

The response of insect faunas to glacial–interglacial climatic fluctuations

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SUMMARY

The extinction of species of small invertebrates is difficult to recognize. However, in deposits that date from the past few million years, insect fossils are remarkably common and provide objective data on the history of the organisms that constitute the biotic communities of the present day. It might have been expected that the great climatic oscillations of the glacial–interglacial cycles should have caused widespread extinctions, if their effects on the large vertebrates is taken as our model. Yet the record of Quaternary fossil insects shows no high extinction rates during this period. Constancy of species and communities of species can be demonstrated to be the norm for at least the last million or so years (= generations).

The enigma of how such constancy was sustained in the face of large-scale climatic fluctuations remains a puzzle though several possible solutions are suggested. These solutions carry implications for our estimates of present and future extinction rates.

1. INTRODUCTION

Extinction may be easy enough to define in theory but in practice it is much more difficult to recognize even among the most conspicuous inhabitants of our planet. Among the very small and often cryptic animals such as many species of insect, extinctions may be almost impossible to demonstrate, despite the subjective conviction that a great many species are currently being exterminated by the burning of rain forests or the drainage of marshlands. Even if we cannot quantify their extinction rates under these circumstances, the fact can hardly be doubted that at this moment, the Earth is losing a wealth of biodiversity at a higher rate than at any time in its geologically recent past. This is regardless of the fact that during the latest 2.4 million years of earth history (the Quaternary period), our planet has been subject to the frequent and intense climatic changes of the glacial–interglacial cycles, which are well known to have had drastic effects by redistributing the biota of the times and were apparently the cause of widespread extinctions of the megafauna. It is well to remember that these climatic oscillations have not come to an end and that there can be little doubt that the present-day climate represents an interglacial interlude in an otherwise dominantly glacial period. The latest phase of arctic climate in Britain came to an end a mere 10 000 years ago.

How did insects respond to the challenge of such drastic environmental changes? Fortunately there is a wealth of fossil (or rather subfossil) evidence that can provide objective information as to how the insects actually met these challenges. It is now possible to

answer some hitherto unanswerable questions. For instance, were there episodes of global extinction of insect species, followed by major speciation events, paralleling for instance, the extinctions and evolution among the mammals at this time?

In the light of the global-warming hypothesis, we may ask to what extent have our faunas (and floras) ‘seen it all before’ at the start of every interglacial? Can they be expected to weather the coming storm in the same manner as they did in the past? In other words, will the stratagems that they adopted then in response to natural hazards, suitably equip them to survive those of human origin? In short, does the past provide a key to understanding the future?

2. QUATERNARY ENVIRONMENTAL CHANGE

To understand the structure and development of the Earth’s biota of the present day, it must be set against the backdrop of the extraordinary events of Quaternary environmental change. During the past two million years there have been numerous and intense climatic oscillations that were widespread and as severe as any recorded in the earliest phases of our geological history. Because of the proximity of this period to the present day, it has been possible to document these events in more detail by both quantifying the changes involved and by providing a more precise chronology than can be obtained in the more remote parts of stratigraphical history.

With the advent of deep ocean coring programmes in the past few decades it has been possible to obtain long continuous records of climatic events that were

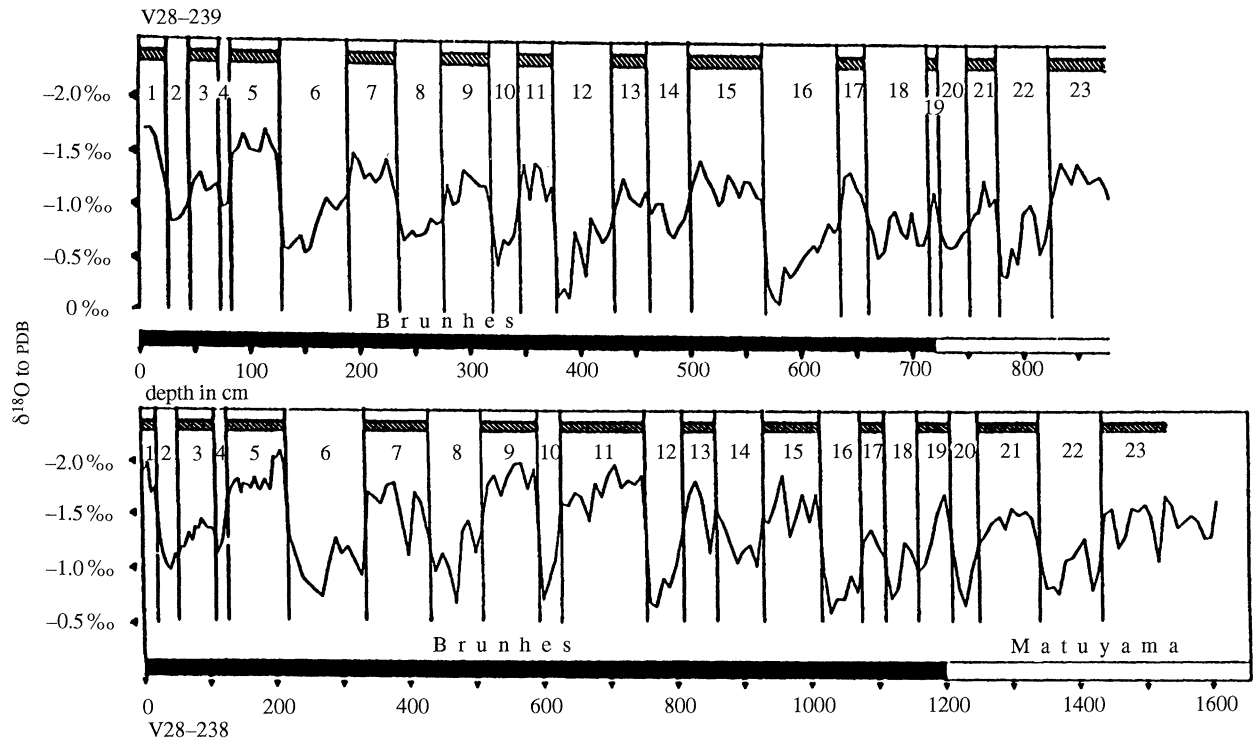


Figure 1. Oxygen isotope records of cores V28-238 (below) and V28-239 (above). These levels are largely controlled by variation in global ice volume. The numbers along the top of curves indicate the isotope stages, odd numbers indicate periods of relatively low ice volume (i.e. more temperate) and even numbers indicate periods of relatively high ice volume (i.e. more glacial) periods. The Brunhes-Matuyama magnetic reversal boundary is globally dated at about 735 000 years ago and is situated in isotope stage 19. The present-day interglacial is represented by isotope stage 1. (From Shackleton 1977; by permission of Oxford University Press.)

global in their effects (Shackleton 1977). Figure 1 illustrates the past 750 000 years of this record. It has now become apparent that the climatic oscillations were more numerous than hitherto suspected from a traditional interpretation of the terrestrial record, and that the climates changed with great rapidity and intensity during this period. It has also become evident that the climatic régime of the present day is unusual in this long term context in which normality would seem to be represented by a glacial rather than an interglacial climatic mode.

The drilling of deep cores into the world's ice-caps such as those of Greenland and Antarctica, have shown even more intimate evidence for the suddenness of these climatic changes. By counting annual ice layers it has been possible to give a more precise measure of the times involved. Thus the transition from the Last Glaciation to the present-day interglacial appears to have taken place in about fifty years (Dansgaard *et al.* 1989). Similar rates of climatic change towards the close of the Last Glaciation were inferred from studies of fossil insect communities in western Britain (Coope & Brophy 1972). If these rates of change are typical for other transitions between glacial and interglacial climates, they provide some measure of the scale of the climatic challenges posed by the fluctuations in the natural environment of the geologically recent past; challenges that were faced by the direct precursors of the present-day fauna and flora.

A more extensive treatment of these Quaternary climatic changes will be given in Coope (1994); there are also numerous synopses that deal with the more detailed response of the various components of the biota to the broad environmental changes (e.g. Bowen 1978; Lowe & Walker 1977).

According to the traditional interpretation it might have been expected that widespread extinctions would result from such frequent, intense and rapid climatic changes with their attendant ice sheets periodically covering large parts of the continental masses and global sea level varying by as much as 100 m. The mass extermination of many of the large mammals and birds during the Quaternary period would appear to support this expectation. However, the less well known and certainly less spectacular insect fossils tell a very different story.

3. QUATERNARY FOSSIL INSECTS

The only objective evidence of the animals and plants that actually lived in the prehistoric past is fossil evidence. On the basis of living organisms alone it is of course possible to make inferences about their biogeographic histories, possible evolutionary changes or even extinction events, but in the end it is the test of palaeontology that determines how close our surmises have been to reality. Fortunately, there are now enough insect fossils from various phases of the Quaternary to permit a number of generalizations to

be made about their biogeographical history, evolution and possible extinctions in the face of the great climatic oscillations of the glacial–interglacial cycles.

The insect fossils that concern us here may be found in great numbers in a wide variety of sediments, provided that they have remained more or less waterlogged and preferably anoxic since the time of their deposition. Suitable localities include lake basins or even relatively small pools into which terrestrial debris has been continuously washed from the adjacent land surface. Places such as these often preserve fairly continuous sequences that may date back for many thousand years. Overbank deposits on the flood plains of ancient rivers, left behind at the present day as terrace remnants, can extend the record still further back in time to hundreds of thousands of years but in such cases the sequences are discontinuous and often represent short-term events only. Many peat bogs provide continuous inventories of faunal and floral changes over the past 10 000 years and archaeological excavations into wet deposits can bring the story up to the threshold of historic time and the commencement of scientific record keeping.

Unlike most of the fossils of classical palaeontology, Quaternary insect fossils are not mineralized but are represented by the original chitin of their exoskeletons. Because insect taxonomy is largely based on exoskeletal characters and because we are dealing with the original material, it is possible to make precise comparisons of the fossil with modern specimens. Thus the fossils can be identified by using exactly the same criteria that are employed by entomologists to differentiate between present-day species. The same species concept can thus be used in both entomology and palaeoentomology and the same nomenclature can be adopted for both modern and Quaternary specimens.

In the discussion that follows, most of the conclusions will be drawn from the Coleoptera (the beetles) simply because their robust skeletons make such good fossils. It must be born in mind, however, that the beetles are in no way exceptional with regard to their evolutionary and biogeographic histories; i.e. what applies for beetles, applies for other orders of insect too. Some of these orders are well represented in the fossil assemblages but are rather more difficult to study. They have up to now been overshadowed by the more conspicuous and exciting Coleoptera. Thus the Diptera are particularly abundant but often in a very crushed state of preservation. On the other hand chironomid larval heads are frequently so common that they can be analysed statistically to give significant evidence on limnic environments (Walker *et al.* 1988). Hymenoptera are represented by numerous highly distinctive skeletal elements but in this case the problem seems to be that modern taxonomy makes secure identification very difficult. Hemiptera are fairly common also and would certainly merit specialist attention. Trichoptera were probably one of the earliest colonizers of lakes and ponds after the retreat of the ice and their larval sclerites provide much palaeolimnological information (Wilkinson 1984, Williams 1988). Odonata are represented by undiagnostic segments and the robust central part of the heads of

damsel flies. Orthoptera are almost completely absent from our fossil assemblages and Lepidoptera occur only as occasional caterpillar jaws.

The literature on Quaternary Entomology is widely scattered and often rather inaccessible. To overcome this problem a bibliography and literature review has been recently compiled (Buckland & Coope 1991). In this review it will be seen that most of the early workers in this field (i.e. up to the 1950s) attributed Quaternary fossils to new species, basing their interpretations on the notion that speciation and extinction was widespread among insects at the present day and that the fossils dating from tens, or even hundreds of thousands of years ago must therefore represent extinct species that had either died out or evolved into something else. The challenge of the complex Quaternary climatic changes appeared to provide ample justification for this expectation and the immense diversity of insect species reinforced this sense of rapid, ongoing evolution.

This view that successive glacials and interglacials caused widespread extinctions of insect species and complementary speciation events cannot now be sustained. In the past few decades, intensive investigations of Quaternary insect fossils in Britain, Sweden, Denmark, France, Russia and North and South America, have all shown that species remained constant both in their morphology, and in their environmental requirements throughout the whole of the Quaternary period. From the British Isles alone there are now over 2000 species of beetle represented by fossils that are the precise match of their present-day equivalents. What is more, there is no large backlog of distinctive but unidentified fossil that could represent the remains of extinct forms.

Outlined below are a selection of species that have been found in Quaternary deposits in Britain but did not resemble any familiar European species. These species originally seemed to be suitable candidates to be considered as extinct species. However, each has subsequently been found living at the present day, albeit in rather unexpected places.

1. *Carabus maeander* Fisch. This is a North American and Asiatic species whose present-day range in Siberia reaches as far west as the Lena river. It has been found as a fossil in deposits that date from the Upton Warren Interstadial, in the middle of the Last (Devensian, Weichselian or Wurm) Glaciation (Coope 1962; Briggs *et al.* 1985)

2. *Helophorus obscurellus* Popp. This species is a predominantly Siberian species that lives today on the tundras that border the Arctic Ocean and also on the high cold steppes of central Asia. Its nearest locality to Britain today is the Kanin Peninsula in arctic Russia. As a fossil this species has been found commonly in Britain, and on the adjacent continent, in deposits laid down under cold conditions. It only became extinct in Britain about 10 000 years ago. The fossils were originally described as *H. wandereri* by d'Orcymont in 1927, in the belief that they represented an extinct species, but were recognized as representatives of a living species by R. B. Angus (in Coope 1968).

3. *Helophorus arcticus* Brown. This is an almost

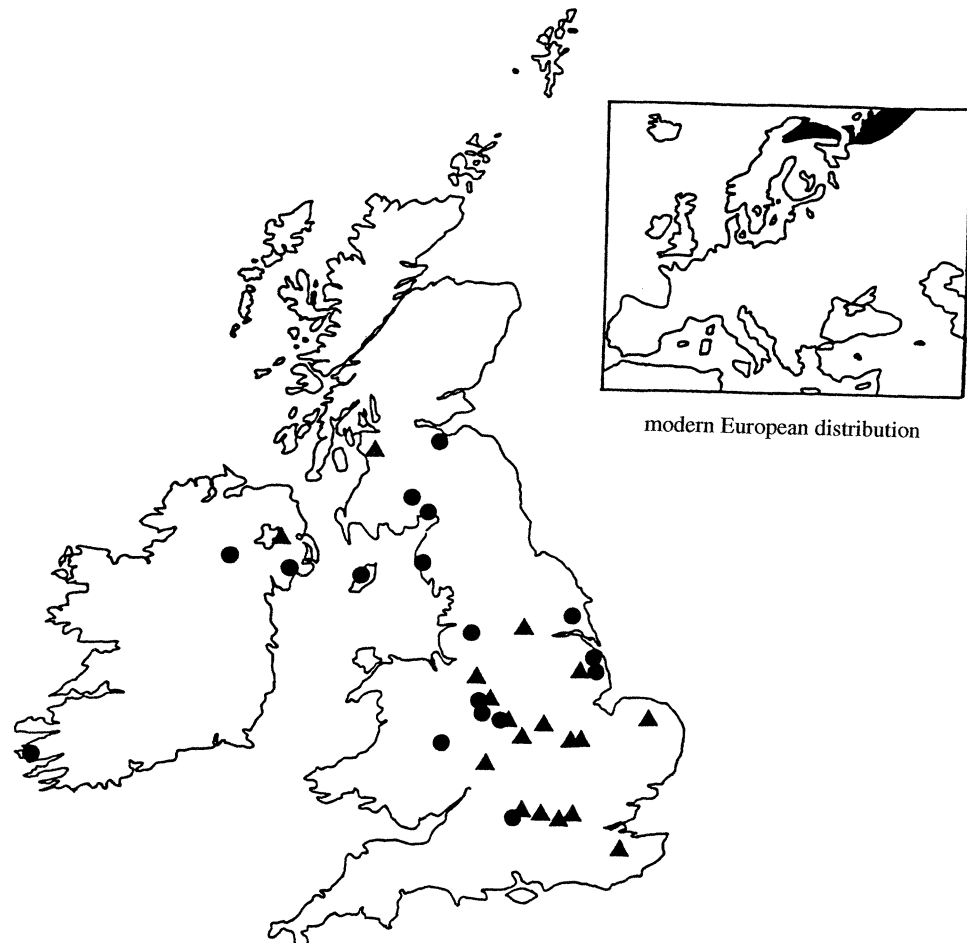


Figure 2. Locations of fossil sites in the British Isles for *Diacheila arctica* Gyll. Filled triangles, Devensian (=Weichselian) Glacial and Interstadial sites; filled circles, Devensian Lateglacial (cold) sites.

exclusively arctic North American species that has also been recorded from the northwest of the Kamchatka Peninsula in eastern Siberia (R. B. Angus, personal communication). As a fossil it has recently been recovered from Middle Pleistocene deposits at Ardleigh, Essex. (G. R. Coope, unpublished data).

4. *Micropeplus dokuchaevi* Rjaburkhin. This species has a significant taxonomic history. It was first described by Matthews (1970) from Pliocene deposits in Alaska that were sealed by a lava flow from which a date of 5.7 million years was obtained. He named the species *M. hoogendorni* in the belief that it was extinct and could be the precursor of a present-day species. Matthews' species has subsequently been equated with the living Siberian species *M. dokuchaevi* Rja (M. J. Campbell in correspondence to Scott Elias, 1993). As a fossil it has been found at three Middle Pleistocene sites in the English Midlands (Shotton *et al.* 1993).

5. *Oxytelus (Anotylus) gibbulus* Epp. This species is almost entirely confined at the present day to the Caucasus mountains, but there is a single enigmatic record from the Ussuri region of eastern Siberia (Hammond *et al.* 1979). This species was at times the most abundant staphylinid beetle in deposits at a number of sites in the English Midlands that date from the interglacial equivalent to 'isotope stage 7' (see figure 1), namely from about 200 000 years ago. It continued to occur sporadically in Britain up to the

Upton Warren Interstadial in the middle of the Last Glacial period where the distinctive head was illustrated in the hope that, if it was still living, someone might recognize it (Coope *et al.* 1961).

6. *Tachinus jacuticus* Popp. Today this species is almost totally confined to Siberia with only a single outpost in northeastern Russia. It occurs in Britain as a common fossil in deposits that accumulated during the middle phases of the Last Glaciation (Ullrich *et al.* 1974). It recolonized the British Isles as the ice-sheets finally retreated, only becoming extinct here about 10 000 years ago when the climate suddenly ameliorated at the beginning of the present interglacial.

7. *Tachinus caelatus* Ullrich. At the present day this species appears to be restricted to the mountains near Ulan-Baator in Mongolia (Ullrich 1975). As a fossil it has been found frequently in England in deposits that were laid down under cold continental climatic conditions (Taylor & Coope 1985).

8. *Aphodius holdereri* Reitt. Today, this species is confined to the high plateau of Tibet and the adjacent parts of northwestern China. As a fossil, this species was the most abundant large dung beetle in Britain during the cooler parts of the Last Glaciation (Coope 1973).

Many other examples could have been chosen from the Quaternary fossil record but they all carry the same message; that there is no evidence to support the

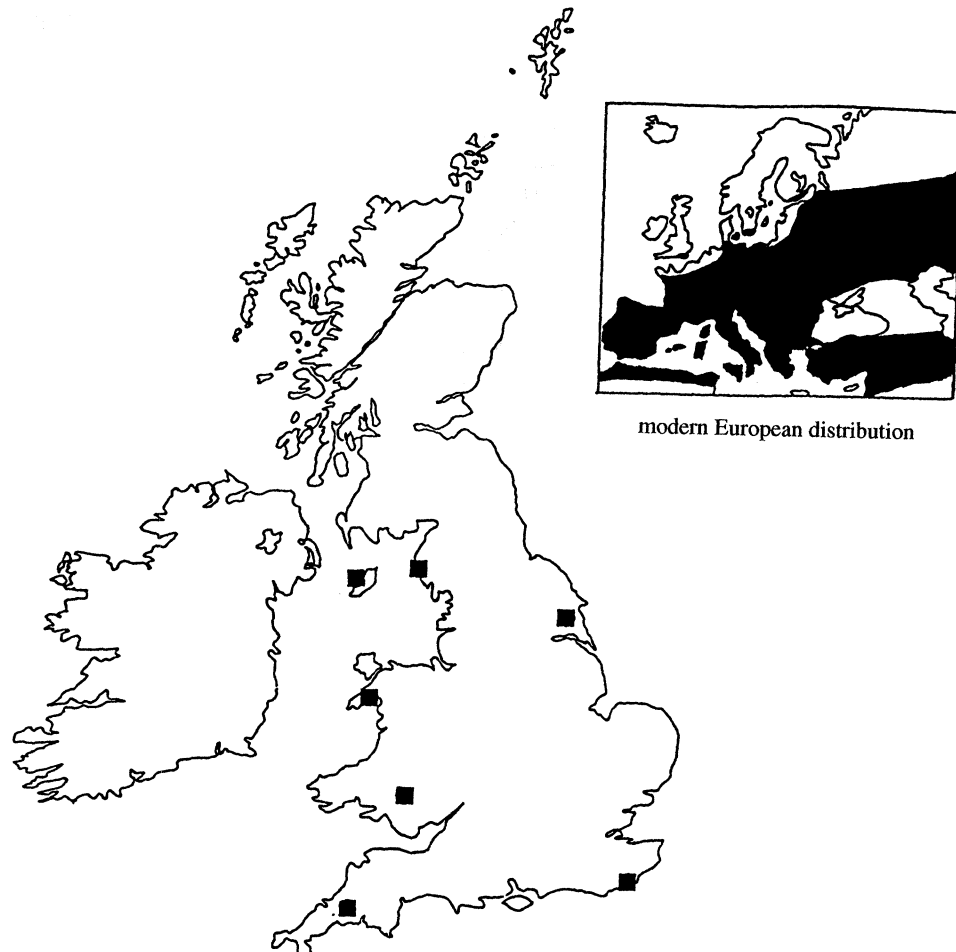


Figure 3. Locations of fossil sites in the British Isles, for *Bembidion octomaculatum* Goeze. Filled squares, Devensian Lateglacial (warm) sites.

view that major episodes of global extinctions of insect species resulted from the numerous large-scale climatic changes of the Quaternary period. Certainly these climatic changes caused local, often catastrophic extinction events but, enigmatically, global extinctions would seem to have been remarkably rare.

The above examples also show the enormous changes in the geographical ranges of insect species that had been forced upon them by the severity of the Quaternary climatic changes. In most of these cases, the changes of range have taken place within the Last Glacial and the ensuing Postglacial (present-day interglacial) but ample evidence is now building up that indicates that similar species movements accompanied each of the major climatic oscillations.

To further illustrate the ways in which geographical distributions of species have altered in both space and time, even within the relatively short period of the latest glacial–interglacial cycle, two species have been selected to represent the shifts in range of ‘northern’ and ‘southern’ species (for further examples see Coope (1994)). The locations of fossil occurrences in the British isles of each species are shown together with a small map of its present-day European distribution in figures 2 and 3. These examples also serve to illustrate the wealth of data on the biogeographic history of

insect species that is gradually being built up from Quaternary fossils.

1. *Diacheila arctica* Gyll (figure 2). This species was a frequent member of the Glacial fossil assemblages in the British Isles where it was found in company with numerous other arctic and many Asiatic species. During the period maximum ice sheet expansion at about 18 000 years ago when the climate was at its most severe, the species may well have become extinct in Britain. The map shows that it returned to both Britain and Ireland after the retreat of the ice, during the Lateglacial period. After this there are no fossil occurrences of this species in Britain.

2. *Bembidion octomaculatum* Goeze (figure 3). This species is extremely rare today in the south east of Britain where it does not seem to be able to establish viable populations. As a fossil it has been found in England during a short temperate period between 13 000 and 12 500 years ago, well to the north of its present-day range. Even as far north as Cumbria it would seem to have been sufficiently abundant to represent a breeding group (Coope & Joachim 1980). It then disappeared from Britain during the cold period that ensued but returned again well to the north of its present-day range, at the time of the sudden climatic warming shortly after 10 000 years

ago. The contraction of its range is apparently a postglacial phenomenon.

4. DISCUSSION

We are now in a position to answer the first of the questions posed earlier in this chapter; how did the insects respond to the challenges of large-scale climatic changes of the geologically recent past? It would seem that a species has three possible responses to any major environmental change: (i) it may evolve out of trouble; (ii) it may move out of trouble; or (iii) it may become extinct. As pointed out earlier, the rates of change of past climates were often dramatically sudden, so that conditions have changed from fully glacial to fully interglacial within the time span of one human lifetime. The rapidity of such events makes adaptation by genetic change almost impossible. On the other hand, the mobility of insects is such that they can readily alter their ranges as the climate changes and suitable climatic areas can be tracked across the continents. Paradoxically therefore, the conditions in which a species actually lived remained effectively constant, regardless of the climatic changes. In a relative sense, under these conditions it is the geography that changes. Thus, provided that the mobility of a species is adequate and land space is available, there should be no greater risk of extinction just because the climate swings back and forth between glacial and interglacial extremes.

If, however, the mobility of a species is restricted for some reason, say because its photoperiodic requirements make it impossible to change latitude, any necessary tracking of acceptable climates may be impossible and extinction a likely outcome. This hypothesis can be tested. The major climatic oscillations in the northern hemisphere appear to have begun quite suddenly at 2.4 million years ago (Ruddiman & Raymo 1988) and the obligation for thermally sensitive species to follow the location of suitable climates must have been initiated at about the same time. It is therefore interesting to note that in studies of Upper Tertiary insect faunas from Alaska and arctic Canada by Matthews (1974, 1976), and from the far north of Greenland by Böcher (1986), among the many species that are identical to modern ones, there are a few that appear to be genuinely extinct and which do not seem to have survived into the succeeding Quaternary period. Their extinction seems to have occurred in late Tertiary times. These species may represent those that failed to track the appropriate climatic conditions after the great oscillations began at the beginning of the Quaternary, 2.4 million years ago. A corollary to this hypothesis is that any species that could survive the first major challenge could, by adopting the same stratagem, survive all succeeding ones. It is as if we view figure 1 as a hurdle race in which any species that could leap the first gate successfully, could leap all the rest.

Another way in which a species might be denied the necessary mobility is by isolation on an island from which escape is impossible. An oceanic island or equatorial mountain top would suffice. Under such

conditions of long-term isolation only two of the three alternatives remain as possible responses to environmental change; to evolve out of trouble or to become extinct. Any environmental changes have to be endured on the spot.

For the bulk of species, i.e. those on the continental masses, this is of course not a problem, but for island populations it is indeed severe. Evolution and extinction of island species must thus be seen as atypical in a global context. The maintenance of long-term species constancy and low rate of extinction in the insects discussed above is thus a 'mainland effect' only, in contrast to rapid evolution and high extinction rates that would seem to characterize island faunas. One can not extrapolate from the one to the other.

The apparent paradox of the prolonged constancy of insect species versus the extreme inconstancy of the Quaternary climate may be resolved as follows (Coope 1978). The high frequency, intensity and suddenness of these climatic oscillations, coupled with the great mobility of insect populations, means that the geographical ranges of species are essentially transitory stages in a state of constant dynamic flux as they react to shifting climates. The large-scale tracking of acceptable climates means that these populations were continuously splitting up and fusing again as they progress to and fro over the complex land-surface. The numerous episodes of temporary isolation and subsequent coalescence ensure that the gene-pools of the species were kept well stirred. Sustained evolution under such circumstances must have been well nigh impossible. Thus paradoxically, it was the climatic inconstancy that was, at least in part, responsible for the maintenance of specific constancy.

The ability to track acceptable climates from place to place across the continental masses has another evolutionary consequence. It means that the environment in which a species lives remains effectively constant regardless of the climatic changes. Under these conditions, species constancy could be reinforced by stabilizing selection throughout the whole of the Quaternary period regardless of its highly unstable climate.

There is a problem of credibility here. How can stabilizing selection operate with such precision that it can maintain species constancy in all its intimate detail for the several million generations represented by the Quaternary fossil record? This is a problem that confronts all evolutionary biologists when faced with the longevity of so many fossil species. In the case of the fossil insects discussed here, this is a problem that cannot be avoided or explained away on the traditional basis that palaeontologists and neontologists have such different concepts of species that we are not comparing like with like. The Quaternary fossil insects show species constancy in exactly the same features that are used to differentiate present-day species. The mechanism whereby species stability is maintained remains a problem.

Information is therefore necessary on the way, or ways, in which species stability could have been maintained for several million generations in the geologically recent past. This becomes important if we

are to estimate the chances of survival of insect species in any climatic changes in the near future; in conditions of global warming for instance. Some speculations on the mechanism governing long term species constancy are therefore inescapable.

Two factors appear to be important in understanding this mechanism. Firstly, it is well known that insect species are fairly rigidly adapted to their environmental niches, making any deviation from the status quo highly precarious and speciation a profound risk. Secondly, all natural populations of insects are very heterozygous suggesting that the stereotyped wild individual is sustained by a genetic complex in such a way that a wide variety of different combinations result in the emergence of very similar 'wild types'. This wild phenotype appears to have been honed, by stabilizing selection for millions of generations, to fit its narrowly defined environmental niche. There would seem to be another paradox here in which phenotypic sameness is maintained by an elaborate conspiracy of polygenic controls. Under such circumstances the effects of natural selection would be diminished. In contrast, if heterozygosity were to be reduced in a population, the constraints that maintain species constancy would be correspondingly weakened, increasing the likelihood of novelties being expressed in the phenotype and thus be made available to natural selection.

If this hypothesis is correct, then phenotypic diversity can be the result of moderate impoverishment of the gene pool (early stages of domestication would fall into this category). The ultimate in genetic impoverishment (i.e. homozygosity) will, of course, result in a return to phenotypic monotony (late stages of domestication would fall into this latter category). As the fossils are representatives of natural populations, it is to be expected that their proven species constancy could have been maintained, in part, by their high degree of heterozygosity which, in turn, was continuously being sustained by the constant stirring of the gene-pools as the species changed their distribution patterns in response to the climatic oscillations.

We are now in a position to contribute some tentative solutions to the second of the questions posed at the beginning of this chapter; will the stratagems so successfully adopted by insect species in the past to deal with glacial-interglacial climatic changes, suitably equip them to survive any impending climatic changes? Two important factors have to be born in mind. First, there is the essential ability of insect species to track the movements of acceptable climates thus freeing them from the necessity of having to adapt afresh to each successive climatic oscillation. Second, there is the proven capacity for insect species to maintain constancy for millions of generations. Both these factors, although fitting the species well enough for survival in the climatic 'hurly-burly' of the geologically recent past, may be of little value in the humanly contrived environmental chaos of the near future.

At the present time, human impact on the landscape is taking place on an unprecedented scale. On the negative side, the drainage of marshlands or the

destruction of ancient forests and on the positive side, the widespread blanket of intensive agriculture or the corduroy plantations of monotypic forestry, all make tracking of habitats difficult or impossible. The effects of habitat destruction on insect species have been considered by Thomas & Morris (this symposium) listing losses in recent years and by Buckland *et al.* (1993) drawing upon fossil evidence of postglacial extinctions in the British Isles. The list is impressive and depressing.

If species are going to be denied the option of tracking the changes in the location of acceptable environments, the solution that they have adopted so successfully in the past, there can be little doubt that the coming extinction event will be on a truly unprecedented scale. Particularly vulnerable will be the species that are adapted to the shrinking natural environments mentioned above. The list of extinctions from such habitats could be the vanguard of a very long procession indeed.

No such vulnerability is likely to effect the species that are well fitted to the new man-made environments, that is unless in our efforts to eliminate pest species we impose such intense selection pressures upon them that their gene pools shrink so much that the constraints maintaining species constancy are relaxed and natural selection allowed full play with the resulting novelties. Evolution rather than extinction may be their future.

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Discussion

A. S. WILKINS (*BioEssays, Company of Biologists Ltd, Cambridge, U.K.*). In evaluating the generality of Professor Coope's findings, one would like to know something about the general range of temperature tolerances in beetles, in particular, and in insects, more generally, relative to other animal groups that have experienced more numerous extinctions during the past 2 million years. Can he comment on this please?

G. R. COOPE. The temperature tolerances of beetles differ greatly from species to species. In the absence of adequate experimental data for most species, we have to estimate the thermal tolerances from the geographical ranges of each species. Those with widespread ranges we view as eurytherms whereas those with more restricted ones we see as stenotherms. Certainly these restricted ranges follow well known climatic zones, giving support to this procedure. I am aware that this is a rough-and-ready method of determining temperature tolerances but, for the present, it is all that we have.

Although it is difficult to estimate temperature tolerances of extinct animals, it would seem likely that they also had restricted geographical ranges and would thus exhibit varied thermal requirements also. Temperature tolerance alone does not seem to provide an explanation why some species seem to be vulnerable to extinction whereas others do not. In the spectacular case of the extermination of the Quaternary mega-vertebrates, it would appear that they experienced lethal predation by human hunters so theirs is a special case. I discuss, in the written paper, other factors that may go some way to explain why insects (and other invertebrates also) were able to avoid extinction during the frequent and intense oscillation of the Quaternary climate.