
Pleistocene Reindeer and Global Warming

DONALD K. GRAYSON* AND FRANÇOISE DELPECH†

*Department of Anthropology, Box 353100, University of Washington, Seattle, WA 98195, U.S.A., email grayson@u.washington.edu

†Institut de Préhistoire et de Géologie du Quaternaire, UMR 5199 du CNRS, Avenue des Facultés, Université Bordeaux I, 33405 Talence, France

Abstract: *Current concerns for the future of reindeer and caribou (*Rangifer tarandus*) in the far north under conditions of global warming focus on the increased energetic and predation costs associated with warmer winters and on vegetation change and increased insect harassment caused by warmer summers. At the Grotte XVI archaeological site (Dordogne, southwestern France), episodes of summer warming between about 36,000 and 12,000 radiocarbon years ago appear to be associated with lowered relative abundances of reindeer. As the Pleistocene ended and summer temperatures climbed higher, reindeer were extirpated from southern France. A similar phenomenon appears to have occurred here during the prior Eemian interglacial. These records suggest that increased summer temperatures under conditions of global warming may have a direct negative effect on reindeer and caribou populations, including a northward displacement of their southern distributional boundary.*

Key Words: caribou, Grotte XVI, *Rangifer tarandus*

Renos del Pleistoceno y Calentamiento Global

Resumen: *La preocupación por el futuro de renos y caribú (*Rangifer tarandus*) en el lejano norte bajo condiciones de calentamiento global se concentra en el incremento de los costos energéticos y de depredación asociados con inviernos más cálidos y en el cambio de vegetación y el incremento de hostigamiento por insectos causado por veranos más cálidos. En el sitio arqueológico Grotte XVI (Dordogne, suroeste de Francia) los episodios de calentamiento estival hace entre 36,000 y 12,000 años radiocarbónico parecen estar asociados con disminución en las abundancias relativas de renos. Al término del Pleistoceno y a media que las temperaturas estivales aumentaron aun más, los renos fueron extirpados del sur de Francia. Un fenómeno similar parece haber ocurrido durante el interglacial, Eemian, previo. Estos registros sugieren que el incremento de temperaturas estivales bajo condiciones de calentamiento global puede tener efectos negativos directos sobre poblaciones de reno y caribú, incluyendo el desplazamiento hacia el norte de su límite sureño de distribución.*

Palabras Clave: caribú, Grotte XVI, *Rangifer tarandus*

Introduction

By the year 2080, Arctic summer temperatures are predicted to increase by 4.0–7.5° C, accompanied by a 10–20% increase in precipitation. Winter temperatures are predicted to rise by 2.5–14.0° C, with a 5–80% increase in precipitation (Anasimov et al. 2001). Such predictions have caused deep concern among scientists (e.g., Gunn 1995; Gunn & Skogland 1997; Gitay et al. 2002) and na-

tive peoples (e.g., Turi 2000) for the future of reindeer and caribou (*Rangifer tarandus*) populations in the north.

The predicted climate changes are expected to have multiple negative impacts on these animals. In winter, greater snow depth would increase the energetic costs of movement, make food more difficult to find, and may make caribou more vulnerable to predation. Greater snow depth and density, coupled with freeze-thaw episodes and the multiple ice crusts that result,

would increase energetic demands on reindeer and caribou as they attempt to dig through snow for food (Russell 1993; Brotton & Wall 1997; Gunn & Skogland 1997; Klein 1999). Warmer winter temperatures could also lead to increased survival and transmission rates of parasites (Brotton & Wall 1997). Not surprisingly, extreme winter snow accumulation and ice crusting are associated with historic population declines in reindeer and caribou (e.g., Klein 1968; Meldgaard 1986), whereas warm and wet winters are correlated with a reduction in calving success (Lee et al. 2000).

The most obvious potential impacts of predicted changes in Arctic summer temperatures on reindeer and caribou are indirect. A variety of insects attack these animals, including mosquitoes (*Aedes* spp.), warble flies (*Hypoderma tarandi*), and nasal bot flies (*Cephenemyia trompe*). Insect harassment of reindeer and caribou increases as temperature increases, with activity peaks reached above approximately 15° C (Helle & Tarvainen 1984; Russell 1993; Nilssen 1997; Mörschel 1999). These attacks occur at a time when energy and nutrient requirements for reindeer and caribou are at their peak (Weladji et al. 2002)—lactating females have their highest yearly energy demands but their lowest yearly body fat reserves (Walsh et al. 1992), males must add fat prior to the autumn rut (Brotton & Wall 1997), and young must add weight quickly to survive the winter (Mörschel & Klein 1997; Mörschel 1999). An increase of 2–4° C in summer temperature and the attendant increase in insect harassment have been estimated to cause a 7% decrease in feeding (Russell 1993) as well as energetically expensive insect avoidance behaviors (White et al. 1975; Downes et al. 1986; Russell 1993). In addition, blood loss to insects can amount to 125 g/day (Helle & Tarvainen 1984). Thus, severe insect harassment can lead to increased mortality during the following winter and to decreased pregnancy rates among surviving females (Brotton & Wall 1997; Mörschel & Klein 1997; Mörschel 1999; Colman et al. 2001). Weladji et al. (2002) suggest that the impact of insects on reindeer and caribou provides the most important causal link between warm summers and poor physical condition in these animals.

The direct impact of summer temperatures on reindeer and caribou may also be significant, although the evidence here is less clear. Some experimental evidence suggests that these animals can tolerate summer temperatures of at least 45° C when given access to unlimited water (Rosenmann & Morrison 1967), and that they are as well adapted to heat as are some desert herbivores (Yousef & Luick 1975). On the other hand, three of the six animals in these experiments died and other work suggests that heat stress may be a significant factor in reindeer and caribou well-being. Because reindeer have few functional sweat glands and remain well insulated in summer, they may undergo heat stress under even moderate temperatures (Soppela et al. 1986b). Reindeer

calves, for instance, increase their respiration rate, heart rate, and oxygen consumption sharply above an ambient temperature of 20° C, changes that are accompanied by an increase in internal body temperature (Soppela et al. 1986a,b; Soppela 2000). In addition, caribou may feed less and move more at temperatures above 20° C even in the absence of insects (Mörschel & Klein 1997). They also increase the rate at which they ingest snow as temperature increases, with ingestion peaking at temperatures above approximately 16° C (Ion & Kershaw 1989). Indeed, the southern edge of caribou distribution (Hall 1981) coincides fairly well with the southern edge of the distribution of three species of spruce (*Picea engelmannii* Parry ex Engelm., *P. glauca* [Moench] Voss, and *P. mariana* [Mill.] B.S.P.) that do not exist where July average temperatures exceed approximately 23° C (Thompson et al. 2000).

Although some researchers have found no correlation between elevated summer temperatures and either reindeer calf survival or fluctuations in reindeer population numbers (Aanes et al. 2000; Lee et al. 2000), a prolonged increase in summer temperatures can be expected to affect reindeer and caribou negatively as a result of increased insect harassment and, perhaps, heat stress. Vegetation change driven by temperature increases is also expected to affect reindeer and caribou abundances (Lenart et al. 2002), but current research does not allow precise predictions of what this effect might be.

Researchers have called for the analysis of long-time series of population-history data on *R. tarandus* and have suggested that archaeological and paleontological records could play an important role in these analyses (Klein 1999; Weladji et al. 2002). We present such a time series from the Grotte XVI archaeological site in the Dordogne region of southwestern France.

Grotte XVI Reindeer and Climate Change

The historical distribution of *R. tarandus* did not extend farther south than 46°N (Geist 1998). During the late Pleistocene, however, this species was found as far south as northern Mississippi (33°N) in the Americas (McDonald et al. 1996) and as far south as western Italy (43°N) and northern Spain (42°N) in Europe (Bedetti et al. 2001; García & Arsuaga 2003). For tens of thousands of years before their extirpation near the Pleistocene-Holocene boundary, reindeer formed a significant part of human diets in southwestern Europe (Grayson & Delpech 2002).

The record we present here is from the archaeological site of Grotte XVI (44.5°N, elevation 190 m), one of a series of caves and rock shelters in the limestone cliffs that overlook the Céou River near its confluence with the Dordogne in southwestern France (Fig. 1). Excavations at this site, completed in 2001, revealed a stratigraphic sequence of deposits >3 m deep (bottom of sequence was not reached) that begins with archaeological units

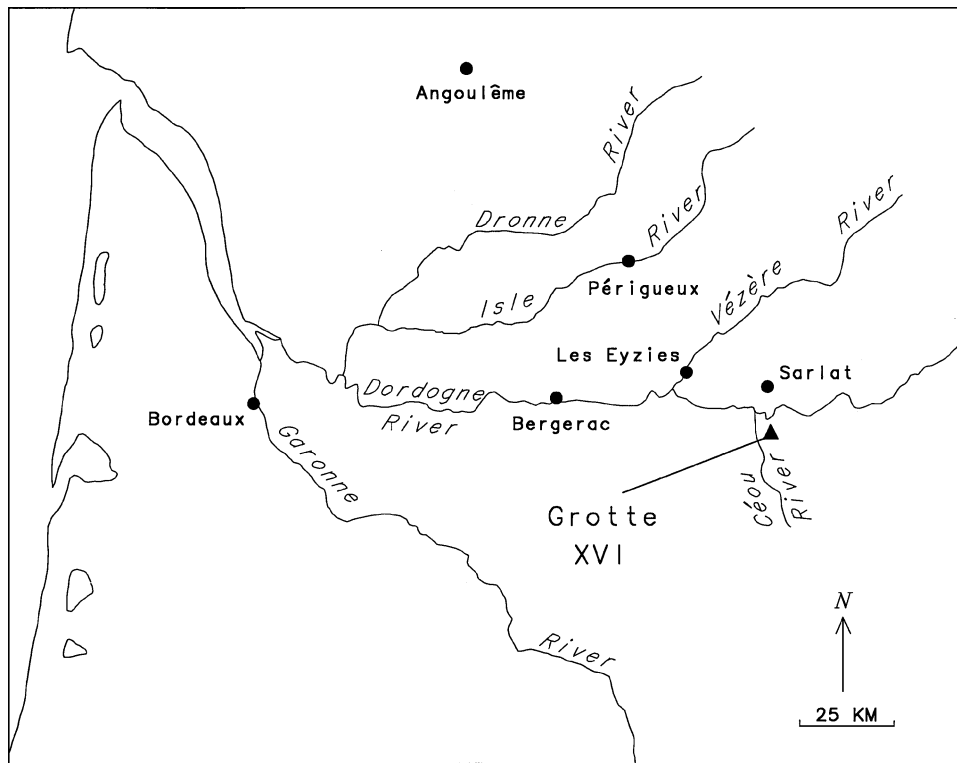


Figure 1. The location of Grotte XVI in France.

attributed to the Mousterian (to date, always associated with Neanderthals) and continues through the latest Paleolithic tradition in the region, the Magdalenian (Rigaud et al. 1995). The depositional sequence begins prior to 60,000 years ago and ends at about 12,000 radiocarbon years ago. Radiocarbon dates are available for five of the Grotte XVI stratigraphic units (Table 1) and our analysis focuses on these five units (strata B, Abb, Abc, As, and 0), although we also present data for undated stratum Aib.

Substantial vertebrate faunal samples were obtained and identified for these six Grotte XVI strata. The ungulate component of these assemblages (Table 2) was introduced by people, and changing ungulate abundances across these strata represent differential human hunting success, but we lack data on the seasons during which these remains were deposited (Grayson et al. 2001; Grayson & Delpech 2003).

Reindeer relative abundance increased steadily from Châtelperronian stratum B, the oldest radiocarbon-dated unit, to Magdalenian stratum 0. In each stratum, the abundance of reindeer compared with that of all other ungulates differed significantly from that in adjacent strata as assessed by chi-square (at $p < 0.05$ for the Aib-Abb comparison and at $p < 0.01$ for all others). In an earlier analysis (Grayson et al. 2001), this pattern of increasing reindeer relative abundance through time could not be accounted for by differential sample sizes, differential transport of bones to the site by its human occupants, differential bone fragmentation across taxa and strata, or any other known mechanical or human behavioral mechanism that

Table 1. Summary of the stratigraphy and chronology of Grotte XVI (from Grayson et al. 2001).

Stratum	Archaeological tradition	Radiocarbon age BP ± SD
0	Magdalenian	12,285 ± 100
As	Solutrean	12,530 ± 105
		20,070 ± 330
		20,230 ± 270
		20,280 ± 220
		20,410 ± 380
Abc	Gravettian	20,460 ± 260
		26,430 ± 470
		28,140 ± 405
Abb	Aurignacian	29,285 ± 420
		29,710 ± 510
Aib	Aurignacian	undated
B	Châtelperronian	35,000 ± 1200
		38,100 ± 1670
C	Mousterian	>39,800 ^a
D-K	Mousterian	64,600 ± 3100 ^b
		undated

^aAssumed to pertain to underlying Mousterian stratum C.

^bAverage of six thermoluminescence dates.

might have affected these assemblages. This result suggests an exogenous cause for the pattern.

No detailed paleoclimatic reconstructions are available for southwestern France for the times of interest here, but a reconstruction is available for eastern France (Guiot et al. 1989; Guiot 1990; Pons et al. 1992), which is based on

Table 2. Number of identified specimens by stratigraphic unit and taxon at Grotte XVI.*

Scientific name	Stratum						Σ
	0	As	Abc	Abb	Aib	B	
Bos/Bison	2	4	26	38	17	26	113
Capra sp.	10	14	99	141	58	103	425
Capreolus capreolus	2	5	6	12	1	11	37
Cervus elaphus	24	22	173	260	79	122	680
Equus sp.	30	23	58	114	25	26	276
Megaceros giganteus	0	0	0	1	0	0	1
Rangifer tarandus	2049	409	1011	887	235	248	4839
Rhinoceros	0	0	0	0	0	2	2
Rupicapra rupicapra	27	18	35	54	23	37	194
Saiga tatarica	26	3	0	0	0	0	29
Sus scrofa	2	5	12	21	11	14	65
Σ	2172	503	1420	1528	449	589	6661
R. tarandus (%)	94.3	81.3	71.2	58.1	52.3	42.1	

*Twenty-five mammoth tusk specimens excluded because all are, or are likely to be, present only because of their use as tools.

the pollen records available from Les Echets (Beaulieu & Reille 1992) and La Grande Pile (Beaulieu & Reille 1984). This reconstruction is consistent with a separate analysis of pollen assemblages from Lac du Bouchet, 140 km east-northeast of Grotte XVI (Pons et al. 1992). There is little reason to think that the directional changes indicated by this reconstruction do not apply to the Dordogne as well.

Estimated July temperatures varied widely between 40,000 and 10,000 radiocarbon years ago (Fig. 2). Each successive increase in the abundance of reindeer at Grotte XVI was associated with colder summer temperatures. Examined from the top down, increasingly warmer summer temperatures were associated with decreasing reindeer relative abundances. Although neither mechanical nor human behavioral variables seem capable of explaining the steadily increasing relative abundances of reindeer at Grotte XVI through time, climate change can.

Arrayed the Grotte XVI ungulate assemblages against the equivalent curves for winter temperature and winter precipitation showed no relationship between these climatic variables and reindeer abundance. There was, however, a positive relationship between summer precipitation and that abundance: reindeer abundance increased as summer precipitation increased.

We are unaware of any data suggesting that reindeer and caribou respond positively to increased summer precipitation per se, but it is possible that these variables interacted to produce the Grotte XVI pattern we have described. For instance, if increased precipitation were accompanied by increased cloud cover, insect harassment may have been reduced from levels predicted from tem-

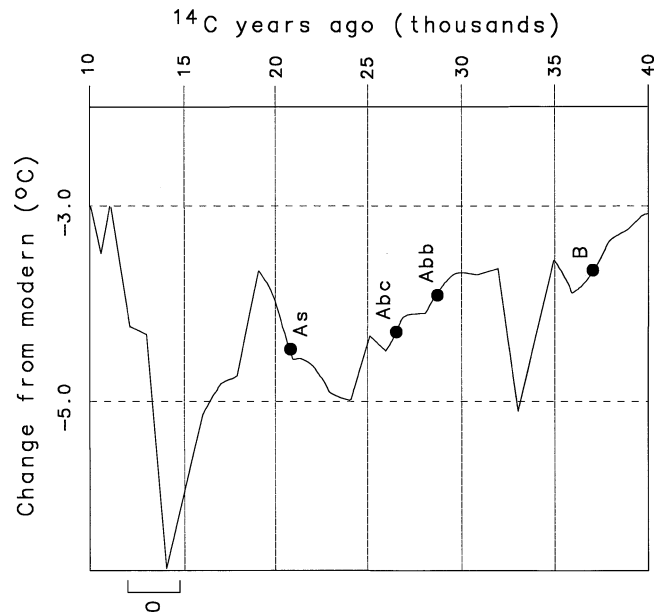


Figure 2. The relationship between July temperatures, expressed as departures from modern (Guiot 1990) and the Grotte XVI ungulate faunal assemblages for which radiocarbon ages are available (B, Abb, Aib, As, and 0 are strata). Stratum 0 is plotted as a range because the dates for this stratum are associated with a significant plateau in the relationship between radiocarbon and calendar ages (Stuiver et al. 1998) and because of the nature of the radiocarbon control in this portion of the paleoclimatic record (Woillard & Mook 1982; Beaulieu & Reille 1984; Guiot 1990).

perature alone because insect activity depends in part on light intensity (Downes et al. 1986; Nilssen 1997; Mörschel 1999). In addition, some experimental evidence suggests that reindeer and caribou show poor resistance to water deprivation (Rosenmann & Morrison 1967) and thus may fare better on a well-watered landscape.

It is also possible that changing summer temperature and precipitation acted together to alter vegetation quality and quantity. It has long been assumed that the changing nature of ungulate communities on the later Pleistocene landscape of southwestern France was driven by a complex combination of changing climate and vegetation (e.g., Delpech 1983, 1999, 2003).

Unfortunately, there are no detailed, pollen-based vegetation reconstructions for the Dordogne region relevant to the times of interest here, nor do we have a small mammal sequence from Grotte XVI that might help to address this issue.

On the other hand, reindeer became extinct in the Dordogne near the Pleistocene-Holocene boundary shortly after stratum 0 accumulated at Grotte XVI, an event associated with increased summer temperatures alone. There was no significant decline in precipitation at this time.

Thus, we suggest that the mechanism that drove changing reindeer relative abundances at Grotte XVI was summer temperature. We do not deny, however, that changing precipitation may have interacted with those temperatures to produce aspects of the pattern evident at this site.

That the relative abundances of reindeer increased as summer temperatures decreased does not necessarily mean that absolute abundances of these animals increased as well. Colder summers may have caused the abundances of other ungulates to decrease (red deer [*Cervus elaphus*], for instance), thus increasing the proportion of reindeer. Nonetheless, as summer temperatures decreased, reindeer became an increasingly important part of the local ungulate fauna. As summer temperatures increased, reindeer became a less important part of that fauna. At the end of the Pleistocene, as summer temperatures increased even more, reindeer were extirpated from this part of southern France (Delpech 2003), just as they were from the Pyrenees to the south (Straus 1995), the Alps to the east (Bridault et al. 2000), and elsewhere in southern Europe.

This was not the first climatically driven extirpation of reindeer from southern France. These animals were present here during the Riss glaciation, prior to about 130,000 years ago. They disappeared during the Eemian interglacial, roughly 130,000 to 116,000 years ago (Kukla 2000), returning as temperatures cooled and global ice volumes increased (Delpech 1989). The climate reconstructions provided by Guiot (1990) suggest that the Eemian interglacial was warmer and wetter than the times immediately before and after, when reindeer were present. Although we lack the chronological precision needed to provide a detailed correlation between the paleontological record for Eemian reindeer extinction and the climate reconstructions, this deeper history also suggests that it was temperature, not precipitation, that played the critical role in determining reindeer abundances.

Pleistocene Reindeer and Global Warming

It is well established that winters marked by deep snows and multiple ice-crusting events can extract a significant toll on reindeer and caribou populations (Klein 1968; Lee et al. 2000). The Grotte XVI sequence suggests that warm summers may have a similar negative effect on these populations, just as scientists working with modern reindeer and caribou populations have hypothesized.

We cannot determine whether the effects of increased summer temperatures on reindeer in the Grotte XVI area were direct (determined by reindeer thermoregulatory capabilities), indirect (determined by the impacts of temperature on insect activity, vegetation structure, and competitive interactions with other mammals), or caused by a combination of all these variables. We suspect that the direct impacts were significant, given that reindeer

retreated from their southern late Pleistocene habitats throughout Europe and North America and that this retreat coincided with the climatically driven extinction of a variety of large herbivores throughout the Northern Hemisphere (Grayson & Meltzer 2002).

If this is the case, the current southern boundary of reindeer and caribou distribution may in part be determined directly by summer temperatures, not only by interactions with predators and other ungulates (e.g., Bergerud 2000). If so, a temperature increase of 4 to 7.5°C in the far north may be expected to cause heavy mortality in reindeer and caribou populations, and this mortality may be accompanied by a significant retreat of the southern boundary of the distribution of these animals.

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