

Avifaunal Responses to Warm Climate: The Message from Last Interglacial Faunas

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ABSTRACT. The possible effect on avifaunas of a hypothetical future warmer climate has recently caused much speculation, frequently ill-founded. On the other hand the actual effects of past warmer interglacials on avifaunas have strangely enough attracted no interest. This paper is an effort to remedy this, by reviewing the avifaunas of the previous interglacial (MIS 5e, 117–130 Ka BP). This interglacial was significantly warmer than the present one, about 2°C in the North Temperate zone and 5°C or more in the Arctic, and may have been the warmest interval since the Pliocene. Most of the known Last Interglacial avifaunas are from the temperate parts of North America and Europe. The scarcity of avifaunas from other areas are due both to a scarcity of Pleistocene avifaunas in general and to rudimentary Quaternary chronologies, which makes it difficult to date faunas older than the last glaciation. In North America, the largest collections are from California and Florida. The Californian faunas are similar to modern faunas, both for seabirds and landbirds, while the Florida faunas contain a number of extralimital Central American and South American species. A small fauna from Arctic Canada (Old Crow Basin) is also similar to modern faunas. In Europe, several faunas from Central Europe differ little from extant faunas in the same areas, while faunas from Great Britain contain some southern (Iberian) species. Material from the southern hemisphere is very limited, and consists of one small fauna from New Zealand which is similar to modern faunas from the same area. The only LIG avifauna that shows dramatic differences from present-day conditions is from southwestern Egypt. This area is now extreme desert but had a rich Afrotropical avifauna during LIG, presumably due to a northward expansion of the African Monsoon. In general it seems that a temperature rise of the order of 2°C does not have a very dramatic impact on temperate avifaunas, while in the tropics changes in precipitation patterns may be more important than temperatures.

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The possible effect on avifaunas of a hypothetical future warmer climate has recently caused much speculation. However the actual fossil data on avifaunas during past warmer interglacials have attracted very little or no interest. This paper is an effort to address this oversight.

The last interglacial (MIS 5e, about 130–117,000 years BP) is of special interest in this context. It was apparently about 2°C warmer than modern climates globally and up to 10°C warmer in large parts of the Arctic (e.g., Velichko *et*

al., 2008, CAPE-Last Interglacial Project Members, 2006), while sea-levels were a few meters higher than at present, though the exact figure is very uncertain. As a matter of fact to judge from the $\delta^{18}\text{O}$ record MIS 5e was the warmest interval since the Pliocene (ca. 2.5 Ma), and to find a sustained period of lower $\delta^{18}\text{O}$ one has to go back about 4 million years to the Early Pliocene warm period (Lisiecki & Raymo, 2005).

Because the last interglacial *sensu stricto* (i.e. MIS 5e) is known by a variety of local names (Sangamonian,

Eemian etc.) the term Last Interglacial (LIG) will be used in this paper.

In general, fully interglacial avifaunas are disproportionately rare compared to faunas from colder intervals, particularly in cave environments. The reason for this is not well understood.

The LIG has a much better avifaunal record than the two preceding interglacials with approximately equal peak temperatures (MIS 9 and 11) but even so, avifaunas which are securely dated to the LIG and are diverse enough for meaningful paleoecological studies are unfortunately almost exclusively available from North America, Europe and northern Africa. Only a single small fauna is known from the southern hemisphere (Table 9).

This geographical limitation is to a large extent due to the fact that in most parts of the World dating of Pleistocene faunas to specific glaciations or interglacials is not yet possible beyond the range of C14 dating.

Methods

To study the effect of climate on the avifaunas the arealogram method (Grichuk, 1969, 1984) was used. This is done by superimposing the modern ranges of all the species in the fossil fauna. The area where all species coexist today defines their common range and the range of environments acceptable to all the species.

If there is no area where all the species of the fossil fauna occur together today, this may either indicate that the environmental conditions have no exact modern counterpart, that the modern range of some of the species have been modified by human action, or that the ecological requirements of some of the species have changed since the LIG. The latter possibility is difficult to evaluate, but seems unlikely to be important over such a relatively short period (ca. 100,000 years).

This method has been much used for plants, including LIG floras (see for example Velichko *et al.* [2008] and references cited therein) and also for mammals, but rarely for birds, probably because of their great mobility (e.g., Harris, 1985). For migrant birds it is moreover necessary to include both wintering areas and areas through which they migrate, unless breeding can be proven by the presence of unfledged juveniles or individuals with medullary bone.

No extinct species have been used in the analysis, since their modern range is not obtainable. Only determinations regarded as secure were used in the analysis. In some cases determinations to genus, e.g., *Cygnus* sp., have been used. In such cases the total range of all species in the genus were used. A further restriction in such cases is that no extinct species belonging to the genus must be known from the applicable area and time interval.

The following sources have been used for range data: North America—The Birds of North America (BNA) (<http://bna.birds.cornell.edu/bna/>), and Price *et al.*, (1995). Europe—Cramp *et al.* (1977–1994), and Hagemeijer & Blair (1997). Africa—Sinclair & Ryan (2003), and Moreau (1972). New Zealand—P. Harrison (1983). Nomenclature and the species order follow Clements (2007). For extinct taxa not found in Clements the nomenclature follows Tyrberg (2008, 2009).

Results

North America. In North America extensive LIG avifaunas are known from southern California and central Florida, with only a few sites from other parts of the continent (Fig. 1).

Los Angeles basin. The LIG climate in southern California is relatively well known from studies of marine deposits. Offshore sea-surface temperatures may have been as much as 3°C warmer than at present while coastal faunas indicate temperatures only slightly higher than today (Muhs *et al.*, 2002, 2006). This is in accord with palynological evidence about the coastal flora which also indicate temperatures similar to or slightly warmer than at present (Heusser, 2000).

The avifaunas from the Los Angeles basin in southern California derive from more than a dozen sites in the LIG marine Palos Verdes Sand (Table 1). Most, if not all, avian remains derive from the “fossil hash” bed. This is an event bed, possibly a tsunamite (Jacobs, Marks & Brown, 2001), which means that the emplacement of the layer was geologically instantaneous though it may of course incorporate older deposits. There seems to be no definite information on the stratigraphic position of this bed within the LIG. This fauna is unusual because while it consists mostly of an exceptionally rich seabird fauna, it also has an appreciable landbird component, probably as a result of its unusual mode of deposition. This makes it possible to analyze conditions both in the sea and on land at the time of deposition.

The composite fauna from the sites in Table 1 consists of 48 analyzable taxa, of which 28 are analyzable as marine or coastal and 20 as land-birds. *Phoebastria albatrus* was not used, since it is now so rare as a result of excessive hunting that its range can not be determined, though it seems to have been the most common albatross in the area during the LIG. Both subfaunas are very similar to the modern avifauna of southern California. The co-occurrence area for the landbirds is a very limited area in the central San Joaquin Valley and the one for the seabirds a short stretch of coast



Figure 1. Sites with Last Interglacial avifaunas in North America.

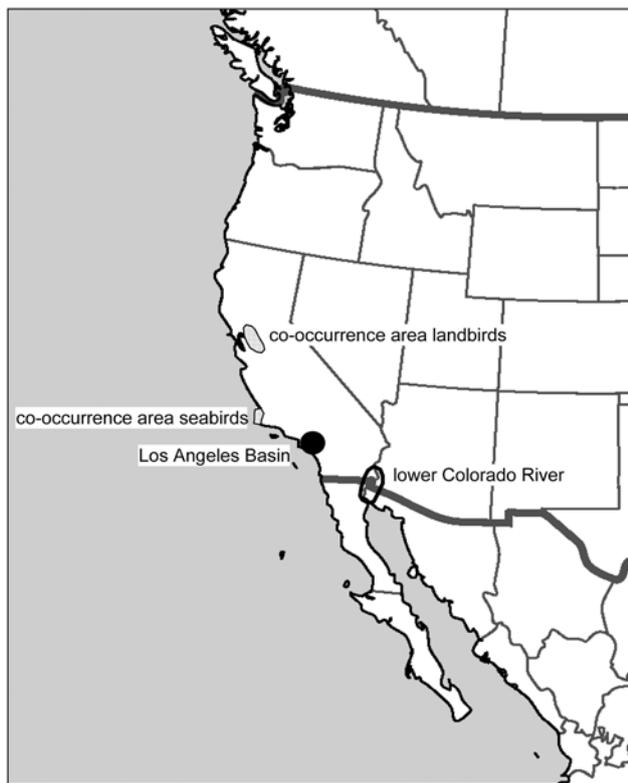


Figure 2. Modern co-occurrence for LIG seabird and landbird faunas from the Los Angeles Basin (shaded areas). The unshaded area on the lower Colorado River marks an area where 19 out of 20 landbirds occur.

in the Lompoc area just northwest of the Los Angeles Basin (Fig. 2). However all landbirds except one also occur along the lower Colorado River 200 km east of the Los Angeles Basin. The species that do not occur in the Los Angeles Basin today are almost exclusively dependent on wetlands or wet meadows, so the avifaunas suggest temperatures similar to the present both on land and in the sea, but with more wetlands than at present.

Florida

The LIG climate of Florida is not well understood due to a paucity of securely dated organic deposits. However the Florida climate is very much determined by the surrounding ocean, and sea-surface temperatures are known to have been similar to or slightly warmer than at present (Muhs *et al.*, 2002) and this is supported by the limited data available on terrestrial vegetation (e.g., Heusser & Oppo, 2003). The maritime influence would presumably have been even stronger than today since sea-level was slightly higher than at present, and southern Florida (south of the present Lake Okeechobee) was a shallow marine/mangrove habitat similar to the modern Florida Bay. To the west along the Gulf coast limited pollen data from LIG beach barrier complexes indicate vegetation similar to modern conditions (Otvos, 2005).

There are a total of seven LIG sites with avifaunas known from central Florida, of which two (Haile VIIA and VIIIA) contain, respectively, only *Meleagris* and *Coragyps atratus*, so are not included in the analysis (Table 2). In contrast to other areas the Florida LIG avifaunas are largely derived

from karstic sites (sinkholes). In all the faunas comprise 104 taxa, of which 7 are extinct. The largest fauna is from Haile XIB with 64 analyzable taxa. Of these, the maximum number of co-occurring taxa at the present time comprises 58 taxa along the upper Texas coast and 56 taxa in south-central Florida (Fig. 3).

The results for the other sites are similar. Rock Springs, with 36 species has all species co-occurring in northern Florida including around the find locality (Fig. 4). Arredondo IIA with 29 analyzable species has a larger area of maximum co-occurrence with 27 species occurring in central and northern Florida and in a coastal belt from Texas to South Carolina (Fig. 5) while Reddick IB/D has 18 from a total of 23 analyzable species co-occurring in a very similar area (Fig. 6). The odd one out in this group is Arredondo IA with 12 species and with two areas of maximum co-occurrence of 11 species each, one in central Florida and one in the mountains of northern Virginia and Maryland (Fig. 7). This strange distribution is due to the presence of *Bonasa umbellus* in the fauna. There is some evidence that *Tsuga* was more widely distributed in southeastern North America during the LIG than during the Holocene (Heusser & Oppo, 2003), but even so it seems unlikely that *Bonasa umbellus* would have occurred in Florida under fully interglacial conditions. It seems more likely that the Arredondo IA fauna is misdated and actually dates at least in part from one of the late cool phases of MIS 5 (i.e. MIS 5b or 5d).

Since the areas of maximum modern co-occurrence (except for Arredondo IA as noted above) are close to or overlap the fossil sites the extralimital species are of particular interest for determining deviations from current environmental conditions.

The extralimital species mostly fall into three groups:



Figure 3. Modern areas of maximum co-occurrence for the Haile XIB avifauna (64 analyzable taxa).



Figure 4. Modern areas of co-occurrence for the Rock Spring avifauna (36 analyzable taxa).



Figure 6. Modern area of maximum co-occurrence for the Reddick IB/D avifauna (23 analyzable taxa).



Figure 5. Modern area of maximum co-occurrence for the Arredondo IIA avifauna (29 analyzable taxa).



Figure 7. Modern areas of maximum co-occurrence for the Arredondo IA avifauna (12 analyzable taxa).

Table 2. Last Interglacial (LIG) faunas from localities in central Florida. Extinct taxa are indicated by a †. List of localities: (1) Haile XIB; (2) Rock Spring; (3) Arredondo IA; (4) Arredondo IIA; (5) Reddick 1B–D. Sources: Brewer (1969); Brodkorb (1957, 1959, 1967, 1978); Emslie (1998); Frailey (1972); Hamon (1964); Holman (1961); Ligon (1965); Olson (1974); Steadman (1976, 1980); Woolfenden (1959). Florida Museum of Natural History Collection database.

species	1	2	3	4	5	species	1	2	3	4	5
<i>Branta canadensis</i>	●	—	—	—	—	<i>Fulica americana shufeldti</i>	—	●	—	●	—
<i>Aix sponsa</i>	●	●	—	—	—	<i>Aramus guarauna</i>	—	●	—	—	—
<i>Anas platyrhynchos</i>	●	—	—	—	—	<i>Grus canadensis</i>	—	●	—	—	—
<i>Anas fulvigula</i>	—	●	—	—	—	<i>Vanellus chilensis</i>	●	—	—	●	—
<i>Anas discors</i>	●	●	—	●	—	<i>Charadrius vociferus</i>	●	—	—	—	—
<i>Anas clypeata</i>	●	—	—	●	—	<i>Recurvirostra americana</i>	●	—	—	—	—
<i>Anas acuta</i>	●	●	—	—	—	<i>Actitis macularius</i>	●	—	—	—	—
<i>Anas [crecca] carolinensis</i>	●	●	—	●	—	<i>Tringa solitaria</i>	—	—	—	●	—
<i>Anas</i> sp.	—	●	—	—	—	<i>Tringa melanoleuca</i>	●	—	—	●	—
<i>Aythya collaris</i>	●	●	●	—	—	<i>Numenius americanus</i>	●	—	—	—	—
<i>Aythya affinis</i>	●	●	—	—	—	<i>Limnodromus scolopaceus</i>	sp.	●	—	—	—
<i>Clangula hyemalis</i>	●	—	—	—	—	<i>Gallinago delicata</i>	●	—	—	—	—
<i>Bucephala albeola</i>	●	—	—	—	—	<i>Scolopax minor</i>	●	—	—	—	—
<i>Lophodytes cucullatus</i>	●	—	—	●	—	<i>Larus</i> sp.	—	●	—	—	—
<i>Mergus serrator</i>	—	●	—	—	—	<i>Zenaida macroura</i>	●	—	—	●	—
<i>Bonasa umbellus</i>	—	—	●	—	—	† <i>Ectopistes migratorius</i>	●	●	●	—	—
<i>Tympanuchus cupido</i>	●	—	—	—	—	<i>Coccyzus americanus</i>	●	—	—	—	—
<i>Meleagris gallopavo</i>	—	cf	●	●	cf	<i>Tyto alba</i>	●	—	—	—	—
<i>Colinus virginianus suilium</i>	●	—	●	●	●	<i>Megascops asio</i>	●	—	—	●	—
† <i>Neortyx peninsularis</i>	●	—	—	—	—	<i>Athene cunicularia</i>	—	—	—	—	—
<i>Gavia immer</i>	—	●	—	—	—	<i>Strix varia</i>	—	●	—	—	—
<i>Podilymbus podiceps</i>	●	●	●	●	—	<i>Asio flammeus</i>	●	—	—	●	—
<i>Podiceps auritus</i>	—	●	—	—	—	<i>Megaceryle alcyon</i>	—	●	—	—	—
<i>Phalacrocorax auritus</i>	—	●	—	—	—	<i>Melanerpes erythrocephalus</i>	●	—	—	—	—
<i>Anhinga anhinga</i>	—	●	—	—	—	<i>Melanerpes carolinus</i>	—	—	—	●	—
<i>Botaurus lentiginosus</i>	●	●	—	—	—	<i>Picoides borealis</i>	—	●	—	—	—
<i>Ardea herodias</i>	—	●	—	—	—	<i>Colaptes auratus</i>	●	—	—	●	—
<i>Ardea alba</i>	—	●	—	—	—	<i>Lanius ludovicianus</i>	—	—	●	—	●
<i>Egretta thula</i>	●	—	—	—	—	<i>Vireo griseus</i>	●	—	—	—	—
<i>Butorides virescens</i>	●	—	—	—	—	<i>Cyanocitta cristata</i>	—	—	—	●	●
<i>Nycticorax nycticorax</i>	—	●	—	—	—	<i>Aphelocoma coerulescens</i>	●	—	●	—	●
<i>Platalea ajaja</i>	—	●	—	—	—	<i>Pica hudsonia</i>	●	—	—	—	●
† <i>Ciconia maltha</i>	—	●	—	—	—	<i>Corvus brachyrhynchos</i>	●	—	—	●	—
<i>Coragyps atratus</i>	—	●	—	—	—	<i>Corvus ossifragus</i>	●	●	●	—	●
(†) <i>Coragyps [atratus] occidentalis</i>	—	●	—	—	●	† <i>Tachycineta speleodytes</i>	●	—	—	●	—
<i>Gymnogyps californianus amplus</i>	—	—	—	—	●	<i>Troglodytes aedon</i>	●	—	—	—	●
<i>Cathartidae</i> sp.	—	—	—	—	●	<i>Cistothorus platensis</i>	●	—	—	—	—
<i>Pandion haliaetus</i>	—	●	—	—	—	† <i>Cistothorus brevis</i>	—	—	—	—	●
<i>Ictinia mississippiensis</i>	—	—	—	—	●	<i>Mimus polyglottos</i>	●	—	—	—	—
<i>Haliaeetus leucocephalus</i>	—	●	—	—	—	<i>Toxostoma rufum</i>	●	—	—	—	●
<i>Accipiter cooperii</i>	●	—	●	—	—	<i>Geothlypis trichas</i>	●	—	—	—	—
<i>Buteo platypterus</i>	●	—	—	—	—	<i>Pipilo erythrophthalmus</i>	●	—	●	—	●
<i>Buteo jamaicensis</i>	—	●	●	—	—	<i>Passerculus sandwichensis</i>	—	—	—	●	—
<i>Caracara cheriway plancus</i>	●	—	—	—	—	<i>Ammodramus savannarum</i>	●	—	—	—	—
<i>Milvago chimachima readei</i>	—	—	—	●	●	<i>Ammodramus henslowii</i>	●	—	—	●	●
<i>Falco sparverius</i>	●	—	—	●	—	<i>Cardinalis cardinalis</i>	●	●	●	—	●
<i>Falco peregrinus</i>	●	—	—	●	—	<i>Dolichonyx oryzivorus</i>	—	—	—	—	●
<i>Coturnicops noveboracensis</i>	●	—	—	—	—	<i>Agelaius phoeniceus</i>	—	—	—	●	●
<i>Laterallus exilis</i>	●	—	—	—	●	<i>Sturnella magna</i>	●	—	—	●	●
<i>Rallus elegans</i>	●	—	—	●	—	<i>Quiscalus quiscula</i>	●	—	—	—	●
<i>Rallus limicola</i>	●	—	—	●	—	<i>Molothrus ater</i>	●	—	—	—	●
<i>Porzana carolina</i>	●	—	—	●	—	† <i>Cremaster tythius</i>	●	—	—	—	—
<i>Porphyrio martinica</i>	●	—	—	●	—	† <i>Pandanaris floridana</i>	●	—	—	●	●
<i>Gallinula chloropus</i>	●	●	—	●	—						

currently South American taxa (*Milvago chimachima*, *Laterallus exilis*, *Vanellus chilensis*), currently western prairie species (*Tympanuchus cupido*, *Numenius americanus*, *Pica hudsonia*) and boreal waterbirds that do not currently winter as far south as Florida (*Branta canadensis*, *Bucephala albeola*, *Clangula hyemalis*). The South American taxa probably indicate warmer conditions than at present, and at least *Tympanuchus cupido* would seem to indicate the presence of prairie habitat while the presence of *Pica hudsonia* might be due to the presence of megafauna. *Numenius americanus* would probably have been wintering,

and its presence in Florida, east of its modern range, may be connected with the presence of extensive prairies in central North America during at least parts of the LIG (Curry & Baker, 2000; Zhu & Baker, 1995). On the whole the extralimital species suggest rather warmer conditions and the presence of more prairie habitat in central Florida than at present. The presence of boreal anatids south of their modern winter range may seem paradoxical, but is confirmed by a small LIG fauna from Chatham county in Georgia (Table 3) with *Cygnus columbianus*, well south of its modern winter range.

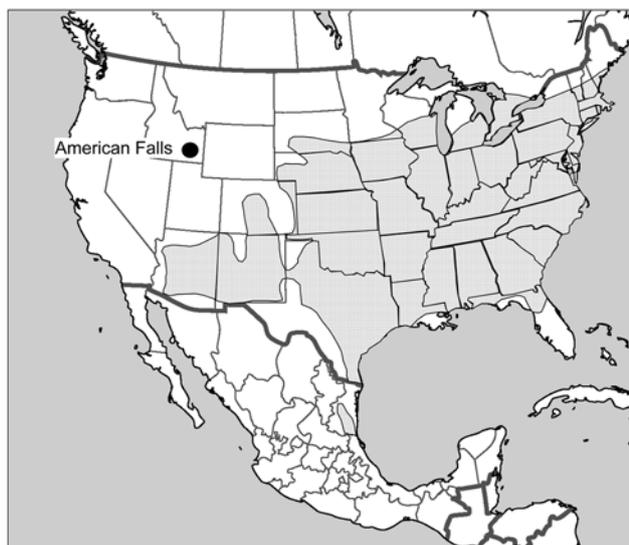


Figure 8. Modern areas of co-occurrence for the American Falls avifauna (6 analyzable taxa).

Table 3. LIG faunas from localities in Chatham County, Georgia. Source: Hulbert & Pratt (1998); ● = present.

species	Isle of Hope	Mayfair
<i>Cygnus columbianus</i>	—	●
<i>Anas americana</i>	—	●
<i>Anas rubripes/platyrhynchos</i>	●	—
<i>Meleagris gallopavo</i>	—	●

The American Falls fauna from Idaho comprises 7 taxa (one extinct) (Table 4) that define a large area of co-occurrence well to the east of the fossil site (Fig. 8). The most climatically significant taxon in the fauna is the Turkey, *Meleagris gallopavo* which has not occurred naturally in the northern Rocky Mountain area during the Holocene. Since introduced turkeys do survive in some parts of the northern Rockies the species' presence in the American Falls fauna does not necessarily indicate very different conditions from today, but the fact that the Turkey managed to disperse to Idaho presumably require the presence of at least riparian woodland corridors across the prairie zone at some stage of the Sangamonian.

The avifauna from the LIG fluvial beds of the Old Crow basin in northwestern Yukon is the only LIG arctic avifauna yet described. It is a small fauna (six species) dominated by widely distributed wetland species (Table 5).

Table 4. LIG fauna from American Falls, Idaho. Sources: Becker (1982), Brodkorb (1963), Howard (1942), Jefferson *et al.* (2002), Pinosof (1992, 1999), Steadman (1980).

American Falls, Idaho
<i>Branta canadensis</i>
<i>Anas platyrhynchos</i>
<i>Anas</i> sp.
<i>Meleagris gallopavo</i>
<i>Ardea herodias</i>
† <i>Ciconia maltha</i>
Cathartidae sp.



Figure 9. Modern areas of co-occurrence for the Old Crow River avifauna (6 analyzable taxa). Note the smaller isolated area south of Hudson Bay, in the St Lawrence valley and the Maritime provinces.

The LIG climate in the area was at least 2°C warmer than at present, forest reached the shore of the Arctic Ocean and large *Larix* and *Picea* logs and several southern extralimital plants and insects occur in the same layer as the birds (CAPE Last Interglacial Project Members, 2006; Harington, 1990; Matthews *et al.*, 1990). The mutual range of the avifauna (Fig. 9) is in line with this climatic information. It comprises a large part of the taiga zone but barely reaches the Old Crow River basin.

Table 5. LIG fauna from Old Crow River, Localities CRH 12,44,45,60, Yukon. Sources: Fitzgerald (1991), Harington (1989).

Old Crow River, Yukon

cf. *Anser/Chen* sp.
Anas americana
Anas clypeata
Anas [crecca] carolinensis
Anas sp.
Melanitta perspicillata
Clangula hyemalis
Tetraonidae sp.
Gavia sp.
cf. Charadriiformes sp.
Passeriformes sp.

Europe

In central Europe most of the sites with avifauna are calcareous tufas (travertines). For some reason that is not well understood, cave sites with deposits of LIG age are extremely rare if not entirely absent on the European mainland. Most or all Eemian tufa sites seem to derive from the early, warmest, part of the interglacial (pollen zones 1–4, *Helicigona banatica*-fauna (Wenzel, 2007)). This was apparently the warmest and driest part of the Eemian which in accordance with conditions in the current interglacial when tufa formation in Sweden was limited to the early part of the interglacial with a continental warm and dry climate (Gedda, 2001).

Interesting exceptions to the absence of cave faunas are two small faunas from coastal caves in Wales (Table 7). These like the Los Angeles faunas, permits comparison of landbird and seabird faunas.

Germany

The climate in Europe during the last interglacial has been well studied. During the early, warmest, part of the interglacial temperatures in central and southern Germany were about 2°C warmer than at present in summer but only slightly warmer than at present (< 1°C) in January (Aalbersberg & Litt, 1998; Kaspar *et al.*, 2005; Klotz *et al.*, 2003).

The largest German LIG avifauna is from Stuttgart-Untertürkheim (Table 6). This is a tufa fauna and the other fossils from the tufa clearly indicate a warm climate, for example Honeysuckle tree, *Lonicera arborea*, a currently

Table 6. LIG faunas from German localities. List of Localities: 1, Stuttgart-Untertürkheim, Biedermannsche Steinbruch, (Unterer Travertin); 2, Burgtonna, travertines; 3, Taubach, travertines; 4, Weimar, Parktravertin; 5. Schönfeld, Brandenburg. Sources: Adam, Bloos & Ziegler (1987); Andree (1939); Fischer (1991); Fischer & Mauersberger (1989); Heinrich (1984); Heinrich & Jánossy (1978a,b); Jánossy (1977); Lambrecht (1933); Wenzel (1998).

species	Europe				
	1	2	3	4	5
<i>Anser anser</i>	●	—	—	—	—
<i>Anser</i> sp.	●	—	—	—	—
<i>Cygnus cygnus</i>	—	—	cf	—	—
<i>Cygnus</i> sp.	●	—	—	—	—
<i>Tadorna tadorna</i>	—	—	cf	—	—
<i>Anas penelope</i>	—	—	cf	—	—
<i>Anas platyrhynchos</i>	●	●	●	—	—
<i>Anas acuta</i>	—	—	—	—	●
<i>Aythya ferina</i>	—	—	—	—	●?
<i>Bucephala clangula</i>	—	—	●	—	●
<i>Mergus merganser</i>	—	—	●	—	—
<i>Perdix perdix</i>	●?	—	—	—	—
<i>Ixobrychus minutus</i>	—	—	—	—	●
<i>Pandion haliaetus</i>	—	—	●	—	—
<i>Accipiter nisus</i>	—	—	—	●	—
<i>Rallus aquaticus</i>	●?	—	—	—	—
<i>Porzana parva</i>	cf	—	—	—	—
<i>Tringa ochropus</i>	—	—	—	—	●
<i>Tyto alba</i>	●?	—	—	—	—
<i>Asio flammeus</i>	—	—	●	—	—
<i>Dendrocopos major</i>	—	—	●	—	—
<i>Eremophila alpestris</i>	cf	—	—	—	—
<i>RiparialHirundo</i> sp.	●	—	—	—	—
<i>Sylvia</i> sp.	●	—	—	—	—
<i>Erithacus rubecula</i>	●?	—	—	—	●
<i>Luscinia</i> sp.	●	—	—	—	—
<i>Oenanthe</i> sp.	●	—	—	—	—
<i>Turdus merula</i>	—	—	—	—	●
<i>Turdus iliacus</i>	cf	—	—	—	—
<i>Turdus philomelos</i>	—	—	—	—	●
<i>Sturnus vulgaris</i>	—	—	●	—	—
<i>Prunella modularis</i>	—	—	—	—	●?
<i>Prunella</i> sp.	●	—	—	—	—
<i>Motacilla</i> sp.	●	—	—	—	—
<i>Anthus pratensis</i>	●	—	—	—	—
<i>Anthus</i> sp.	●	—	—	—	—
<i>Emberiza citrinella</i>	cf	—	—	—	—
<i>Fringilla coelebs</i>	●	—	—	—	—
<i>Fringilla montifringilla</i>	●	—	—	—	—
<i>Loxia</i> cf. <i>curvirostra</i>	●	—	—	—	—
<i>Carduelis chloris</i>	●	—	—	—	—
<i>Pyrrhula pyrrhula</i>	●	—	—	—	—
<i>Coccothraustes coccothraustes</i>	●	—	—	—	—
<i>Fringillidae</i> sp.	●	—	—	—	—
<i>Montifringilla nivalis</i>	●	—	—	—	—



Figure 10. Modern areas of co-occurrence for the Stuttgart-Untertürkheim avifauna (22 analyzable taxa).

Table 7. LIG faunas from the coastal sites in southwest Wales: 1, Bacon Hole (Layers D–F); 2, Minchin Hole. Sources: C.J.O. Harrison (1977, 1987), Stringer *et al.* (1986), Stewart (2007).

	1	2
<i>Calonectris diomedea</i>	●	—
<i>Milvus milvus</i>	●	—
<i>Arenaria interpres</i>	●	—
<i>Calidris alpina</i>	●	●
<i>Alca torda</i>	●	●
<i>Corvus coronelfrugilegus</i>	●	—
<i>Alauda arvensis</i>	●	●
<i>Hirundo rustica</i>	●	—
<i>Oenanthe oenanthe</i>	●	—
<i>Turdus merula/torquatusa</i>	●	—
<i>Sturnus vulgaris</i>	●	—
<i>Sturnus</i> cf. <i>unicolor</i>	—	●

Mediterranean species. The fauna contains 22 species of which 21 define an area of co-occurrence that is quite large despite the large number of species (Fig. 10), and does not indicate any definite deviation from the extant climatic conditions. The single extralimital species, *Montifringilla nivalis*, is a high-altitude montane form, which might be expected in a glacial avifauna, but not in an otherwise clearly interglacial context.

Three tufa faunas in Thuringia (Burgtonna, Taubach, Weimar Park-Travertin) (Table 6), when merged comprise only 8 species which delineate a very large area of co-occurrence (Fig. 11). This too only confirms the generally interglacial character of the faunas, but gives no specific information about deviations in climate from modern conditions. The species reported on the basis of eggshells by Stephan (1977, 1984) were not included since the determinations were considered uncertain.

The fauna from Schönfeld in Brandenburg (nine species) (Table 6) is unusual in being derived from a lake basin.

The area of co-occurrence in this case is situated largely to the south and east of the fossil site (Fig. 12), suggesting slightly warmer and/or more continental conditions than at present.



Figure 11. Modern areas of co-occurrence for the Thuringian avifaunas (Burgtonna, Taubach, Weimar) (8 analyzable taxa).

Wales

The only known European cave avifaunas of LIG age are from two coastal caves, Bacon Hole (Layer D–F) and Minchin Hole, in southwestern Wales. The combined fauna is relatively small, 10 landbird and 2 seabird taxa (Table 7), but interesting since it is the only European LIG avifauna that indicates conditions significantly warmer than at present. Both the seabirds and the landbirds suggest conditions similar to that found in parts of the Iberian peninsula today (Fig. 13).

There is a discrepancy between the LIG climate of southern England as reconstructed on the basis of palynology compared to that based on insects (Coleoptera). The latter indicate July temperatures 4°C warmer than at present (Cope, 2001) while plants indicate about 2.5°C warmer in July and 2°C colder than at present in January (Kaspar *et al.*, 2005). The birds would seem to support the higher temperatures indicated by Coleoptera. The lower temperatures suggested by the plants may be due to their lower mobility than the volant birds and insects; plants restricted to warmer habitat may simply not have had time to reach the British Isles before



Figure 12. Modern areas of co-occurrence for the Schönfeld avifauna (9 analyzable taxa).

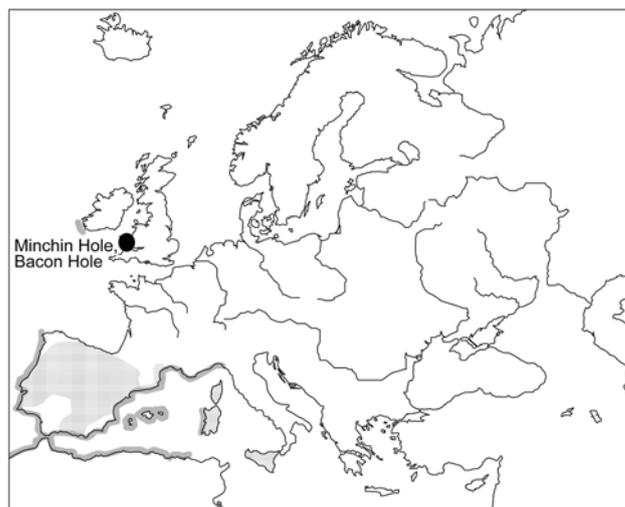


Figure 13. Modern areas of co-occurrence for the Welsh coastal cave avifaunas (Bacon Hole, Minchin Hole) (8 analyzable taxa). The shaded land area and coastal strips indicate the co-occurrence areas for landbirds and seabirds respectively.

they were isolated by rising sea levels. This phenomenon has been noted as skewing interglacial temperature reconstructions too low in Japan (Okuda *et al.*, 2007), which is in a somewhat similar biogeographical position. Sea-surface temperatures, which are important for seabirds, were 1.5–3°C warmer than at present in summer during the LIG, while winter temperatures were similar to current conditions (Burman & Pâsse, 2008).

Africa

The only African site with an appreciable LIG avifauna is Bir Tarfawi, “Grey Lake 2” deposits. At the present time Bir Tarfawi is situated in one of the most extreme desert areas on Earth, but during the LIG the area was a savannah with shallow permanent lakes. This environment indicates much higher precipitation than at present. The avifauna comprises 18 species (Table 8). 16 of which occur together today in the Sahel savannah belt where annual precipitation is in the 500–1000 mm range (Fig. 14), confirming the environmental reconstruction from other climate proxies. The two remaining species *Chlamydotis undulata* and *Pterocles senegallus*, are of special interest since they currently occur in semi-desert environment at the northern edge of the Sahara Desert (Fig. 14). The presence of these species in an otherwise Afrotropical fauna suggests that the eastern Sahara north of Bir Tarfawi was narrow during the LIG, and may not have contained any extreme desert. The fact that the fauna is predominantly Afrotropical and the few Palearctic forms are arid-adapted suggests that increased precipitation was mainly due to a northward extension of the African monsoon system rather than a southward extension of temperate weather systems from the Mediterranean. Such a northward expansion of the monsoon during the LIG has been documented from several climate proxies (Fleitmann *et al.*, 2003; Osmond & Dabous, 2004; Smith *et al.*, 2004; Szabo *et al.*, 1995) and for a brief period may even have meant a virtual disappearance of the hyperarid zone in northeastern Africa and southwestern Asia (Vaks *et al.*, 2007).

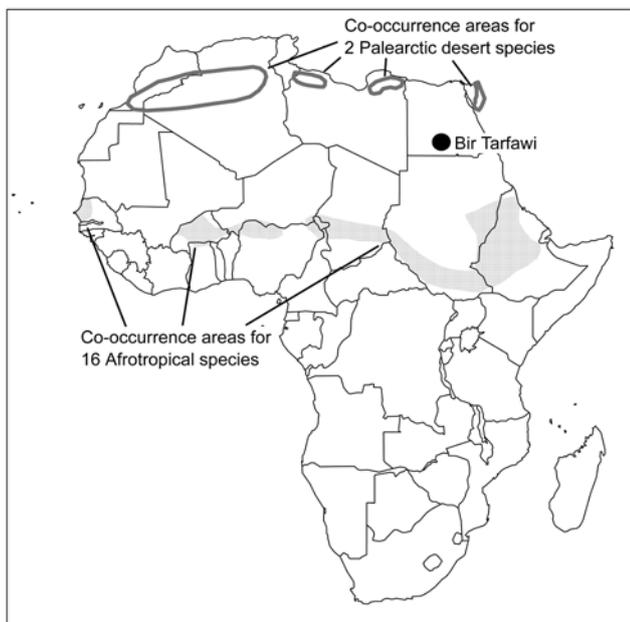


Figure 14. Modern areas of co-occurrence for the Bir Tarfawi avifauna (18 analyzable taxa). The shaded area marks the co-occurrence area for the 16 Afrotropical taxa and the unshaded area the co-occurrence area of *Chlamydotis undulata* and *Pterocles senegallus*.

Table 8. LIG fauna from Bir Tarfawi, SW Egypt. Sources: Bocheński (1991, 1993); Kowalski *et al.* (1989); G.M. Miller (1993).

Africa
<i>Struthio camelus</i>
<i>Phalacrocorax africanus</i>
<i>Ardea cinerea</i>
cf. <i>Bubulcus ibis</i>
<i>Nycticorax nycticorax</i>
<i>Plegadis falcinellus</i>
<i>Gyps africanus</i>
<i>Turnix cf. sylvaticusa</i>
<i>Porzana cf. pusilla</i>
<i>Gallinula chloropus</i>
<i>Fulica cristata</i>
<i>Chlamydotis undulata</i>
<i>Pterocles cf. senegallus</i>
<i>Pterocles</i> sp.
<i>Oena capensis</i>
<i>Corvus albus</i>
<i>Corvus</i> sp.
<i>Riparia cf. riparia</i>

New Zealand

The only avifauna from the southern hemisphere that is reasonably securely dated to the LIG and large enough for environmental reconstruction is from Cape Wanbrow on New Zealand.

The LIG climate of New Zealand was 2–3°C warmer than at present (Marra, 2003) while sea-surface temperatures were about 1°C warmer than at present in the Tasman Sea immediately west of New Zealand (Pelejero *et al.*, 2006).

The fauna comprises 11 species, five landbirds and six

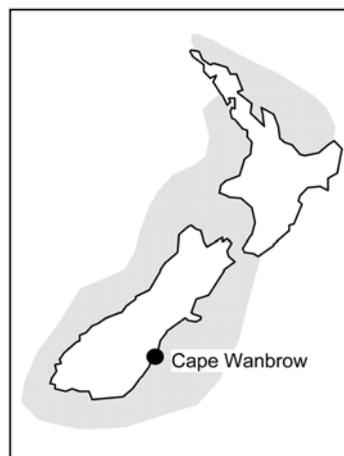


Figure 15. Modern area of co-occurrence for the Cape Wanbrow marine avifauna (5 analyzable taxa).

Table 9. LIG fauna from Cape Wanbrow (sites J41/f8710, f8214, f8227), New Zealand. Sources: Worthy & Grant-Mackie (1993); Boessenkool *et al.* (2008).

New Zealand
† <i>Emeus crassus</i>
† <i>Pachyornis elephantopus</i>
† <i>Megadyptes waitaha</i>
<i>Eudyptula minor</i>
<i>Puffinus griseus</i>
<i>Puffinus gavia/huttoni</i>
<i>Pelecanoides urinatrix</i>
<i>Phalacrocorax punctatus</i>
† <i>Harpagornis moorei</i>
<i>Nestor meridionalis</i>
† <i>Sceloglaux albigacies</i>

seabirds (Table 9), of which four and one respectively have gone extinct during the late Holocene. Because the modern range of extinct species cannot be defined, only the common foraging range of the seabird component of the fauna can be determined (Fig. 15). This comprises the coastal waters around most of New Zealand, and does not indicate any significant difference compared to modern conditions.

Discussion

Initially it must be noted that the identification of the studied sites as being of LIG age on biostratigraphic and chronostratigraphic grounds is confirmed by the avifaunas. Only in two cases are there records of species that seem out of place in a fully interglacial environment, Arredondo IA (*Bonasa umbellus*) and Stuttgart-Untertürkheim (*Montifringilla nivalis*).

The avifaunas also mostly conform quite well to the environmental and climatic conditions indicated by other proxies. However, in some cases the avifaunas suggest differences between modern and LIG conditions that are not obvious in earlier reconstructions, for example the presence of wetlands in the Los Angeles area, prairie habitat in northern Florida and the presence of desert taxa with northern affinities in the Bir Tarfawi area.

One somewhat mysterious matter is the presence of boreal swans, geese and ducks south of their present winter range in eastern North America. A possible explanation might be that the known very warm arctic LIG climate (e.g., CAPE Last Interglacial Project Members, 2006) meant much larger breeding populations, which needed larger wintering areas than the extant populations. Another possible explanation is increased seasonality. There is some evidence for this from southern Europe where winter temperatures seems to have been lower than at present at the beginning and the end of the LIG when winter insolation was low at mid-latitudes, despite summer and annual average temperatures being higher than at present (Allen & Huntley, 2009; Rousseau *et al.*, 2006).

As for the effect of the generally warmer climate during the LIG it seems clear that differences on the order of 2°C or less, both on land and in sea-surface temperatures, are barely, if at all, detectable in the avifaunas. The Old Crow River fauna, with a temperature differential probably slightly more than 2°C seems to be a borderline case.

It is unfortunate that there are no quantitative data on LIG climate in Florida, since the faunas there show small but significant differences compared to modern faunas from the same area.

On the other hand the Welsh coastal faunas show a quite clear climatic signal, which is associated with a summer temperature differential of 4°C, judged by the entomological data.

The strongest climatic signal by far is of course the one connected to the Bir Tarfawi fauna which is completely different from the (almost nonexistent) fauna occurring in the area today. In this case it is however, not the temperatures but the precipitation that is the determining factor.

It might be noted in this context that a recent very thorough review of changes in numbers and distribution of the Swedish avifauna during the last 30 years failed to find any identifiable effects of climatic change, though the average annual temperature has risen nearly 1°C during this period (Ottvall *et al.*, 2009).

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