin and prolamin and similarly, the quantam of mono- and oligosaccharide as compared to starch content is by far higher in C. capsularis than in D. esculentum . Besides the possibilities mentioned here, some other nutritional factors (not covered in the present study) of C. capsularis may also be responsible in boosting the fecundity of S. obliqua.

III. DRY MASS BUDGET

Relative consumption rate (RCR) may change both within and between instars, presumably reflecting physiological changes during development. Later instars tend to have lower RCR values than earlier ones (Slansky and Scriber, 1985; Mohanty and Mitra; 1991) but only a few species have been studied and these data must be interpreted with caution (Slansky, 1993). The findings in the present study on S. obliqua and S. casigneta corroborate the above proposition

i.e. reduction in RCR values (dry weight) with the advancement in instars. The fact has also been found true for the instars of the acridid species, A. crenulata. The change in the RCR value between the early and late instars may be due to feeding behaviour since the early nymphs skeletonize leaves feeding on softer tissues whereas later instars consume most of the leaves including veins (Wagner and Leonard, 1979; Salinas 1984).

Insects that feed on foods of lower nutritional quality often show higher rates of consumption than similar insects feeding on more nutritious foods. Insects may thereby compensate for lower food quantity by increasing consumption to obtain sufficient nutrition for development (Farrar et al. 1989). This hypothesis does not apply well in the study of the arctiid species, as far as nutritional parameters of the fern and the angiosperm hosts are concerned. Since the ferns in the present context appear to be of a better nutrient value than the angiosperm, a lower RCR value was expected in the larvae. In fact the values especially in the early instars are higher on D. esculentum, which imply that some factors other than the concerned nutrients and allelochemicals may be responsible. However, an insect's behavioural response to a food

source may be an important determinant of consumption rate than its physiological state. This seems empirically obvious and is evidenced by bioassays in which an insect's behavioural response is altered by addition of stimulant or deterrent compounds to a food source (Farrar et al. 1989). Further, plants exhibit many qualitative and quantitative changes in nutrients and allelochemicals along with leaf maturation, with chemical fertilization, and between species etc. that might affect food consumption independent of a compensatory response to decreased nutrient level (Slansky, 1993).

In case of A. crenulata the comparison of RCR values supports the earlier hypothesis of Farrar et al. (1989). On the nutritionally richer C. crinipes, the acridid species in general has a lower RCR value than the angiosperm C. capsularis. The dietary parameters studied are quite indicative and supportive of the expected phenomenon.

Since relative growth rate (RGR) depends on consumption rate and efficiency of conversion of ingested food (ECI) (Barbosa and Greenblatt, 1979), the reduced consumption rate in the advanced instars may account for the decreased growth rate which is evident with minor variations in all the three insect

species studies, irrespective of the host plant. The difference in the RGR values which are usually more on the nutritionally rich hosts i.e. D. esculentum for S. obliqua and S. cassigneta , and C. crinipes for A. crenulata , can be readily understood. It is well known that in addition to the life style and feeding pattern, the vast difference in the overall growth rate between species of the same trophic level can also be accounted to some extent by food quality (Scriber and Slansky, 1981). Factors such as nitrogen, energy, mineral and toxin contents of the food significantly influence the growth rate through feeding rate (Gordon, 1972; Mattson, 1980; Slansky and Fenny, 1977).

According to Muthukrishnan and Pandian (1987) most lepidopterans belong to the short lived species group whereas the orthopterans belong to long lived species group. The former group is known to maximise energy accumulation by accelerating the rate of food consumption and conversion without prolonging the feeding period and thus, reducing the metabolic costs of maintenance. In this group the growth rates are several times faster than the long lived forms. In the present study, similar faster growth rates have

been noted for the lepidopteran species when compared to the lower values of the long-lived orthopteran species.

Greater consumption can result from prolonging larval development time which may include extra instars. So, slower growth and lengthened development frequently occur in caterpillars feeding on suboptimal foods. There seems to be enough evidences to atleast strongly suggest that insects exhibit compensatory feeding in responses to changes in the nutrient levels in their typical food plants, although other factors like allelochemicals may also affect food intake. When nymphs of Locusta migratoria were fed on a diet with reduced protein content, brought about by addition of cellulose, they increased food consumption by feeding more frequently (Simpson and Abisgold, 1985).

Dietary proteins can be divided into four fractions based on their solubility i.e. albumin, globulin, glutelins and prolamines. Albumins and globulins tend to be the highest quality proteins, glutelins intermediate and prolamines the poorest (Slansky and Panizzi, 1987; Draper, 1976). Caterpillars may not have evolved to compensate through increased feeding for reduced protein quality, probably because greater intake would only increase the metabolic costs

of catabolising and excreting the imbalanced amino acids. As an example, caterpillars of Spodoptera eridania consuming diet with zein (a poor quality protein) although ingested similar amount of nitrogen as larvae consuming the diets with casein (a high quality protein) excreted over three times more uric acid and had respiration rates about twice as high as the latter caterpillar (Karowe and Martin, 1989).

The dry mass budget of S. casigneta that include a higher assimilation and production on D. esculentum , as compared to M. indica can be substantiated by a better nutritional quality of the former. For the situation arising out of the budget of S. obliqua on two of its hosts, a different interpretation is required. The high production and reduced respiration in S. obliqua reared on C. capsularis inspite of lesser assimilation may be understood through the qualities of protein. As mentioned earlier, in an unpublished observation the quantum of albumin and globulin (high quality protein) is found to be higher in C. capsularis when compared to that of D. esculentum. The above facts may be supported by findings of Karowe and Martin (1989) where the higher nutritional quality involves lower respiration rate and metabolic costs.

The mass budget of A. crenulata on C. crinipes, as expected, shows a better production index because of the food quality. Possibly presence of a higher phenol and fibre in C. capsularis results in a higher respiration inspite of better assimilation. Further, the enhanced cost of maintenance of A. crenulata on C. capsularis may be explained by referring to its increased food consumption resulting from low nutrient level and higher amount of indigestible material (fibre) that dilutes the nutrient concentration. Greater consumption may result from eating faster and for longer period which also involves higher expenditure of energy (Slansky, 1992, 1993).

Compensatory feeding is generally adaptive because it mitigates the deleterious impact of reduced nutrient level on herbivore performance (Simpson and Simpson, 1990; Wheeler and Slansky, 1991). However, ingestion of an increased dose of a potentially deleterious allelochemical may exceed herbivores capacity of coping with it. This does not seem to be the case for some insects apparently well adapted to allelochemicals in their food ; compensatory feeding leading to consumption upto three fold more food has little deleterious impact from ingestion of additional allelochemicals (Slansky, 1992). In the present study, the higher respiration and maintainance cost of the

arctiid moths on D. esculentum may be indicative of the fact that the allocation of energy from metabolic pool to respiration has taken place. Such a phenomenon may result from activity of detoxifying enzymes against unusual toxins (allelochemicals) on occasion of switch over to alternate food plants that appear to be energetically more expensive (Muthukrishnan and Pandian, 1987). So, the possible explanation for constantly higher respiration on the fern D. esculentum than the angiosperm, C. capsularis or M. indica , may be due to some functions related to the neutralization of the fern toxins or allelochemicals that have not been considered in the present study. Judging by the lower respiration and maintenance cost of A. crenulata on C. crinipes it seems that this species of fern host is relatively free from the allelochemicals.