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IMPLICATIONS OF A 'GREENHOUSE CLIMATE' FOR BRITISH BIRDS

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PART 1. CLIMATIC CONSIDERATIONS

Is there a 'greenhouse effect'?

Despite the widened debate on this topic over the last two years, there are still some climatologists who question its reality or significance. In the opinions of a minority, it remains an interesting hypothesis which has been made a dumping ground for recent diverse anomalies of weather. As recently as November 1989, a report from the Washington - based George C. Marshall Institute suggested that 20th century global warming had been due primarily to heightened solar activity. Another view is that absorption of greenhouse gases (carbon dioxide, methane and others) by the oceans will mitigate the potential greenhouse effects to an extent not yet ascertained (Pearce 1989b). Kelly, of the UEA Climatic Research Unit, has opinioned that if the greenhouse effect is genuine then it could take 20 years for the reality to become fully established (Gribbin 1988); the British Meteorological Office (Bracknell) has also predicted a time-lag through oceanic absorption of CO_2. Whilst an overall rise in mean global temperatures during this century has been more pronounced in the 1980s, making it the warmest decade since recording began, alternative factors which may apply (perhaps in conjunction) are:

1: short-term natural climatic oscillation, comparable to the well-known Arctic amelioration between 1890-1940;

2: the El Nino events of 1982-83 and 1986-87 (these begin in the Pacific but their effects ripple outwards), for the global warming trend has been more marked in the southern hemisphere than in the north;

3: intensified solar activity;

4: a depleted ozone layer allowing more ultraviolet radiation to warm the troposphere.

To keep matters in perspective, the increase in mean global temperature over the last 100 years (i.e. Man's industrial age) has been just 0.5°C (Kelly and Granich 1989). It is the enhanced trend over the last ten years which has caused concern.

In the northern hemisphere the warming trend during the 1980s has affected mainly the continental interiors, probably because oceans are slower to warm up than land. Hence there are maritime edge anomalies. The North Atlantic area (east Canada/south Greenland/northwest Europe) has actually cooled over the last 20 years, with mean reductions of 0.9°C in Scandinavia and 0.3°C in Britain (Gribbin 1988). Also, parts of Antarctica have cooled by up to 1°C. Moreover, since mid-1988 there has been a cooling of mean global temperatures (these having returned to the 1950-1980 average); but this is thought to be connected to a La Nina counterpart of the 1986-87 El Nino oscillation, in which case the observed effects should be only temporary (Pearce 1989a). This emphasizes the extent to which global figures are influenced by events in the southern hemisphere, with its much larger extent of ocean.

The foregoing serves to underline the problems of assessing what is happening to world climate, with its combination of short-term anomalies and long-term trends. It is, however, fair to say that the case for there being a greenhouse effect is now widely accepted. The remainder of this document is written on an assumption that the latter view will prove to be correct.

Climatic change: the general situation

Computer models predict that greenhouse warming will be least in the tropics and most marked at the poles (Pain 1988). There seems to be a consensus that over the next 50 years mean world temperatures are likely to rise by about 3°C, with increases of about 1°C at the equator and up to 5°C at the poles. Some models predict a global increase of 6°C, and up to 12°C at the poles, sometime during the 21st century. But it is not safe at present to look further ahead than about 50 years, for the range of uncertainties includes Man's effectiveness in seeking to slow down or reverse the trend. However, corrective measures might need several decades to take effect.

A warmer world climate would lead to increased evaporation (especially from the oceans), so that rainfall would also rise. Yet increased, denser cloud cover could inhibit sunshine and perhaps slow down the rate of global warming, provided that the water vapour did not itself act as a heat trap (as it might). The development of a greenhouse climate could be slower than allowed for in current predictions.

Regional patterns of rainfall and humidity can change with any disturbances to wind circulations, there being most risk of such changes between 30°N and 30°S latitudes. Another potentially major change would be to sea-levels, which would rise in part through the natural expansion of warmed water and in part through melting of glaciers and polar icecaps. The likely extent of the latter is still conjectural. The Arctic icecap (which is largely sea ice) has thinned measurably during the last 10-15 years, though the Antarctic ice-sheet (which is largely on land) has not. The worst possible scenario of the future would allow complete melting at both poles. The recent widely-publicized claim by Ark, that sea-levels would rise by up to 5.7 m by the year 2050, was such an extreme, which distorted the view of its own technical adviser through ignoring wide confidence limits on time-scale (New Scientist, 22 April 1989). More responsible predictions are for sea-levels to rise by 0.8-1.65 m over the next 50-60 years (Robin

1986). Even that may prove pessimistic, for the reason given in the previous paragraph.

Climatic change: British Isles

Hitherto, computer modelling of climatic change has been in the form of broad (mostly global) overview. Only now is predictive work beginning of what the implications might be for our small cluster of islands. The view has been offered by Kelly and Granich (1989) that UK temperatures may rise by up to 3°C over the next 40 years, with increased rainfall but a marked change in its seasonality. The climate of southern England may come to approach that of present-day south-west France, while eastern England may acquire a drier, more Mediterranean type of regime as an extension to the Continental trend. The rest of the country is expected to become warmer but wetter, with rainfall rising by up to 20%.

It is likely that, as happened in the 1890-1940 amelioration, the Icelandic low will decline and move northwards while the Azores high will expand. This will tend to push North Atlantic fronts more towards the north-east so that they affect mainly the northern half of Britain. The rest of the country will receive its depressions from the south-west, bringing in warm maritime air from the subtropical Atlantic. Yet the development of more persistent high pressure to the south and east of Britain in summer should lead to rainfall becoming largely a winter feature, at least in the southern half of the country. Thus there will be more risk of summer droughts, and of lower water levels in rivers, lakes and reservoirs at that season.

The forecast rise in sea-level (of around 1-1.5 m) will cause problems for coastal protection, particularly along the soft coastlines of eastern and southern England. These problems will be exacerbated if there is a continuance of the recent trend for the north-eastern Atlantic to become rougher (Carter and Draper 1988). Coastal erosion will occur, especially of dune system, clay cliff and upper saltmarsh, though resulting sediments will be deposited elsewhere and build up those coastlines. A higher mean sea-level will narrow the inter-tidal zones of mudflat and saltmarsh, so that the slopes of shores will become steeper as they become narrower. Initially at least, coastal towns and agricultural land will be protected by strengthening existing sea wall defences, but eventually it may be necessary to build new lengths of sea-wall inland on higher ground and abandon some lower ground to the sea (Boorman et al 1989). The latter circumstance would create exciting new opportunities for coastal nature reserves (Thomas et al 1989). Higher sea levels will also lead to salt water penetrating further up rivers, leading to more brackish conditions there as well as in coastal lagoon systems such as the East Anglian broads. Disadvantageous hydrological changes would also affect other low-lying areas of conservation importance, including the Outer Hebridean machair which is only 1-3 m above sea level now.

The forecast temperature rise (of 3°C) is equal to the present mean temperature difference between southern England and northern Scotland, and this would soon have repercussions for the terrestrial flora and fauna also. It is well to remember, however, that distributional change is not new, but is an on-going consequence of the dynamism of living organisms responding to alterations to their environments. Past distributional changes documented in Britain include examples from most major Classes of the animal and vegetable kingdoms (Johnson and Smith 1965, Hawksworth 1974). An entire volume has been devoted to status changes amongst British breeding birds within historical times (Parslow 1973). It is the possible rapidity and profoundness of the changes which could happen in response to a developing greenhouse climate which have aroused concern.

PART 2. IMPACTS ON BRITISH BIRDS

Factors governing bird distributions

Brown and Gibson (1983) championed the hypothesis that the distributions of species are determined primarily by climatic factors, related to latitudinal variation in the levels of input of solar energy. Root (1988a, b) showed that the winter northern distribution limits for a range of North American bird species were related to temperature, determined by the ability of the birds to meet the energy expenditures required to compensate for colder ambient temperatures. In Britain this concept has been taken up by Turner et al (1987, 1988), and extended to seasonal bird distributions using data drawn from the BTO Breeding Atlas and Winter Atlas (though only a limited range of insectivores was studied). These authors concluded that British bird distributions conform well to the climatic/solar energy hypothesis, while failing to provide any support for the alternative theories of historical distribution (i.e. recolonisation after past glacial retreat) or of structural (=habitat) dependence. Regression analysis consistently singled out temperature (though not sunshine hours - with one exception) as the most significant correlation with observed seasonal bird distributions, rejecting the alternative independent variables of habitat type, habitat diversity, altitude, distance from the coast, interval since the last glacial retreat, latitude and longitude.

The problem with such analyses is that statistical correlation is easier to demonstrate than causal (biological) connection. The climatic hypothesis is attractive, but is it universal? How does one determine when species are limited in distribution by their own climatic tolerances or by those of their key foods (plant or animal)? Yet it has to be said that most birds eat too wide a variety of foods to be themselves limited by the distribution of any one of them. But in combination? - that would require more complex analysis.

Turner et al may well be right to challenge previous assumptions of animal distributions being determined by habitat (physical features and their vegetation). However, it is necessary to remember that the point at issue is distribution limits rather than dispersion within a species' range. Moreover, 'habitat' includes series of plant species (and associated microfauna) which are themselves subject to external influences on conditions for growth and reproduction. Few bird species are closely associated with individual species of tree or other plant, and even these throw up certain anomalies. Thus Reed Warbler and Bearded Tit have much more restricted ranges than does Phragmites reed; while Ireland possesses sessile oakwoods which Redstarts, Wood Warblers and Pied Flycatchers seldom reach.

For many passerines at least, it does seem that habitat association is less with species composition of the vegetation than with its structure, e.g. in terms of height, spacing, density of understorey and degree of shrub layer (MacArthur et al 1962, Hilden 1965); see also Thomas (1984) for a detailed study of Sedge Warbler habitat preferences in relation to plant densities. Some of these factors will, of course, be influenced by geology (=soil type). Cliff-nesting seabirds have an essentially seasonal association with land; their gross distributions seem more likely to be determined by marine productivity, itself related to climatic influences on ocean currents.

In summary, it does seem plausible that climate is an ultimate factor influencing distribution limits, with habitat availability being but a proximate factor. The web of interdependence within a community of plants and animals is no less real for its constituent species being susceptible to gradual spatial shifts under external (climatic) influences. Nor is this changed by the greater capacity for dispersal conferred upon birds (and some insects) by the power of flight.

Implications for British birds; northern influences

The prospects, outlined earlier, are for a Britain in which by the year 2050 the average temperatures may be 3°C higher than at present, rainfall has increased but probably become more seasonal, and sea-levels may be 1 m or more higher than now. Thereafter, climatic change will continue to an extent which we cannot yet quantify; even after Mankind initiates determined countermeasures, it could take decades to stabilize the atmospheric levels of greenhouse gases. Given this background, much of the biotic uncertainty is related to how quickly (or not) the vegetational zones and their associated faunas will change. Yet with all computer models predicting bigger effects at higher latitudes than in lower ones, the first major avifaunal changes to affect Britain may arise in the Arctic.

One of the zones most vulnerable to climatic warming is that of the northern tundra which, it has been predicted (Woodward 1989), will shrink noticeably within a decade as scrub taiga and then forest invade northwards with a thaw of the permafrost. Moreover, such a thaw would lead to severe erosion and collapse of the soil; while a resumption of normal decomposition of tundra plant material (now locked into the permafrost layer) would itself release vast amounts of additional carbon (as CO_2) into the atmosphere to fuel the greenhouse changes. A major shrinkage of the tundra zone would have serious consequences for the numbers of swans (especially Bewick's Swan), geese, ducks and high arctic waders which breed there and either winter or occur on passage in western Europe (including Britain). In practise, most of the duck species prefer wooded tundra (taiga) and would be less affected, though three reach their greatest abundance on open tundra (these being Pintail, Scaup and Long-tailed Duck). Amongst the waders, these most at risk are the northern species of the genera <u>Pluvialis</u>, <u>Calidris</u>, <u>Limosa</u> and <u>Numenius</u>.

These aquatic species (wildfowl and waders) will also experience problems in winter as rising sea levels affect the extent of coastal saltmarsh and mudflat, and the diversity and abundance of marine organisms within them (Boorman et al 1989). Higher mean sea levels will not only reduce the densities of food sources available to shorebirds on the mudflats, but will also reduce the period of their accessibility because mudflats will be exposed for a shorter period within each tidal cycle. The effect of reducing feeding time - a decline in wader numbers - can be seen now where Spartina has invaded the mud (Goss-Custard and Moser 1988).

On the other hand, species which breed in the boreal zone and winter inland, by fresh or brackish water, may be affected less - including most ducks and the Tringa sandpipers. However, British Redshanks will suffer serious loss of breeding habitat as saltmarshes become more frequently inundated at high tides. We in Britain may also find that more of the northern thrushes and finches will be able to winter successfully north to east of our islands, as less severe winter conditions come to apply there and (in the longer term) the deciduous (or mixed) forest zone extends northwards.

The other potentially serious effect of warming within the Arctic will arise if there is permanent reduction in the extent of polar sea ice, and a $5^{o}C$ temperature rise over 50 years would cause this to happen. Seasonal sea ice is vital to the Arctic ecosystem, for it is the algae which grow in abundance on the under-side of the ice which form the basis of the food chain on which Arctic marine life depends (Pain 1988). Moreover, it is the cold, descending Arctic waters which, when they meet continental shelves, produce the upwelling conditions which permit high levels of marine productivity there. Large concentrations of seabirds (both breeding and non-breeding) feed in such regions. Britain and Ireland probably could not retain their large and spectacular populations of petrels, skuas, terns and auks - at least at present levels - if marine productivity in the Arctic and on the continental shelf of north-western Europe was to decline significantly through warmer waters and the changes these would make to the ocean currents.

Implications for the composition of the British breeding avifauna

Despite the significant change that there would be to the British climate, following a $3^{o}C$ rise in average temperatures, it is unlikely that floral and faunal changes will be profound by the year 2050. Sixty years is a short period on the evolutionary time-scale. And we are not yet in a position to predict beyond then with any measure of confidence.

Except under plantation conditions, trees are long-lived. Their natural reproduction declines as conditions become less favourable (fewer seeds germinate or saplings become established), but mature specimens are able to live out their normal spans. As vegetational zones move northwards gradually, replacement tree species from the south - broad-leaved evergreens such as the Mediterranean holm oak - may be slow to reach Britain due to our island situation, but there are already introduced specimens to provide a nucleus. Our present deciduous trees, no longer needing to shed their leaves in winter, will be able to extend further towards or into Scotland and (there) be less stunted than their present counterparts. Sitka spruce will become unsuited to the new climate (it needs a period of winter dormancy) so that forestry interests will eventually have to rethink their planting strategy. Given time, the tree line could rise altitudinally to include moorland and all but the higher mountain slopes. However, the key determinant of the extent of this trend may prove to be grazing pressure, which will depend on Man's land-use policies. In general, a vertical expansion of the tree-line by 500 m is equivalent to horizontal expansion of 250 km (Pain 1988).

The growing season for plants will be extended under warmer conditions. Vegetation will become more lush (taller and of increased complexity) under a wetter regime; this, however, may not apply to south and east England which are predicted to become drier and prone to summer droughts as they fall less under the influence of Atlantic weather and (in the east) assume a more Mediterranean character. With an extended growing season, and with increased atmospheric CO_2 to enhance the efficiency of photosynthesis, farming should prosper though it may have to accept crop changes and (in southern England) the need for summer irrigation. The insect fauna may change in species composition in response to the new conditions, but it is unlikely to decline in quantity; indeed, warmer temperatures all year round will aid overwinter survival, in much the same way that present-day aphid populations increase after a mild winter (Kelly and Granich 1989). In wetter regions, mildew growth will be encouraged also. Hence agrochemicals are likely to continue firmly as part of the farming scene.

With the majority prediction that the sea level rise will not exceed 1.5 m by the mid-21st century (and may be only half that), conventional sea defences should be able to prevent major permanent inundations on that time-scale. It is likely to be further into the future before the value of low-lying land is exceeded by the cost of protecting it. (The present concentration of reserves and other protected areas on the vulnerable low-lying coastal fringe of eastern Britain should be noted.) Even so, temporary flooding will become a higher risk, as when (a) North Sea tidal surges breach coastal defences, and (b) when river run-off of heavy rainfall coincides with high tides, higher than at present, in the estuary. Hence the recent trend for low-lying marshes and water meadows to be converted from grazing to arable may be reversed locally.

It is against this background that one may speculate on bird community changes, on the hypothesis that climate (=solar energy input) is an important determinant of distributions. With gradual northward shift of the climatic and vegetational zones, the long-term trends will be for boreal species to retreat northwards and become scarcer here if they do not disappear altogether (except as winter visitors); while warm-temperate and southern species will be able to expand in Britain, especially in the drier regions of the south and east.

Table I. British breeding species whose breeding ranges in western Europe do not extend south of 50°N latitude (marine and introduced species excluded)

Black-throated Diver	Wood Sandpiper
Red-throated Diver	Green Sandpiper
Red-necked Grebe	Greenshank
Slavonian Grebe	Purple Sandpiper
Wigeon	Temminck's Stint
Pintail	Dunlin*
Scaup	Red-necked Phalarope
Goldeneye	Little Gull
Common Scoter	Common Gull*
Eider*	Snowy Owl
Red-breasted Merganser*	Shore Lark
Whooper Swan	Redwing
Merlin*	Twite*
Red Grouse*	Scarlet Grosbeak
Golden Plover*	Parrot Crossbill
Dotterel	Brambling
Ringed Plover*	Lapland Bunting
Whimbrel	Snow Bunting

NOTES:

1. Sources are Voous (1960) and Harrison (1982).

2. Occasional British breeding species are included provided there has been such a record (one or more) since 1950.

3. Dotterel has nested in the Alps, but this is extralimital.

4. While there are no breeding Shore Larks in western Europe south of 50°N, there are isolated populations in the Balkans and North Africa (different races).

5. Those marked with asterisks were located in 10% or more of 10-km squares during the Breeding Atlas.

Table II. British breeding species whose range in western Europe do not extend further north than 60°N latitude (marine and introduced species are excluded).

Black-necked Grebe	Bee-eater
Little Grebe*	Wood Lark
Bittern	Grey Wagtail*
Little Bittern	Stonechat*
Garganey	Black Redstart
Red Kite	Nightingale*
Marsh Harrier	Bearded Tit
Montagu's Harrier	Cetti's Warbler
Hobby	Savi's Warbler
Quail*	Grasshopper Warbler*
Stone Curlew	Marsh Warbler
Black-winged Stilt	Reed Warbler*
Kentish Plover	Dartford Warbler
Avocet	Firecrest
Mediterranean Gull	Golden Oriole
Black Tern	Chough
Rock Dove*	Hawfinch*
Turtle Dove*	Goldfinch*
Barn Owl*	Serin
Hoopoe	Cirl Bunting
Kingfisher*	Corn Bunting*

NOTES:

1 Sources and definitions as in Table I.

2. Red-backed Shrike may now belong to this group, following widespread decline in western Europe (Hilden and Sharrock 1985).

3. Those marked with asterisks were located in 10% or more of 10-km squares during the Breeding Atlas.

Table I lists the basically northern species which at present reach their southern limits in Britain and corresponding latitudes of western Europe. It will be seen that over 75% of these are non-passerines, with substantial emphasis on aquatic species (divers, grebes, waterfowl and waders). Most of the 36 species in this table have small and localized British breeding populations (or nest only irregularly), with only nine of them having been found in 10% or more of 10-km squares during the 1968-72 Breeding Atlas. All could be expected to lose ground in a warmer Britain that came more firmly within the broad-leaved zone. Recent colonists from the north, which comprise half the species in Table 1, are likely to be lost completely; of course, a few of these (such as Snowy Owl and Lapland Bunting) were never serious candidates for successful colonization of Scotland. In the future, only the higher Scottish mountains may continue to provide outposts of these northerners.

The counterparts to the above are the basically southern species which reach their present northern limits in Britain and corresponding European latitudes; these are listed in Table II. It will be seen that the composition differs significantly, these southern species comprising only 26% aquatic non-passerines but 52% passerines and near-passerines. Moreover, one-third of these are already widely distributed in Britain (present in over 10% of 10-km squares), whilst a similar proportion are recent or attempted colonists from the south. These represent the kinds of birds which one would expect to do well under a greenhouse climate, particularly in a drier eastern England in respect of southern in-comers.

For these essentially southern species, the predictions of a Mediterranean-type climate for eastern England will be important since they require warm and (especially) dry summers. Over the last 100 years north-west Europe has experienced declines of a number of such species (e.g. White Stork, Roller, Hoopoe, Red-backed Shrike) following an eastward extension of the Atlantic climate which involved increased summer rainfall (Voous 1960). This trend will be reversed if the greenhouse predictions prove correct. Further, a hotter and drier climatic regime over Europe as a whole (especially in the continent's interior) may encourage a range of eastern species to resume the westward expansions they began in the 1920s and 1930s but which have since faltered - examples are Greenish Warbler, Red-breasted Flycatcher and Penduline Tit.

Moreover, there is a variety of other bird species which breed around the Bay of Biscay but not further north (Table III). These should be able to spread northwards within France as a changing climate leads to habitat modification in their favour; the migrants amongst them already cross the English Channel sea barrier as rare visitors to Britain. Perhaps the most likely candidates for future British breeding status are such migratory landbirds as Scops Owl, Crag Martin, Tawny Pipit and the range of warblers.

It is well to remember that species and populations are aggregates of individuals, and that distribution changes are

Table III. Species which breed around the Bay of Biscay (north Spain, south-west France) but are known to have done so in Britain.

Purple Heron	Tawny Pipit
Night Heron	Fan-tailed Warbler
Little Egret	Great Reed Warbler
Black Kite	Melodious Warbler
Booted Eagle	Orphean Warbler
Short-toed Eagle	Bonelli's Warbler
Whiskered Tern	Woodchat Shrike
Scops Owl	Rock Sparrow
Short-toed Lark	Ortolan Bunting
Crested Lark	Rock Bunting
Crag Martin	

initiated by individuals. In response to habitat and environmental changes of the kind being discussed here, some individuals within an existing population will stay put, but experience declining breeding success (as conditions for them deteriorate) and eventually die out in that area. Other individuals, however, will pioneer new peripheral sites which become available through these same environmental changes. As greenhouse changes take effect, and southern bird populations expand northwards in response, this will be through pioneering by individual birds rather than through any form of "population pressure" to vacate previous breeding areas which become too hot or arid.

Implications for the ecology of British breeding birds

The species included in Tables I and II, those at the limits of their breeding ranges in British latitudes, represent only 40% of British breeding birds (marine and introduced species excluded). The larger proportion have wide latitudinal distributions from Scandinavia southwards to France or Spain, and therefore already live under a range of climatic conditions. These species are listed in Table IV, where they are divided into residents, partial migrants and summer visitors.

With the exceptions of a few specialist species, discussed later, these Table IV birds should be able to cope with greenhouse climate changes. In particular, those resident species which are now prone to hard-winter mortality - notably the small passerines such as Wren and Long-tailed Tit - should achieve more consistent population levels in a warmer climate, in that the large fluctuations which now occur should in future be smoothed out. For aquatic and some farmland species, however, the beneficial effects of warmer winters may be counterbalanced by the problems of summer droughts (at least in the southern half of the country). This is considered further below.

Under greenhouse conditions the incidence of partial migration will decline, except perhaps where this arises from age-related winter resource partitioning (as currently in the case of the Mistle Thrush) - though the distribution of winter resources will themselves be changed by the new climatic regime. The partial migration strategy has always offered individuals within a species the alternative of either wintering close to their breeding area, with the benefits of more spring territory choice and earlier breeding opportunities, or of moving southwards to improve their winter survival prospects. Future change seems inevitable. Those individuals whose migratory behaviour was triggered by environmental conditions (such as the onset of severe winter weather) will experience different conditions from before; hence the incidence of cold-weather movement will decline. Moreover, the relative survival of individuals that differ genetically (in their migratory behaviour) will change because their environment has changed; the resident strategy will come to have selective advantage over the migratory one. The winter food requirements of individual birds will become less in warmer

Table IV. British breeding species which are neither at the northern nor southern limits of their European breeding ranges (marine and introduced species are excluded).

Resident in Britain	Partial migrants in Britain	Summer visitors
Mute Swan	Great Crested Grebe	Honey Buzzard
Greylag Goose	Grey Heron	Osprey
Mallard	Teal	Spotted Crake
Golden Eagle	Gadwall	Corncrake
Buzzard	Shoveler	Lt. Ringed Plover
Sparrowhawk	Pochard	Common Sandpiper
Peregrine	Tufted Duck	Ruff
Ptarmigan	Goosander	Cuckoo
Black Grouse	Shelduck	Nightjar
Grey Partridge	Hen Harrier	Swift
Water Rail	Kestrel	Wryneck
Moorhen	Oystercatcher	Swallow
Coot	Lapwing	House Martin
Woodcock	Snipe	Sand Martin
Stock Dove	Curlew	Tree Pipit
Woodpigeon	Black-tailed Godwit	Yellow Wagtail
Collared Dove	Redshank	Ring Ouzel
Tawny Owl	Black-headed Gull	Wheatear
Green Woodpecker	Long-eared Owl	Whinchat
Great Sp. Woodpecker	Short-eared Owl	Redstart
Lesser Sp. Woodpecker	Meadow Pipit	Bluethroat
Skylark	Pied Wagtail	Sedge Warbler
Rock Pipit	Mistle Thrush	Blackcap
Wren	Song Thrush	Garden Warbler
Dipper	Fieldfare	Whitethroat
Dunnock	Blackbird	Lesser Whitethroat
Goldcrest	Robin	Willow Warbler
Great Tit	Siskin	Chiffchaff
Blue Tit	Linnet	Wood Warbler
Coal Tit	Redpoll	Spotted Flycatcher
Crested Tit	Crossbill	Pied Flycatcher
Marsh Tit		Red-backed Shrike
Willow Tit		
Long-tailed Tit		
Nuthatch		
Treecreeper		
Starling		
Jay		
Magpie		
Jackdaw		
Rook		
Carrion Crow		
Raven		
House Sparrow		
Tree Sparrow		

(Table IV continued)

Chaffinch		
Greenfinch		
Bullfinch		
Yellowhammer		
Reed Bunting		
50 (44%)	31 (27.5%)	32 (28.5%)

NOTES:

These are the British breeding species not included in Tables I and II.

Species in the first and second columns are considered further under habitat preference in Table V.

conditions, since less energy will need to be expended on the regulation of body temperature.

Yet this prospect of resident species being able to achieve more consistent population levels may have implications for the summer visitors. It has been argued (Herrera 1978, O'Connor 1981) that migrants are primarily exploiters of those breeding season resources that are left under-used by residents whose population levels are regulated by climate in winter and density-dependent (i.e. territorial) behaviour in summer. It is implicit to this hypothesis that each breeding area (irrespective of habitat type) has a particular carrying capacity for birds, so that migrants can increase only when residents have declined. At present there is rather little evidence for direct competition between resident and migratory birds; and it may be that migrants are able to exploit seasonal over-abundance of food resources in the unstable mid-succession stages of woodland growth in which (it is confirmed) the higher proportions of migrants occur (Karr 1976, Helle and Fuller 1988). Nevertheless, it is clear that the proportions of summer migrants within regional avifaunas increase with latitude, being highest where there is greatest contrast between the extent of winter and summer food resources (MacArthur 1959), so that there is also regional correlation between the percentage of migrants and the average temperature of the coldest month (Alerstam 1985). Hence some disturbance to the resident:migrant ratio, to the disadvantage of summer migrants, can be expected in Britain under a greenhouse climate in which winters become warmer and vegetation has a longer growing season.

Summer visitors will also be influenced by changing conditions on their migration routes and in their winter quarters. At present, there are contradictory views on whether global warming will result in drier or wetter conditions in the Sahel region (Forse 1989), for this will be influenced also by ocean temperatures and currents. What seems clear is that the western Mediterranean basin, including the southern half of Iberia, will eventually become drier and dominated by sparse or desert-like vegetation (Woodward 1989) and therefore may become less suitable as staging areas (i.e. the laying down of fat deposits) for trans-Saharan migrants. The Mediterranean/Sahara crossing seems destined to become a bigger problem for such birds. Yet in the changed conditions it may be that more species will follow the examples of Blackcap and Chiffchaff, in which many individuals already winter in Europe. Indeed, these could become new partial migrant species. Such behavioural changes could occur quite quickly. In genetical terms, small passerines have generation lengths of only one year. Sixty generations by the year 2050 AD would be sufficient for major genetic changes to occur, provided there is sufficient genetic variation to start with; and if migration behaviour depends in part on the reactions of individuals to their environment, the changes could occur even faster. The Lesser Black-backed Gull changed its migration habits over a period of a mere 20 years (Barnes 1961, Baker 1980), whilst English Canada Geese established a moult migration to the Beauly Firth, Scotland, over a similar time-scale (Dennis 1964, Walker 1970); both of these species have mean generation intervals that are <u>longer</u> than those of most trans-Saharan migrants.

Table V. The resident and partially-migratory British breeding species, divided according to their key habitats

<u>Woodland</u>	<u>Farmland</u>	<u>Wetland/ coastal</u>	<u>Upland/ moorland</u>
Sparrowhawk	Kestrel	Gt.Crest. Grebe	Hen Harrier
Woodcock	Grey Partridge	Grey Heron	Golden Eagle
Tawny Owl	Lapwing	Mallard	Buzzard
Long-ear. Owl	Stock Dove	Teal	Peregrine
Green Woodp.	Woodpigeon	Gadwall	Ptarmigan
Gt.Sp. Woodp.	Skylark	Shoveler	Black Grouse
Lr.Sp. Woodp.	Pied Wagtail	Pochard	Curlew
Wren	Mistle Thrush	Tufted Duck	Short-ear. Owl
Dunnock	Fieldfare	Goosander	Meadow Pipit
Song Thrush	Blackbird	Shelduck	Dipper
Robin	Magpie	Greylag Goose	Raven
Goldcrest	Jackdaw	Mute Swan	
Great Tit	Rook	Water Rail	11 (13.5%)
Blue Tit	Carrion Crow	Moorhen	
Coal Tit	Greenfinch	Coot	
Crested Tit	Linnet	Oystercatcher	
Marsh Tit	Bullfinch	Snipe	
Willow Tit	Yellowhammer	Black-t. Godwit	<u>Urban/suburban</u>
Long-t. Tit		Redshank	
Nuthatch		Black-head Gull	Collared Dove
Treecreeper		Rock Pipit	Starling
Jay		Reed Bunting	House Sparrow
Tree Sparrow			
Chaffinch			
Siskin			
Redpoll			
Crossbill			
27 (33.5%)	18 (22%)	22 (27%)	3 (4%)

NOTES:

1. These species are the resident and partial migrant subsets from Table IV.

2. Some of the above habitat allocations are rather arbitrary; more importance has been attached to feeding habitat.

The resident and partial migrant subsets from Table IV are extracted and regrouped under their habitats in Table V. In some cases, habitat allocation is arbitrary (e.g. Blackbird densities are higher in suburbia than in natural situations), but the preferred type is usually known.

Most British woodland birds occur at higher densities in deciduous woods than in conifers, with mixed woodland occupying an intermediate position. Important factors here are the numbers of insect species associated with particular types of tree, and the feeding adaptations of individual bird species to exploit them. Since it is already known that alien trees tend to attract fewer insect species (Southwood 1961), it cannot be assumed that southern broad-leaved evergreens will be able to sustain bird population levels equal to those of our currently indigenous trees. Consequently, our woodland birds may fare better (at least during the transitional decades) in central and northern Britain where vegetation will be more akin to that to which they are already adapted. Britain's woodland birds include few conifer specialists; the prospects for such species as Common Crossbill, Coal Tit and Goldcrest will probably be linked to changes in afforestation policy and practice. Sitka spruce will not grow to commercial standards in a warmer Britain, but there are other (southern-origin) conifers which do not require winter dormancy. It is impossible at present to predict what will happen to Scots pines of the Caledonian Forest, with their endemic populations of Crested Tit and Scottish Crossbill.

At the present time, farmland birds can be placed into two broad categories: those which occupy copses, shelterbelts and hedgerows as woodland overflow but without exploiting farming opportunities in any marked way (Wren, Robin and the tits are clear examples), and those which depend upon farming activites for feeding and breeding sites. It is the latter which will be affected by agricultural changes.

While Britain is expected to become wetter overall, the prospects of much drier summers in the south and east will create problems there for farmland species which either select the proximity of damp situations (hirundines, wagtails) or feed in summer on soil invertebrates that become less accessible in dry conditions (thrushes, Jackdaw, Rook). The 1976 summer drought showed well how the breeding success and post-fledging survival of such species fall in those conditions. Long-term declines in dry regions seem inevitable. Yet there could be mitigation through farmers being compelled to irrigate their land at that season. Warmer weather may encourage farmland insect pests, but (as noted earlier) the use of chemicals may limit the extent to which birds can exploit these. In warm and dry conditions, annual plants (i.e. weeds) will have selective advantage over perennials, and southern weed species can be expected to invade (Pain 1989); but, again, chemical control on farmland may rob birds of much of the potential benefit. The net effect may be that our traditional farmland bird species will eventually become reduced in densities in the drier regions of south and east England.

Summer evaporation may become a problem in eastern England at least. If this becomes serious then it might affect the breeding success of such aquatic birds as grebes and rails when water level recedes below the inner margin of emergent vegetation. The reponse might be to breed earlier while water levels are high. In other parts of the country less subject to rainfall seasonality, heavy rains during the breeding season would be harmful to reed bed species such as the Reed Warbler. Riverside nests of a variety of birds would become more susceptible to flooding.

Under a greenhouse climate, uplands are likely to assume an even larger conservation importance, for only on the highest ground can there be montane outposts for such northern species such as Ptarmigan, Golden Plover, Dotterel and Ring Ouzel. Almost certainly there would be increased agricultural demands on the uplands, as vegetational zones rise. Perhaps only managed grouse moors and conservation areas will survive the twin impacts of farming and afforestation. The amount of open ground remaining will determine the survival of the important upland breeding population of raptors.

One important consequence of a warmer climate that is subject to regional summer drought conditions is an inevitable change in growing seasons for plants. Not only will the growing season be prolonged (as mentioned previously), but in dry regions growth will occur in winter and spring which will be followed by a summer (dry season) dormant phase except where land is irrigated.

Since the breeding seasons of birds are so timed that young will appear at the peak season for food availability (Lack 1968), breeding seasons in Britain should eventually be advanced by a month or more in a greenhouse world, to resemble more the timing in the present-day Mediterranean. Winter breeding should remain atypical (though it may become less exceptional than at present); while an early start to breeding allows individual pairs more time for replacement clutches, should these be needed, there is likely to be a limit to selection pressure in that direction when the environment itself has become less seasonal. The extended growing season will mean that there is better cover for early nests, though (on the debit side) ground-nesters such as waders may have problems with the early growth of vegetation. Species attempting second or third broods will (in south and east England at least) have to fit these in before the onset of the dry season. Yet there is also a broad trend, applying today, for numbers of broods and mean clutch sizes to decline across progressively warmer latitudes (Lack 1968). This may result from a trend towards higher nest predation levels in warmer zones; nests will have more chance of avoiding detection by predators if broods are smaller so that feeding visits by parent birds can be fewer (Snow 1976). Also, lower reproductive rates could arise through competition amongst adult birds for the available summer resources (which females require for egg formation), this being keener in regions where breeding season population levels are normally high in the absence of cold winter mortality (Ricklefs 1980). In time, one might expect a comparable reduction in productivity amongst British birds: breeding seasons are likely to begin earlier, but the length of the season may become shorter, and brood sizes smaller.

Since, in general, moult follows closely behind the breeding season, this could also become advanced in a warmer Britain. There are, however, a variety of species which suspend their moult while they migrate, and complete feather renewal in their winter quarters. This may change. Whilst the onset of moult seems likely to occur earlier, perhaps by a month or more, autumn migration may have to wait for the onset of rains in western (and especially south-western) Europe to create suitable conditions for pre-migratory fat deposition. Hence there will be more time for moult to be completed close to the breeding grounds.

In conclusion, it must be re-emphasised that a time-scale for the major trends indicated in this document remains uncertain, even speculative. It may be another two decades before the reality of the greenhouse effect is established beyond question, and at least as long again before there are clearer signs of shifts in British vegetational zones. By the year 2050 we (rather, our successors) may be detecting the beginnings of the more serious changes forecast here, and these seem unlikely to have major impact until the second half of the 21st century. Only in high latitudes may changes be quicker, for there the temperature rises will be proportionally higher. Of course, this is still a remarkably short time-scale by evolutionary standards; but a mean global temperature rise of even 3°C would make the world a warmer planet than it has been for 100,000 years.

Summary

1. The "greenhouse effect" is still an unproved hypothesis, though becoming increasingly plausible as a consequence of on-going studies. Yet even its adherents acknowledge that it may be 20 years before the reality becomes incontrovertible.

2. Computer predictions are for "greenhouse effects" to increase with latitude. It is suggested that by the year 2050 (i.e. 60 years hence) Britain will average 3°C warmer, have 20% higher rainfall though this may become more regional and seasonal, and the south-east quadrant of England in particular will acquire a much drier summer regime of Mediterranean type.

3. Whilst vegetational zones must change gradually in response, it is unlikely that these will be profound by the year 2050. Predictions further ahead are unreliable (at present), since Man's future effectiveness in stabilizing greenhouse emissions is an unknown quantity. But even with political will, it would take decades to reduce emissions to the rate of oceanic absorption. Therefore "greenhouse world" changes must be expected to mount during the next century.

4. The forecast is for sea-levels to rise by 0.8-1.6 m over the next 60 years. This is within the capability of present sea-defences, with appropriate reinforcement. No large-scale

coastal inundations are expected on that time scale. On the other hand, river valley flooding may increase when rainstorm run-off coincides with high tide in the estuary. In southern and eastern England, summer waterlevels are likely to fall in rivers and reservoirs, so that drought conditions become less rare.

5. Recent work has proposed that species distributions are influenced primarily by climate (especially temperatures), directly related to latitudinal variation in the input of solar energy. Complex communities of animals and plants ("habitat") are aggregates of species, each subject to the same climatic pressures. If this hypothesis is correct, it simplifies assessments of the consequences of "greenhouse world" climatic changes.

6. One of the quickest reactions to a rise in temperatures is likely to be a thaw of the tundra permafrost, leading to soil erosion and collapse, and invasion by scrub taiga and then boreal forest. This has serious implications for the waterfowl and wader populations which breed on the tundra, and winter in (or migrate through) western Europe where they would meet further problems caused by rising sea levels reducing the extent of coastal mudflats. Moreover, reduction in the extent of high latitude sea ice would affect marine productivity and therefore many seabird populations.

7. A northward retreat of the boreal zone would lead to decline in Britain of bird species of northern origins (Table I). In particular, new 20th century colonists would almost certainly be lost. Eventually, higher proportions of northern winter visitors would winter closer to their breeding areas in northern Europe. The higher Scottish mountains may retain a montane zone effect in the face of climatic change, to aid the continuance of some outlying (extralimital) populations.

8. Southern-origin species should broadly benefit from the climatic changes, consolidating their British status or (in some cases) become newly established here, especially in the drier south and east (Tables II and III). This, however, is with the proviso that long-distance migrants may face greater passage problems due to the forecast of greater aridity in the west Mediterranean, which would affect its use as a staging area for migrants.

9. Under a warmer climatic regime, resident species (Tables IV and V) should be less subject to hard-winter mortality; and the incidence of the partial migration strategy may decline. Yet this may affect the numbers of summer visitors if, as hypothesised, much migrants exploit those resources left under-used by residents (whose populations should be consistently higher when less influenced by winter weather).

10. English resident species may show more nomadism in what will become the dry season, while long-distance migrants are likely to find the Mediterranean-Saharan crossing more arduous so that species additional to Blackcap and Chiffchaff

may begin to winter regularly in Europe. The genetical changes necessary for the latter could occur quite quickly, since small passerines have an effective generation length of only one year.

11. Climatic change would affect bird ecology as well as distribution. With the growing seasons of plants extended to become almost all-year-round, except for a summer dormant phase in the more arid south-east, bird breeding seasons would be advanced. Eventually the known trend for clutch sizes and numbers of broods to decrease across higher temperature zones would be apparent through reductions in Britain also. Probably moult seasons would also be advanced, in line with breeding seasons; but the onset of autumn migration may have to be delayed until autumn rains in south-west Europe create conditions for pre-migratory fat-deposition. Within Britain, year-round feeding conditions would probably be improved, as vegetation becomes more lush and insects also benefit from better conditions for overwinter survival; but in the drier conditions of the south and east, soil invertebrates may become less accessible to such dependent species as thrushes and some crows.

12. It is emphasised that the changes forecast above are long-term ones. Their onset may only just be perceptible by the year 2050. For the most part, the major changes are likely to occur in the second half of the 21st century and beyond, to a degree that will be determined by Man's ability (or failure) to reduce the scale of "greenhouse gas" emissions.

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