Chapter 8 Case studies

To illustrate some of the points made in the previous chapter, various case studies are presented. Firstly, woodlice are described as an example of a 'cryptozoic' animal which illustrates the point that most terrestrial invertebrates are continually in danger of water loss. Secondly, rare butterflies are considered since they represent a particularly specialized group of insect herbivores, whose existence is dependent on attributes of vegetation structure. Four species of dry grassland, one heathland and one woodland species are described. Finally, a detailed study of an orthopteran, the wart-biter (Decticus verrucivorus), is described since, like many of the British butterflies, it occurs at the northern edge of its range in the south of England and occurs in local, isolated populations, and is also very dependent on vegetation structure.

8.1 Woodlice: an example of a cryptozoic animal

Primitive invertebrates generally lead hidden lives since they are more prone to desiccation than more highly evolved forms. This may make these 'cryptozoic' animals more vulnerable to the effects climatic change particularly if they involve increased drought.

8.1.1 Introduction

As their name implies, cryptozoic animals lead hidden lives because they are in constant danger of desiccation and must remain in a damp, moist environment. Apart from spiders and insects, most terrestrial arthropods are cryptozoic and they are mostly rather small. Because they lose water rapidly by transpiration, the majority are active at night and spend the day in sheltered microhabitats. The nocturnal habitat confers several other advantages, even to animals that resist water loss. Enemies are more easily avoided, food more easily obtained and competition reduced (Crawford, 1934). As a result, primitive forms especially tend to be nocturnal. More highly evolved forms are quicker-moving, diurnal and can live in hot, light environments.

Woodlice are the classic example of cryptozoic animals because they form a reasonably homogeneous group containing several common species that show different degrees of adaptation to life on land (Edney, 1954). Lacking an effective waterproof epicuticular layer of wax (Cloudsley-Thompson, 1954), all the species must spend the greater part of their time in an atmosphere that is saturated with water vapour (Waloff, 1942).

However, there is considerable variation regarding their ability to withstand dry air, high temperatures and the period of time during which they can venture into dry places (Edney, 1954; Warburg, 1964, 1968). The most resistant in this respect in Britain is the pill woodlouse (Armadillum vulgare), which can survive in dry places for several hours and is often seen running about in the open during the daytime. Next in the series comes the common woodlouse (Porecellio scaber), easily recognized by its rough, granular integument, then the garden slater (Oniscus asellus) and finally the smaller (Philoscia muscorum) which soon dies from desiccation when exposed to dry conditions (Cloudsley-Thompson, 1962).

8.1.2 Diurnal and seasonal rhythms

Cloudsley-Thompson (1952) showed that the positive response to humidity of O. asellus is less strong in darkness than in light, and still less in the nocturnal phase: it increases with desiccation. Movement away from light is enhanced in animals which have been in darkness for some time, but desiccated animals tend to become photopositive. This can be related to the nocturnal ecology of the species. Woodlice often wander in dry places at night and this is permitted by the reduction in the intensity of their humidity responses. The increased photonegative response after they have been conditioned to darkness ensures that they get under cover promptly at daybreak. On the other hand, if their daytime habitat should dry up, woodlice are not restrained there. Movement away from light is enhanced in animals which have been in the darkness for some time, but desiccated animals tend to become photopositive.

When different species of woodlouse are compared, it is found that the degree of nocturnal activity is correlated with the ability to withstand water-loss by transpiration. P. muscorum, for example, transpires more rapidly, is more strongly photonegative and more strictly nocturnal than O. asellus or P. scaber, whilst A. vulgare is the least intensively nocturnal and photonegative (Cloudsley-Thompson, 1956). Seasonal changes in the response to humidity also occur. Woodlice show a marked response rise in the intensity of their humidity responses in spring. At the same time, seasonal changes in distribution occur and these vary between the species. Whereas P. muscorum remains under stones and litter throughout the year, the tiny Trichoniscus pusillus moves in summer from its winter habitat under stone to litter and dead wood. O. osellus is found mainly under stones throughout the year, but in summer it also occurs on dead wood and trees. Finally, P. scaber, whose winter habitat is at the base of trees, tends to move upwards during the summer. Changes due to succession may also occur, as for example, the log under which woodlice are living rots.

Williams discusses the diurnal and seasonal patterns of activity of carabid beetles (Williams, 1959a, b), harvestmen and spiders (Williams, 1962).

8.2 Rare butterflies

Extinctions among butterflies have been of a greater order of magnitude than those experienced by other groups of wildlife this century. In Britain, four indigenous species have increased in recent years and another seven species have remained stable overall: but the overwhelming majority have declined, in many cases with great rapidity, over large areas of their traditional ranges. To date, national extinctions have been rare in Britain, but in The Netherlands 17 out of 21 indigenous butterfly species have disappeared. Such losses have occurred only at the county level in Britain: for example, 42% of butterfly species have become extinct in Suffolk since the mid-19th century (Thomas, 1991). Losses have occurred in a wide range of biotopes, including nature reserves, and often among species whose foodplants remain common, widespread or abundant in the county. Thus, although many butterfly populations have disappeared from sites that have been destroyed, many have also become extinct in biotopes that look little different from when they supported the species and where the flora (and larval foodplant in particular) remains rich and abundant.

8.2.1 Dry grassland species

a) Maculinea arion (Large blue)

This is unusually specialised: eggs are laid on Thymus praecox and the larvae feed briefly on the flowers and seed before being adopted by Myrmica spp. of ant. Larvae are carried into the ant nests and become predators of ant brood for the next 9 months. The enigma was not that 50 of the species former 91 sites were ploughed or fundamentally changed in the period 1800-1970, but that it gradually disappeared from another 41 sites, including National Nature Reserves (N.N.R.), where Thymus and Myrmica remained abundant (Thomas, 1980).

The explanation lay in the fact that the young stages were more specialized than had been suspected, being specific to just one host, Myrmica sabuleti (Thomas et al., 1989). The need for one particular species of Myrmica, to coincide with Thymus, restricts M. arion to a narrow niche within its biotope. In England, adequate densities occur on southern south-facing slopes where the sward is also grazed to below 2 cm tall, whereas Thymus grows commonly in swards up to 10 cm tall. But M. sabuleti almost certainly needs a warmer microclimate than Thymus: on

British sites, an increase in the height of the sward from 1 cm to 5 cm is enough to reduce spring temperature at the soil surface by about 5 °C: the equivalent cooling effect of transporting the site from the south coast of England to the Orkneys.

By the mid 1970s, all but one British Maculinea arion (large blue) site had been largely abandoned by farmers, and rabbits were a negligible force from the mid 1950s to late 1970s, due to myxomatosis. Swards grew too tall for Myrmica sabuleti which declined to below the level needed to substain M. arion.

b) Lysandra bellargus (Adonis blue)

A similar story emerges for this species which also declined severely in c. 1955-1980 (Thomas, 1983a, 1990). Of the 91 extinct L. bellargus sites, 60 contained higher densities of the foodplant, Hippocrepis comosa (horseshoe vetch), growing over larger areas than the minimum needed to support a population, and there was no correlation between the abundance of H. comosa and the size of L. bellargus populations (Thomas, 1983a). The adults again proved to be specialized during egg-laying, when they selected H. comosa growing in very short turf (i.e. heavily grazed), especially where this grew on steep south-facing banks or in hoof-marks with a hot microclimate. The larvae are tended by ants which are more common in these situations. Suitable growth forms disappeared in many swards, that became overgrown following myxomatosis, leading to the extinction of L. bellargus populations within 2-3 seasons. No colony was found on a former site whose sward had grown above a mean height of 5 cm.

c) Hesperia comma (Silver-spotted skipper)

H. comma larvae feed solely on Festuca ovina (sheeps fescue). This fine grass still dominates much calcareous grassland in Britain, yet the butterfly has never been recorded from most southern downs where the foodplant is dominant, and disappeared from most occupied sites in c. 1955-80 (Thomas et al., 1986). H. comma needs a short warm sward for egg-laying: the ideal Festuca plant is 2 cm tall, 1.7 cm in diameter, and has 75% of its edge abutting onto bare ground, typically chalk or limestone scree. There is some latitude in choice, but most plants in a very short (< 1 cm tall) or dense sward are rejected, as are those growing in a tall one. Selective light rabbit grazing on thin-soiled downs often produces suitable plants. Adult population density of H. comma was correlated with how closely the sward approached the ideal structure for egg-laying. Most sites that had lost H. comma still contained abundant F. ovina, but were too overgrown to be suitable for breeding. Most extinctions of H. comma occurred during a twenty year period, when sites became overgrown after rabbits were killed by myxomatosis.

d) Thymelicus acteon (Lulworth skipper)

The larvae of this species eat only Brachypodium pinnatum (tor grass), but the species has an extremely restricted range in comparison to its foodplant, being confined to south-facing downs and undercliffs in south-east Dorset and to three similar sites in Devon and Cornwall (Thomas, 1983b). This insect increased greatly during the cool wet summers of 1955-80, often on the same sites where L. bellargus declined. By 1978, there existed several T. acteon populations with tens or hundreds of thousands of adults, and the butterfly had spread to occupy many new sites within its traditional range (Thomas, 1983b).

The females are highly selective in their choice of egg-laying sites. They choose large clumps of sheltered B. pinnatum that are at least 10 cm tall and preferably more than 30 cm. Although warmth-loving, the larva escapes the cooling effect of a tall sward by living high up in the hottest vertical zone, a few centimetres beneath the windswept tips (Waterhouse, 1955; Thomas, 1990). Ironically, the same agricultural changes that reduced M. arion, L. bellargus and H. comma populations had the opposite effect on T. acteon. Useless short swards of B. pinnatum were released to grow into tall clumps essential for egg-laying, and the butterfly's previously scarce habitat suddenly became common within its south-facing unimproved calcareous grassland.

8.2.2 A heathland species: Plebejus argus (Silver-studded blue)

The ecology of this butterfly has been studied at the north of its British range in North Wales (C. D. Thomas, 1983, 1985a, b), in Suffolk and Devon (Read, 1985; Thomas, 1991). Larvae eat a wide variety of plants, including Ericaceae, Ulex spp. (gorse) and Lotus corniculatus (birds foot trefoil) (C. D. Thomas, 1985a), yet this is a scarce and declining species that is absent or has disappeared from many apparently suitable sites.

Potential foodplants for egg-laying are chosen only when these grow under very precise conditions especially in the north (C. D. Thomas, 1985a). In Wales, there was a strong preference for laying eggs adjacent to bare ground, in short (< 7 cm tall) patches of vegetation, and on south-facing slopes (C. D. Thomas, 1983, 1985a). This placed them in the hottest available microclimate: on average, slopes facing south were 7 °C warmer than those facing north, and the preferred short swards were 8-13 °C hotter than nearby taller vegetation (C. D. Thomas, 1985a). In these oviposition sites, foodplants produce the tender young growth that alone is palatable to larvae, and there exist high densities of the ant, Lasius niger (garden black ant), which has a close symbiotic relationship with P. argus (C. D. Thomas, 1983). In Wales, the species depends on a 'pioneer' heathland habitat that exists for the first 5 years after a disturbance or fire (C. D. Thomas, 1985 a, b). Its needs are much less exacting in the warmer regions of Devon: colonies are not restricted to south-facing aspects and can breed through the entire 'building' phase of Calluna regeneration lasting from ca. 5-15 years (Read, 1985).

8.2.3 A woodland floor species: Mellicta athalia (Heath fritillary)

This became the most endangered British butterfly after Maculinea arion (large blue) disappeared in 1979. By 1980, an extrapolation of its decline suggested that M. athalia would become extinct within 10-20 years (Warren et al., 1984). Warren (1987a, b, c) found that the larvae need an abundance of Melampyrum pratense (common cow-wheat) growing in early successional stages: populations increase exponentially for 3-4 years after vigorous coppicing is cut, but are completely shaded out after 5 year of regrowth. M. athalia became rare because modern commercial woods seldom possessed continuity of its ephemeral habitat.

8.2.4 Conclusions

In most of the butterfly species described, the young stages were found to require considerably more specialized conditions than had been suspected, which restricted them to narrow niches within their habitats, usually corresponding to a short-lived seral stage and often to a warm microclimate. Thomas (1991) suspected that most butterfly species that are today restricted to very warm microclimates would have become extinct between 4500 and 2500 year ago, had it not been for man's clearances and management of the land. Summer temperatures fell by about 3 °C during this period, a cooling that would have been compensated for by the warm microclimates created within young woodlands, grasslands and heathlands. It seems likely that warmth loving species became restricted to these hot man-made refugia at this time, as well as to south-facing aspects, where they remained trapped for the next 4,000 years. In other words, extinctions were postponed until the present century, when new forms of management resulted in the disappearance of warm microclimates from most types of biotope. The re-implementation of traditional management practices on sites where populations have gone extinct or are seriously declining may provide the necessary microclimatic conditions to permit their recovery. However, if the climate warms up as predicted the availability of suitable sites (i.e. hot spots) may increase and the larval stages of butterflies may no longer be limited to very short vegetation patches.

8.3 The Wart-biter

8.3.1 Introduction

The large ground-dwelling bush cricket, Decticus verrucivorus (L.) (Orthoptera: Tettigoniidae), is widespread in Europe, but appears to be declining in Denmark, southern Sweden and Great Britain at the northern edge of its range (Marshall & Haes, 1988). In Britain, it has only four populations in southern England (three chalk grassland and one heathland site, Haes, 1976; Webb & Tuck, 1984) and as such is one of Britain's most endangered species. The species is listed as fully protected under schedule 5 of the 1981 Wildlife and Countryside Act (Shirt, 1987). Population sizes vary between 20 and 100 adults in most years. Historical records show that the 'wart-biter' has been rare in Britain since at least the early 1800s (Marshall & Haes, 1988). The four remaining populations lie within Sites of Special Scientific Interest (S.S.S.I.) and two are within National Nature Reserves (N.N.R.). Uncertainty as to the species habitat requirements has hampered positive site management for its conservation. This is clearly demonstrated by the loss of a population from a nature reserve in East Kent after a period of excessive grazing in the late 1970s (Shirt, 1987; Marshall & Haes, 1988). Cherrill and Brown (1990a, b) conducted a three-year field study on the largest of the populations, which occurs on chalk grassland in East Sussex, with the aim of providing baseline information on the species' ecology. This programme is ongoing as part of the English Nature Species Recovery Programme.

8.3.2 Life-cycle and population dynamics

Cherrill and Brown (1990a) described the post-embryonic development and distribution of the wart-biter, in relation to microclimate. Egg hatch occurred in mid-April, there are seven nymphal instars and adult emergence occurred in July, although its timing was strongly influenced by weather. During this time, densities fell by 99.3%, yet adult survival was high. The population was estimated to contain at least 290 adults in 1987 and 190 in 1988. After emergence, adult females almost doubled in weight, but did not reach their maximum weight (and potential fecundity) until September. No adults survived beyond mid-October. Realised fecundity may therefore be severely curtailed by poor weather in September.

Many studies have demonstrated a positive relationship between body temperature, as determined by solar radiation, and rates of development and reproductive output in Orthoptera (e.g. Behrens et al., 1983; Remmert, 1985). Nymphal development in D. verrucivorus occurs most rapidly at 33 °C and ceases below 20 °C (Ingrish, 1978). Using the Chorthippus brunneus (common field grasshopper), Begon (1983) has shown that in the field internal body temperatures of 30 °C can rarely, if ever, be achieved in Britain in the absence of sunshine. Thus, the dynamics of British orthopteran populations are likely to be crucially dependent on the amount of sunshine in the spring and summer. An analysis of the numbers of adult D. verrucivorus in Sussex between 1969 and 1987 (Haes et al., 1990) found that 54% of the variation in numbers is explained by the number of sunshine hours experienced by the adults in the summer two years previous. The correlation is probably biologically meaningful, since the eggs usually hatch in the second spring after oviposition (Ingrish, 1986) and fecundity may be determined by insolation (e.g. Begon, 1983).

8.3.3 Habitat requirements and distribution

Within the study site, densities were influenced positively by mean temperatures and were highest on a south-facing slope. Mean temperatures were determined by interactions between weather, aspect and vegetation structure. The vegetation was predominantly below 5 cm in height, but comprised a mosaic of vegetation types, such that sampling units of 25 m^2 typically contained both close-cropped turf and tussocks (Cherrill & Brown, 1990b). Both final instars and adults were found predominantly in patches of tussocky vegetation, which had a height of around 20 cm and covered 25% of the study site. The taller vegetation may provide a preferred microclimate, a greater abundance of food and/or shelter from predators. The latter appears most probable. Cherrill and Brown (1990a, 1992) found that temperatures within grass tussocks were lower than in open areas of turf and that D. verrucivorus is extremely thermophilic. Hence, grass tussocks are unlikely to be selected for their microclimate. Similarly, diet is unlikely to explain their distribution, since both nymphs and adults are omnivorous and catholic in their diets (Cherrill, 1989). Evidence that predation may be important is persuasive. In 1987, 5.2% of adults had severed femora, hind tibiae or ovipositors. A further 13.0% had an entire leg missing, while an adult female was found with triangular beak marks on her abdomen. Final instars weighed 0.7 g and adults up to 2.5 g (Cherrill & Brown, 1990a). They must therefore present an attractive food to vertebrate predators, mainly birds.

8.3.4 Ontogenetic changes

The distribution of male instars and male adults was similar. However, adult females were more frequently in areas of short, open turf than male adults or final instars. Consideration of the species' egg laying behaviour (Cherrill et al., 1991a) suggests that adult females were leaving the shelter of grass tussocks to oviposit in adjacent open areas with small patches of bare soil ('hot spots', Cherrill and Brown, 1990b). Thus, first instars were strongly associated with short, sparse turf, reflecting the oviposition behaviour of females. Subsequent early instars were also found in short, open turf, but at the fifth moult a distinct shift in distribution to dense tussocks occurred. Late instars and adults were strongly associated with these structures, probably to avoid vertebrate predators. Mean temperatures within dense grass tussocks were lower than in short turf, but these highly mobile stages actively thermoregulate by basking on the sides of tussocks. In contrast, areas of short turf may be crucial for the development of the smaller and less mobile early instars and eggs (Cherrill & Brown, 1992b).

Hence, in cases where spatial differentiation of the microclimate occurs on a smaller scale, insects search for the most favourable situation which varies with their stage of development. Lensink (1963) studied the behaviour and microdistribution of three grasshopper species in dry dune grasslands and found similiar ontogenetic changes. The vegetation consisted of a small-scale mosaic of seven types which differed in structure and microclimate. In spring and summer the animals migrate from the warm, open sunny types to the cooler and moister types. Later, the females return to the former types in order to lay their eggs. During cool summers the animals stay longer in the open sunny spots. The highest densities were found where spots with a favourable microclimate for egg laying and hatching of larvae are found close to spots with the most favourable microclimate for larvae and adults.

A mosaic of vegetation structures may also be important in enhancing mate location when population density is low, because propagation of male song is greater over short turf than through dense vegetation (Keuper et al., 1986). Cherrill and Brown (1992b) also mention that, in adult males, the preference for grass tussocks can also be attributed to their use of these structures as song perches. Weidemann et al. (1990)

studied the distribution and population density of D. verrucivorus in a damp meadow in Germany and concluded that larval distribution reflects the distribution of oviposition sites, but the distribution of adult males, though also depending on the distribution of resources and climatic factors, is produced mainly by the acoustic interactions with other males.

8.3.5 Body size and coloration

Adult wart-biters from Sussex lie at the bottom of the size range recorded for continental Europe (Samways & Harz, 1982). In particular, the forewings are unusually short (Cherrill & Brown, 1990a). Cherrill and Brown (1992a) found that specimens from heathland in Dorset were larger than those from chalk grassland in Sussex, as previously indicated by Haes (Marshall & Haes, 1988). They also found sexual dimorphism in body size in the latter population. Females were larger and this was associated with a longer period of development. In other Orthoptera, body size is known to show considerable plasticity in response to environmental factors, such as temperature, food availability (quantity and quality) and density of competitors (e.g. Grayson & Hassall, 1985; Wall & Begon, 1987; Atkinson & Begon, 1988).

The colour of continental specimens is highly variable ranging from green through yellow-brown to blackish brown and even red (Holst, 1986) whereas, the range of colouration described in British material is somewhat limited (Marshall & Haes, 1988). However, Cherrill and Brown (1991b) discovered a wide diversity of colour patterns in the early instars, and three distinct colour forms in the later instars and adults, within the largest population in southern England. They found a high relative abundance of a cryptic green form which suggests that predation by visual hunters has been important in the evolution of colour patterns in this population. Gill (1979) discovered associations between variation in colour-pattern and habitat in the grasshopper, C. brunneus. Fraser Rowell (1971) discussed the variable coloration of the acridoid grasshoppers, the role of genetic and environmental factors, physiological mechanisms and pigments.