7.2.1 Microhabitats

a) Soil cover and rocks

Many invertebrates inhabit cracks or holes in soil, sand or rock especially those in extreme environments, e.g. desert and arctic habitats. The insulating effect of the soil has been demonstrated on a number of occasions. Burrowing to a depth of 6 inches into the soil may have a temperature effect equivalent to climbing 2,000 ft. Diurnal temperature variation in the surface layers is considerable, but decreases with depth and is almost zero below about 50 cm in most places (Cloudsley-Thompson, 1969).

b) Plants

The presence of plants ameliorates climatic conditions to a marked degree. Not only the height of plants, but the architecture, reflectivity and density of herbage will modify microclimatic profiles. The extent of the cooler, damper layer trapped beneath the leaf canopy (Waterhouse, 1950) depends, upon the depth of penetration of the sun's rays and is determined by the angle of leaves, which varies diurnally and seasonally. Such effects can be related to the distributions or feeding patterns of many insects including sawfly larvae (Waterhouse, 1955), caterpillars (Casey, 1976) and ants and bees (Willmer & Corbet, 1981). Casey (1976) found that desert caterpillars moved around their foodplants to utilise favourable microclimates and stabilise their body temperature. Cicadas (Heath & Wilkin, 1970) and psyllids (Hoffman _et al._, 1975) profit from the cooler, moister air on the shaded sides of plant stems. The temperature and relative humidity in summer among the roots of marram grass (_Ammophila arenaria_) on the coastal dunes of the Bay of Biscay have been found to be remarkably constant. These tufts of grass, particularly the older ones, harbour a number of smaller animals such as woodlice, spiders, mites and false-scorpions (Cloudsley-Thompson, 1960a).

i) Leaves

Conditions may vary quite markedly between leaves or other parts on the same plant or even parts of the same leaf. Willmer (1980) found a cool, humid microclimatic zone around a cabbage leaf extending at least 10 mm above the upper leaf surface and 25 mm under the lower surface. Caterpillars of _Pieris brassicae_ (large white) showed changes of water balance which could be correlated with their position on the leaves. In the case of insects which produce leaf rolls, these effects may be even more marked. Nettle rolls made by Pleuroptya (mother-of-pearl) larvae maintain an environment always in excess of 95% relative humidity (Willmer, 1980) and the leaf rolls made by Choristoneura (spruce bud-worm) exhibit a steady internal temperature 8 °C above ambient when insolated (Henson, 1958).

ii) Flowers

Flowers may provide yet more specialized microclimates since their colouration and form may affect the temperature (Hocking & Sharplin, 1965; Kevan, 1975) and humidity (Corbet et al., 1979) within them. In cup-shaped flowers, like buttercups (Lack, 1976), the petals may act as a parabolic reflector producing a hot spot in the centre where small insects may bask (Kevan, 1975). This may considerably aid the thermal balance of arctic insects. Humidity may be very high within corollas (Figure 4), especially when these are of elongate form where the trapped air may equilibriate with nectary water (Corbet et al, 1979). These gradients are relevant to flower-visiting insects both directly and also indirectly through effects on nectar concentrations. In the extreme case of closed buds, where certain insects oviposit, the relative humidity may be around 99% at all times (Willmer, 1980). Staminate flowers of coniferous trees in Canada are commonly at temperatures 5-8 °C above vegetative buds in sunlight. Since the buds, in turn, are above air temperature, this is an important difference for insects like the spruce bud-worm, Choristoneura fumiferana (Wellington, 1950).

Dobkin (1985) found microclimatic variation both among and within individual Heliconia wagneriana infloresences. He demonstrated that hummingbird flower mites (Gamasida: Ascidae) respond to this variation by exploiting thermally favourable locations and avoiding thermally adverse conditions within infloresences. Kingsolver (1979) found pitcher desiccation is a function of microclimate and pitcher size as determined by rainfall patterns and revealed significant differences in larval developmental rate, voltinism, and larval mortality due to microclimatic effects.

c) Tree-trunks and logs

These provide numerous microhabitats for small animals. Different bark types have different thermal properties, microclimates and faunas (Nicolai, 1986). Species with fissured and scaly barks, shade and insulate the inner parts of the bark and harbour a diverse arthropod fauna. However, on smooth and thin barks which show no adaptation to avoid

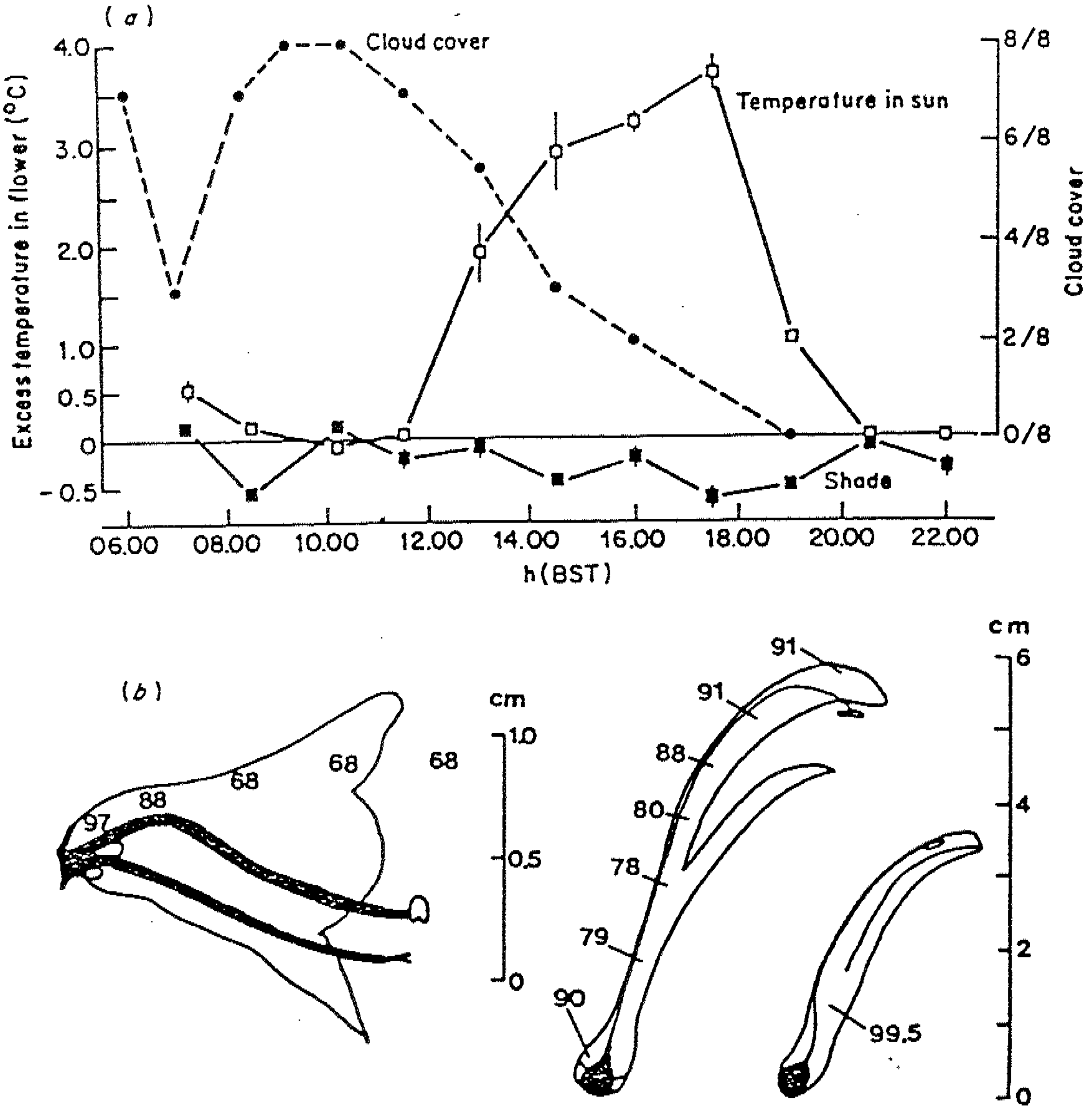

Figure 4. Temperature (a) and relative humidity (b) conditions in flowers. (a) shows the changes in temperature excess recorded in Crataegus flowers in sun (□) or shade (■) through the day (from Corbet et al., 1979)
(b) shows humidity profiles (as % RH) measured using the droplet technique in flowers of Echium vulgare (left) and of Justacia aurea (right: mature flower and bud) (from Willmer, 1982b)

overheating, fewer species are found. Different insect species inhabit sunny and shaded regions on tree trunks or logs. The discontinuous bark cover formed by epiphytic lichens and algae provides a mosaic of habitats for the fauna. The composition of these 'corticolous microcoenoses' is greatly affected by the vegetation stratification on bark (Andre, 1985). Bark beetles lay their eggs within logs to avoid overheating in highly insolated sectors and excessive humidity in the shaded damp areas (Cloudsley-Thompson, 1962). Nesting carpenter bees may choose to make their holes on the more insolated side of available wood for similar reasons (Corbet & Willmer, 1980). The fauna of rotting wood changes with the varying stages of decay so that a succession of animal communities develops, each one dependent on particular type of microhabitat.

d) Leaf-litter and debris

A thick layer of leaf litter and debris tends to conserve moisture and buffer temperature fluctuations. It may support a rich and varied fauna which varies according to the vegetation that produces it. Gradually, it decays and becomes incorporated into the soil humus so that again there is a succession of changes. Even the thin drift on the seashore provides a microclimate within the range of tolerance of many animals and well below the high extremes of unprotected sand surfaces (Barnes & Barnes, 1954).

7.2.2 Physiological effects of the microenvironment

a) Thermal balance

Insects have conventionally been regarded as classic examples of ectotherms, their body temperature reflecting environmental conditions and being 'regulated' only by behavioural mechanisms. Where this is true, their thermal balance should bear a direct and obvious relation to microclimate and to their selection of appropriate conditions. However, as reviews by Heath et al. (1971), Heinrich (1974) and May (1979) have pointed out, a good many cases of endothermy in insects from most of the major orders have now been described.

The available evidence suggests that, in most environmental conditions, insects gain heat principally by radiation (Parry, 1951; Shepherd, 1958) and lose it principally by convection (Digby, 1955; Edney, 1971). Conduction is minimal, since points of contact with the substrate are very small, and evaporation is usually precluded because insects cannot afford the water loss entailed unless overheating becomes critical. Behavioural mechanisms allow insects to maintain body temperature by finding and using more equable microenvironments in which they may heat up or cool down as required. As regards endothermy, the essential strategy is the generation of metabolic heat as a means of regulating body temperature. Some large insects show considerable powers of endothermic regulation, and the mechanisms of wing-beating and shivering to achieve warm-up and blood-shunting to permit cooling may be directly triggered by microclimate, as perceived by the insect's receptors. Such techniques have been demonstrated in bees (Heinrich, 1972, 1974), beetles (Bartholomew & Casey, 1977; Bartholomew & Heinrich, 1978), moths (Heath & Adams, 1967; Hanegan & Heath, 1970), butterflies (Kammer, 1970), dragonflies (May, 1976) and Orthoptera (Heath & Josephson, 1970) and even small syrphid flies (Heinrich & Pantle, 1975). For reviews see Heinrich (1974) and May (1979).

The various sources of heat gain and loss for an insect are influenced in turn by several features of the animal itself: its size, shape and surface area; the colour and microsculpture of its surface; and its orientation or posture. Since these factors affect the rate of heat exchange they also determine the tolerances the species may have in timing its activities and in seeking suitable microhabitats in which to pursue them. Hence, the nature of each insect's microclimatic choice is the end result of the interactions of all these features of environment, physiology and form. Each of these controlling factors can therefore be considered in terms of its contribution to this overall pattern.

i) Size and shape

The interrelation of such factors as size, shape and surface area of insects with their thermal balance has been extensively studied over the last 30 years. Early studies by Parry (1951) on model insects pin-pointed some of the more important relationships, and these observations were extended by Digby (1955) and Church (1960a, b) with actual specimens covering a considerable size range. Larger insects attain a higher temperature excess, but take longer to reach it under constant conditions (Digby, 1955; Willmer & Unwin, 1981). At the upper end of the size range, these effects may be modified by the action of endothermic mechanisms. Also, there is always a shape effect superimposed, the slope of the size/temperature relation being different for elongate 'locust-type' insects and for the rounded 'fly and bee types' (Digby, 1955).

The size of insects therefore affects their needs for appropriate microclimates: larger forms may tolerate less stable environments and intermittently higher radiation, because they will change their body temperature more slowly as their size 'smooths out' some of the variation. They may also become active under cooler conditions with limited solar radiation, as their temperature excess can be greater and they may reach an adequate body temperature more readily than a small insect. Patterns of activity at a particular site can thus be correlated with the size of insects as it relates to their temperature requirements. Willmer (1982b) found that larger-bodied forms, such as Hydromyza (a scatophagid fly), tend to use water lily pads early and late in the day, whilst small dolichopodid flies use them to rest on only around midday in hot conditions, when other habitat may be inhospitable to them (Figure 5). Flower-feeding insects may visit at times and in places where temperatures around the flowers are suitable, rather than visiting at times of maximum nectar or pollen rewards (Willmer, 1983). Some insects may change their effective thermal size by aggregation which may afford some degree of protection against predators (McGavin, 1984). This may allow an increase in body temperature if net surface area is decreased, because metabolic heat can be shared and conserved while convective cooling is reduced. This occurs with caterpillars (Wellington, 1949), sawfly (Seymour, 1974), ants (Jackson, 1957) and locusts (Willmer, 1982a).

ii) Colour

The effects of colour (surface absorptivity or reflectivity) on thermal physiology have been somewhat controversial. Digby (1955) found clear effects when insects were 'painted', but his estimations showed that even a pale and apparently highly reflective insect still absorbed about three quarters of received radiation. Other authors have felt colour to be of negligible importance (e.g. Pepper and Hastings, 1952).

Edney (1971) found that, in desert insects, either black or white was preferred according to the time of day when a particular species was active. Further evidence for the direct importance of colour comes from those insects which may have differently pigmented forms, where dark forms have a higher body temperature under the same conditions. This has been shown for flies (Watt, 1968) and in the honey-bee (Cena & Clark, 1972). The same effect can occur if differently coloured parts of the same insect are exposed, as is the case for a cicada which offers its dark dorsum to the sun at low body temperatures and its white ventral surface if it is too hot (Heath et al., 1972). In a few cases, notably for certain dragonflies (O'Farrell, 1963), grasshoppers (Key & Day, 1954) and beetles (Hadley, 1979), insects may change their colour and thereby thermal balance (O'Farrell, 1963).

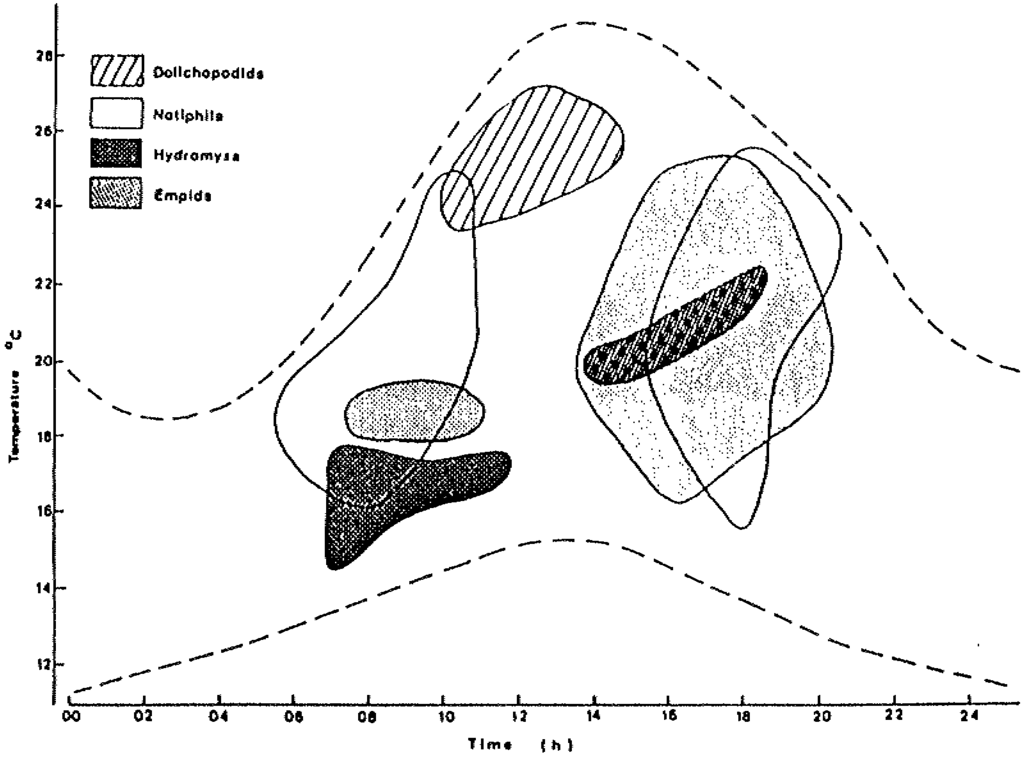

Figure 5. The interaction of microclimate (temperature) and of time in determining insect activities on lily pads. The dotted lines show the limits of recording conditiond, and the periods of maximum occurrence of each type of fly are de-limited by solid lines, the criteria being emphids, dolchipodids, and Notophila brunnipes >10; Hydromyza livens >5 (numbers per 10 min.) (from Willmer, 1982a)

The development of a reflectometer which can be simply constructed and used in the field (Willmer & Unwin, 1981b) has shown that insects of higher reflectivity do heat up more slowly than dark forms of the same size. Recent field studies have demonstrated a relationship between the mean surface reflectance of insects active at particular sites and received radiation at that site as it varies through time (Willmer, 1982b). These studies also confirm that most temperate insects have rather low reflectances, up to 25%. However, white forms in deserts may be much more reflective: Edney (1971) estimated a value of 79% for a white tenebrionid.

iii) Insulation

Insects may be insulated in various ways: by bristles, hairs or scales, and in some dragonflies by internal air sacs, thus creating a very local microclimate. Church (1960b) has shown convincing evidence for a thermal effect of hair in bees and scales in moths, which may be especially important in moving air during flight. The sub-elytral cavity of beetles may also have a useful role in insulation (Cloudsley-Thompson, 1964; Hadley, 1970) staying 2-7 °C hotter than the underlying abdomen.

iv) Behaviour

1. Posture

This may have a very direct effect upon thermal physiology, especially in those forms which live on very hot surfaces and exhibit 'stilting'. This phenomenon is recorded for many long-legged insects, including locusts (Waloff, 1963), grasshoppers (Chapman et al.,1926), tenebrionid beetles (Hadley, 1970; Hamilton, 1971) and tiger beetles (Dreisig, 1980). Simply by raising the body mass a few mm above the sand or rock surface, the insect may move to a microclimate some 10 or 20 °C cooler. By contrast, in conditions of low insolation in the evening, locusts may crouch against the warm ground to gain heat by conduction (Waloff, 1963).

Other clear examples of postural control are familiar from studies of the Lepidoptera (mainly butterflies). Adults may 'bask' either with wings outspread or side on to the sun to maximize radiative gain, or can adopt the alternative stance of wings closed together over the back and directed into the sun, reducing heat uptake (Clench, 1966; Watt, 1968; Kevan & Shorthouse, 1970; Wasserthal, 1975; Rawlins, 1980). During sunshine, Graylings (Hipparchia semele (L.)) present a maximal wing area to the sun's rays when the ambient temperature is relatively low, and a minimal area when it is high ('sunning' and 'heat-avoiding' positions respectively, Findlay et al., 1983). Porter (1982) found that under low ambient temperature, but high solar radiation intensity, the temperature excess of basking larvae of the butterfly Euphydryas aurinia (marsh fritillary) can attain 30 °C.

2. Orientation

This is an extension of postural control, whereby insects can alter their radiative balance by exposing maximum or minimum surface area to the surface. It is especially impressive in insects with elongate bodies (Digby, 1955), and in the Odonata (May, 1976) and Orthoptera (Willmer, 1982a) in particular. In locusts and stick insects, orientation across the windstream during insolation can reduce temperature excess by nearly 50% (Digby, 1955) and even small variations in air movement can be critical (Parry, 1951). Orientation effects also occur in the spruce budworm larva (Shepherd, 1958), and in desert caterpillars (Casey, 1976), where a ten-fold difference in insolated body area occurred as the larvae moved in three dimensions around their food-plant to stabilise body temperature.

3. Burrowing

The fossorial habit is well-established as a means of behavioural thermoregulation, especially in deserts where burrows are generally cooler, and are certainly more constant in temperature, than the surface. Here, beetles frequently use burrows to avoid high temperatures (Hadley, 1970; Hamilton, 1971). In temperate conditions, burrows provide a thermally desirable retreat from tiger beetles (Dreisig, 1980) and for solitary wasps (Willmer, 1982a).

4. Evaporative behaviour

A number of insects when extremely heat-stressed adopt behaviour patterns which allow for evaporative cooling. Bees may extend their tongues and evaporate collected nectar or saliva ('tongue-lashing')(Esch, 1976; Corbet & Willmer, 1980; Heinrich, 1980a, b) which can cool the head and thorax. Some sawfly larvae (Carne, 1962; Seymour, 1974) raise their abdomens and may extrude fluid over their posterior surfaces at temperatures above 37 °C, to keep body temperature below its upper critical limit.

5. Sun-shade alternation

'Shuttling' between sun and shade microclimates is probably the most ubiquitous method for regulating body temperature (May, 1979). Convincing evidence for the alternation of sun-basking and resting in shade to control body temperature is given for cicadas by Heath (1967; Heath & Wilkin, 1970) and for tenebrionid beetles by Edney (1971), who demonstrated control to within 1 °C as the animals moved within their naturally heterogeneous environment.

6. Flight

Flight in insects requires very high metabolic activity in thoracic muscles and, in many larger forms, the heat thus generated provides a means of raising body temperature. However, in small insects, the extra convective losses during flying may exceed any heat gains, and the insect may actually cool down slightly (Digby, 1955). In general, large, stout insects get warm when they fly, whereas slender, small insects get cooler when they fly (Unwin & Corbet, 1991).

b) Water balance

Just as with temperature control, insects may regulate their water balance both by internal metabolic or physiological effects and by behaviour appropriately coordinated with their environment. In the former category are mechanisms such as the production of metabolic water, particularly by the metabolism of stored fats, and the redistribution of solutes or water between different compartments of the body to minimise osmotic stress on critical tissues. In the latter group are behaviour patterns closely allied to those for controlling temperature, all resulting in the occupation of more tolerable microniches. Several reviews of the water relations and osmoregulation of arthropods (e.g. Barton Browne, 1964) all point to the extreme importance of conserving water to most insects at most times. Thus, in general, insects must seek rather cool and very moist conditions to limit losses of water (e.g. Platt et al., 1958; Kingsolver, 1979). However, there is the danger of increased pathogenic attack at high relative humidities, so that near-saturated habitats are in practice often avoided.

As with body temperature, a number of features of the insect itself and of its behaviour will affect its water content in relation to its environment. In some cases, these controlling factors are the same, since thermal and osmotic problems are so intimately linked, but particular effects of each variable may be rather different.

i) Size and shape

The difficulty of maintaining water content for an insect is essentially related to the properties of its exposed surfaces, and hence the parameters of surface area, shape and size are critical to loss of water and in turn to the degree of microclimatic control necessary. Of two insects differing only in scale, the larger will be at an advantage in terms of percentage water loss and its body fluids will therefore become concentrated less rapidly. Similarly, a compact shape without elaborate or flattened appendages will be an advantage. There is of course always the opposing need for reduced size to allow exploitation of small humid zones. Direct evidence is rather difficult to obtain, since other parameters such as permeability and surface ultrastructure may also covary. Willmer (1980) found that smaller third instar caterpillar of Pieris (white butterflies) lost water more rapidly than fifth instars, though here there was some indication that permeability was decreasing as the larvae aged.

ii) Permeability

Perhaps the single most critical factor controlling the water balance of terrestrial insects is the permeability of the exposed cuticular surfaces. The enormous literature on this subject was reviewed by Gilby (1980). Most insects have very impermeable cuticles, but the range of values measured for this material is very large and is well correlated with habitat (Willmer, 1982a). Permeability may vary widely in different areas of any one insect and may also change through the various stages of the life cycle. It may be modified by other factors, both internal and external. The profound effects of temperature upon cuticular properties are well known (Beament, 1958; Machin, 1980; Gilby, 1980). It is also likely that relative humidity can affect cuticle permeability (Loveridge, 1968; Humphrey, 1975).

iii) Behaviour

Most of the behaviour patterns which can help regulate body temperature will also affect water content and those which are used to raise the insect's temperature (sunbasking, and its interrelations with posture and orientation) will usually have adverse effects on water balance. However, most heat-avoidance strategies will take the insect into cooler more humid zones where water loss will be reduced, whether this involves stilting in deserts, burrowing or shade-seeking. In many cases, thermal considerations appear to outweigh the needs of water balance in determining microhabitat choice.

There are also some specific behaviour patterns which affect insect water balance. Mention has been made of techniques for increasing evaporation as an emergency strategy to lower body temperature. Related to this are techniques such as spiracle closing, or changes in the ventilation rate, which may be controlled in relation to ambient temperature, or more directly to humidity and water balance (Bursell, 1957; Miller, 1961, 1964; Loveridge, 1968; Krafsur, 1971a, b). A further example is the extrusion of salivary or excretory fluids. Alternatively, some insects may have the ability to take up water from non-saturated air either by exposing or everting special salivary-coated sacs or by mechanisms involving rectal pumping (Machin, 1979) and such behaviour may therefore be diagnostic of water-stressed insects.

c) Wind and shelter

Air movements have an important role in influencing the distribution of terrestrial arthropods, such as locusts (Rainey, 1958), aphids (Johnson, 1954) and spiders (Duffey, 1956). The nocturnal emergence of woodlice is inhibited by wind which removes the shell of moist air that surrounds a moist animal (Cloudsley-Thompson, 1958). Spiders disperse by 'ballooning', a form of aeronautic behaviour which they initiate by launching themselves into thermal updrafts (Greenstone, 1990). Other tiny wingless arthropods (e.g. immature insects) exploit air velocity gradients at the boundary layer (Washburn & Washburn, 1984). High wind speeds limit both the aeronautic dispersal of spiders (Vugts & van Wingerden, 1976) and the flight activity of insects, such as mosquitoes, horse flies and cicadas (Cloudsley-Thompson, 1960a).

Small, flying insects accumulate in the sheltered zones near to hedgerows (Lewis, 1969, and artificial windbreaks), especially to leeward. The height and permeability of such 'windbreaks', and the angle and speed of the incident wind, largely determine the patterns of distribution in the air (Lewis, 1966a, Lewis & Stephenson, 1966) which are reflected on the vegetation beneath (Lewis, 1965, 1966b). The effect is greater in windy than in calm weather (Lewis, 1969). Microclimatic variations associated with the structure and density of grassland swards, the presence of a litter layer, aspect etc., considerably influence the distribution of invertebrates within grassland and their persistence during adverse weather. Grasses, such as *Dactylis* (cocksfoot), *Deschampsia* (hair-grass), *Holcus* (e.g. *H.*

lanatus, yorkshire fog) and Poa (meadow-grass), with a tussock growth form provide shelter for beetles and other invertebrates in winter (Luff, 1966; Bossenbroeck et al., 1977a, b) and grassy field-edges with a well-developed litter layer provide important winter hibernation sites for carabid beetles (Desender et al., 1981).

Luff (1966) investigated the cold resistance of three beetle species. Under natural conditions, 100% mortality occurred at -8.5 to -10.5 °C with Dromius melanocephalus and D. linearis and between 42 and 65% with Stenus clavicorius. At -5 °C, mortality for all three species was ca. 20%. A clear protection was provided by tussocks of Dactylis glomerata (cocksfoot) in which the temperature did not sink below -4 °C. Between -2 and -4 °C mortality only occurred with D. melanocephalus. Large differences may be found in grass tussocks in the winter in relation to aspect. Stoutjesdijk and Barkman (1992) found that, with an air temperature of 1 °C, the surface temperature at the south side of a tussock of Deschampsia flexuosa (wavy hair-grass) was 19 °C, whereas at the north side it was -2 °C. Stoutjesdijk and Barkman (1992) observed ants (Formica rufa (wood ant) and F. polyctena) concentrating on the south sides of ant hills where temperatures were higher.