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Late-glacial to Holocene transition in northern Spain deduced from land-snail shelly accumulations

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ABSTRACT

Shells of the helicid *Cepaea nemoralis* were studied using taphonomic, isotopic and morphometric measurements to estimate late glacial–Holocene (~12.1–6.3 cal ka BP) environmental conditions in northern Spain. Higher taphonomic alteration among Holocene shells suggests lower sedimentation rates or higher shell-destruction rates than during glacial conditions. Shells preserved the aragonitic composition despite differing degree of skeleton damage. Shell δ^{13} C values were $-10.3 \pm 1.1\%$, $-8.2 \pm 2.3\%$, and $-7.3 \pm 1.6\%$ for modern, Holocene and late-glacial individuals, respectively. Higher δ^{13} C values during the late-glacial and some Holocene periods imply higher water stress of C₃ plants and/or higher limestone contribution than today. Intrashell δ^{13} C values were higher during juvenile stages suggests that during -12.1 - 10.9 cal ka BP conditions were drier and became wetter at -8.4 - 6.3 cal ka BP and today. Intrashell δ^{18} O profiles reveal that glacial individuals experienced more extreme seasonality than interglacial shells, despite possible larger hibernation periods. Shell size correlated positively with δ^{18} O values, suggesting that growth rates and ultimate adult size of *C. nemoralis* may respond to climate fluctuation in northern Spain.

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Introduction

Land snails have been exploited by humans as a food resource and/or for ornamentation purposes since early human civilizations, as evidenced by numerous shell middens globally (e.g., Bobrowsky, 1984; Evans, 1972; Lubell, 2004a,b), however, they have received comparatively less scientific attention than other zooarchaeological remains. Land snail shells are potential retrospective environmental and ecological archives (reviews in Goodfriend, 1992, 1999) which may complement and expand the information extracted from other (more commonly studied) organisms. Land snails interact with the habitat where they live and therefore, their taphonomic condition, geochemical composition and body size reflect the conditions of the environment in which they grew, died and were subsequently buried.

Land-snail taphonomy (= snail fossilization process) is used to estimate shell burial mechanisms and the quality and fidelity of the fossil record (e.g., Cameron et al., 2010; Carter, 1990; Rundell and Cowie, 2003; Schilthuizen et al., 2003; Yanes, 2012; Yanes et al., 2008a, 2011a). Strongly altered shells are often associated with low sedimentation rates or multiple burial–exhumation cycles (i.e., longer exposure of shells to biostratinomic processes). In contrast, weakly damaged samples reflect rapid sedimentation rates and therefore, a rapid burial process and reduced residence time in the taphonomically active zone (e.g., Brett and Baird, 1986). Hence, some important information regarding postmortem processes can be inferred from the study of the taphonomic condition of shells. Yet, these kinds of studies are uncommon for terrestrial gastropod shelly accumulations, especially those from archeological sites (cf. Carter, 1990; Evans, 1972; Gutiérrez-Zugasti, 2011).

The carbon (δ^{13} C) and oxygen (δ^{18} O) stable isotope values of fossil aragonitic shells are used to reconstruct the paleovegetation and past atmospheric conditions (e.g., Colonese et al., 2010a,b, 2011; Kehrwald et al., 2010; Yanes et al., 2011b, c, 2012). The shell δ^{13} C values represent values of consumed plants (Metref et al., 2003; Stott, 2002). Field studies indicate that the relationship between plant and shell is not straightforward because snails ingest limestone (Goodfriend, 1987; Goodfriend and Hood, 1983; Goodfriend et al., 1999; Yanes et al., 2008b; Yates et al., 2002). The contribution of limestone into the shell appears to be negligible among minute (length <10 mm) gastropods (Pigati et al., 2004, 2010), but can be substantial among medium-large size (length >10 mm) snails that inhabit carbonate-rich areas. There is an isotopic offset between shell and diet, varying between ~8 and 22‰ (e.g., McConnaughey and Gillikin, 2008; Metref et al., 2003; Stott, 2002; Yanes et al., 2008b, 2009). Such isotopic offset is the consequence of carbon isotope exchanges between respiratory CO₂ and HCO₃⁻ of the hemolymph from which the shell is precipitated (e.g., McConnaughey and

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Gillikin, 2008). The shell δ^{13} C values may be used to estimate the proportion of C₃/C₄ plants, variations in atmospheric CO₂ levels, or the degree of water stress of C₃ plants in C₃-dominated landscapes (e.g., Goodfriend and Ellis, 2000, 2002).

The shell δ^{18} O values are linked to rain δ^{18} O values and air temperatures (e.g., Balakrishnan et al., 2005b; Lécolle, 1985; Yanes et al., 2008b, 2009; Zanchetta et al., 2005). A snail evaporative steady-state flux-balance model by Balakrishnan and Yapp (2004) demonstrates that such relationship can be complicated because other important atmospheric variables, such as relative humidity and water vapor δ^{18} O values, should be considered when interpreting δ^{18} O values of snail shells. Thus far, the model by Balakrishnan and Yapp (2004) is the most sophisticated mathematical approach available that incorporates the highest number of environmental variables jointly to explain quantitatively shell δ^{18} O values of land snails. The shell δ^{18} O values are fractionated (~1-8‰) with respect to unmodified ambient water as a consequence of body-water loss through evaporation (Balakrishnan and Yapp, 2004). The isotopic offsets between shell and water are larger at drier/hotter sites, where evaporation processes are enhanced (e.g., Yanes et al., 2009). Altogether, the shell δ^{18} O values of land snails are complex to understand though useful to reconstruct ancient atmospheres at the soil-air interface during snail active periods (e.g., Zaarur et al., 2011).

Land-snail body size responds to multiple environmental and biological factors operating jointly, which are sometimes difficult to identify and quantify. Moisture is one of the best-documented environmental driving factor to which shell size responds (see review in Goodfriend, 1986). In arid environments, where water is a limiting factor, snails tend to be larger because they lose less water as a consequence of their lower surface to volume ratio (e.g., Nevo et al., 1983). Other studies have however observed opposite trends (e.g., Goodfriend, 1986), whereas some studies found no correlation between body size and rainfall (e.g., Hausdorf, 2006). Even though humidity may be an important factor, the link between body size and the environment seems to vary in scale and direction across taxa and localities.

In this study, *Cepaea nemoralis* (Gastropoda: Helicidae) shells from late-glacial period (~12.1 cal ka BP), earliest Holocene (~10.9 cal ka BP) and early mid-Holocene (~8.4–6.3 cal ka BP) archeological sites were studied using taphonomic descriptors, stable isotopes and morphometric measurements combined to infer the average (dominant) and seasonal (high-resolution) atmospheric conditions at the late glacial–Holocene transition in Cantabria and Asturias, northern Spain (43°N). This study represents one of the few published works using snail assemblages from the Iberian Peninsula as a paleoenvironmental proxy (cf. Yanes et al., 2011b, 2012). The isotopic results are compared to other published European and Mediterranean snail data and the shell δ^{18} O values are interpreted in the context of a snail evaporative steady-state flux-balance mixing model.

Methodology

Geographical and archeological context

Shells were recovered from five archeological sites in Cantabria and Asturias, northern Spain (Fig. 1), including four Holocene stratigraphic units: Arenillas (AR) shell midden level; Cubío Redondo spit 3 (CR3); Cubío Redondo spit 6 (CR6); El Mazo (EM) level 105; one earliest Holocene unit: La Fragua (LF) level 3; and one late-glacial unit: El Piélago II (EP) level 2. Shells were found directly associated with other archeological remains including vertebrates, charcoal, lithic artifacts and marine mollusks. Land snails were almost certainly collected and probably consumed by ancient human groups (Gutiérrez-Zugasti, 2011).

Radiocarbon dating of charcoal and bones indicates that shell remains range from ~12.1 to 6.3 cal ka BP, embracing the late glacial– Holocene transition (Bohígas and Muñoz, 2002; García-Guinea, 1985; González-Morales, 2000; Gutiérrez-Zugasti, 2011; Ruiz-Cobo and Smith, 2001).

Environmental setting

The study area is characterized by mild winters and cool summers, with an average temperature of ~14°C, ranging from 9.5°C in January to 19.9°C in August (www.aemet.es), and a total annual precipitation above 1200 mm (Table 1; Fig. 2). Precipitation mostly occurs in winter (Table 1; Fig. 2A), associated with mid-latitude Atlantic Ocean storms. The weighted mean δ^{18} O values of the rain vary from -3.4% (SMOW) in May to -6.9% (SMOW) in February (Table 1; Fig. 2B). The annual weighted mean δ^{18} O value of the rain is -6% (SMOW) (www.iaea. org). Average relative humidity (RH) ranges from ~73% in March to ~78% in August (Table 2; Fig. 2B). Average annual maximum RH is ~88% at night and dawn, but can reach up to 100% at certain seasons due to the short distance from the coast. Weighted mean δ^{18} O values of the rain correlate positively with temperature (Fig. 2C) and negatively with precipitation (Fig. 2D).

Samples

The archeological sites were excavated between 1967 and 2010 (Bohígas and Muñoz, 2002; García-Guinea, 1985; González-Morales, 2000; Ruiz-Cobo and Smith, 2001). Shells were obtained from collections archived in the University of Cantabria and the Museum of Prehistory and Archaeology of Cantabria. A total of 172 shells of *C. nemoralis* (Linnaeus, 1758) were available. In addition, living specimens (n = 12) were collected in Cantabria during the winter of 2010 to establish a modern analog previously unavailable for the region.

C. nemoralis is an air-breathing pulmonate gastropod natural from Western Europe but introduced in other continents. *Cepaea* is usually abundant at carbonate-rich and humid localities. In the Iberian Peninsula *Cepaea* is only abundant in the northern (wetter) region (e.g., Gutiérrez-Zugasti, 2011). It typically takes $\sim 1 - 2$ yr for newly hatched snails to reach adulthood, and the average lifespan is ~ 2.3 yr. In occasional cases *Cepaea* can live up to ~ 5 yr more after the lip is segregated. Growth rates seem to vary depending on the ecological context like population density (e.g., Wolda, 1970) and environmental conditions such as temperature and calcium content in soil and decayed vegetation (e.g., Bengtson et al., 1979).

Shell taphonomy and morphometrics

Shells were evaluated for taphonomic condition and diagenetic alterations to assess their quality. X-ray diffraction analyses of two archeological shells (one ~12.1 ka shell from El Piélago and another ~6.3 ka shell from Arenillas) were performed at the Instituto Andaluz de Ciencias de la Tierra (IACT), CSIC-Universidad de Granada. Several taphonomic descriptors, including breakage, corrasion (=biochemical dissolution and/or mechanical abrasion; e.g., Brett and Baird, 1986), carbonate coating and color loss, were also studied under a binocular microscope to evaluate macroscopic damage of shells. The taphonomic study was carried out following Yanes et al. (2008a, 2011a) methodology for twelve modern and 172 archeological shells. The taphonomic data were recorded as binomial variables, where (=1)was assigned for poorly preserved shells and (=0) was assigned for well-preserved shells. The total taphonomic grade (TTG) was scored for each shell as the sum of all taphonomic features (for further details see Yanes and Tyler, 2009). The TTG in this study ranged from 0 (= well preserved) to 4 (= poorly preserved).

Six measurements, including length, width, height of the two last spires, height of the last spire, aperture height and aperture width, were obtained from twelve modern and 164 ancient *Cepaea* individuals following Kerney and Cameron (1979) and Huntley et al.



Figure 1. Geographical setting of the study area and the archeological sites included in this study: (1) El Mazo, (2) El Piélago, (3) Cubío Redondo, (4) La Fragua, (5) Arenillas, (6) Voto (where modern specimens were collected).

(2008) methodology. Measurements were obtained using an electronic caliper to the nearest 0.02 mm.

Stable isotope analyses

Laboratory analyses were performed in the IACT. Shells were cleaned in deionized water and pulverized with an agate mortar and pestle. Shell organics may affect the isotopic composition of the carbonate. However, laboratory tests showed that non-treated and 5% H₂O₂-treated carbonate aliquots from the same shell did not differ significantly (<0.2‰; n = 4) in carbon or oxygen isotopic values. Consequently, shell pretreatments were unnecessary.

Complete shells were used as a proxy for average environmental conditions over the life of an organism. In addition, three specimens from three age intervals (modern, middle Holocene and late glacial) were selected for intra-shell isotopic analysis along shell growth direction. Between 40 and 47 subsequent aliquots were sampled from the same shell using an electronic Dremel drill. The intrashell isotopic profiles were used to evaluate the high-resolution environmental information tracked by a snail through its lifespan.

Shell carbonate (~5 mg) was placed in a 12 ml exetainerTM vial, flushed with helium, and converted to CO₂ by adding ~0.1 ml of 100% phosphoric acid (H₃PO₄) at 50°C during 24 h. The resulting CO₂ was analyzed isotopically using the Gas-Bench II and a Finnigan Delta PLUS^{XP} isotope ratio mass spectrometer (IRMS). Results are reported in δ notation relative to PDB for carbonate and SMOW for water. The δ values are defined as:

$$\delta^{13}C \text{ or } \delta^{18}O = \left[\left(R_{sample}/R_{standard} \right) - 1 \right] \times 1000(\%)$$

Table 1

Current atmospheri	c conditions in	n Santander,	Cantabria	(northern	Spain).
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Month	Rain δ ¹ ‰(SMC	⁸ 0)W) ^a	Temperature (°C) ^b	Precipitation (mm) ^b	Relative humidity (%) ^b
Jan	-5.8	± 0.9	9.5	123	74
Feb	-6.9	± 2.5	9.9	104	74
Mar	-6.5	± 1.7	10.7	105	73
Apr	-5.6	± 1.2	12.0	125	73
May	-3.4	± 0.7	14.6	89	75
Jun	-3.5	± 1.0	17.1	62	76
Jul	-4.2	± 1.0	19.4	52	78
Aug	-4.5	± 1.5	19.9	72	78
Sep	-4.8	± 1.4	18.3	85	78
Oct	-6.3	± 1.1	15.4	135	77
Nov	-6.5	± 0.7	12.2	146	76
Dec	-6.6	± 1.3	10.7	117	73

^a Data taken from the International Atomic Energy Agency (IAEA): www.iaea.org.

^b Data taken from the Spanish Agencia Estatal de Meteorología (AEMET): www.aemet.es.

where R=¹³C/¹²C or R=¹⁸O/¹⁶O. δ^{13} C and δ^{-18} O values were calibrated against three in-house standards. The precision of the analyses was ~0.1‰ (1\sigma standard deviation) for both isotopes based on the repeated measurement of standards (n=30). Replicate analyses of the same shell had a precision of ~0.2‰ (1\sigma standard deviation) for δ^{18} O and δ^{13} C.

Statistical analyses

Statistical analyses were performed using PAST 1.38b (Hammer et al., 2001), considering the significant level at $\alpha = 0.05$. Simple regression analyses were performed to test the potential relationship between one independent and one dependent variable, and to identify the slope and intercept of the relationship. The Mann–Whitney U test was used to test if samples differed in median values. Morphometric data was log-transformed and subjected to a principal components analysis (PCA) on a variance–covariance matrix. PC1 scores were grouped a posteriori into age categories. All six morphometric measures were strongly correlated with PC1. PC1 is hence considered an appropriate proxy of body size because it reflects six measurements jointly (Huntley et al., 2008). In addition, geometric mean of log-transformed shell length was also computed as a second proxy of body size (Huntley et al., 2008; Jablonski, 1997).

Results

Taphonomic condition and body size

Ancient shells were affected by fragmentation, corrasion, carbonate coating and color loss whereas modern shells were basically undamaged (Table 2; Appendix S1). ~8.4-6.3 ka shells recovered from Arenillas, Cubio Redondo 3, Cubio Redondo 6 and El Mazo sites exhibited significantly higher total taphonomic grade (TTG), i.e., higher proportion of shells damaged, than ~12.1-10.9 ka shells from La Fragua and El Piélago II (Fig. 3A). This may be attributable to a longer residence time of Holocene shells in the taphonomically active zone, which in turn suggests lower sedimentation rates and/or higher shell-destruction rates during the interglacial interval (e.g., Brett and Baird, 1986; Yanes, 2012; Yanes et al., 2008a, 2011a). In terms of shell breakage alone, Gutiérrez-Zugasti (2011) observed higher degree of fragmentation in the earliest Holocene shell midden. This was interpreted as a more intense used of the cave by ancient human groups. Thus, taphonomic patterns observed in shells may represent both environmental and anthropogenic processes. Despite the macroscopic alterations of shells (Table 2; Figs. 3A-B), X-ray diffraction analyses revealed that the original mineralogical (aragonitic) composition of shells collected from El Piélago II and Arenillas was unmodified. Accordingly, the shell material is suitable for further geochemical analyses because substantial diagenetic processes were unlikely.

Various bidimensional measurements of shells were highly correlated with each other (Table 3; Appendix S1; Figs. 3C–D). Modern



Figure 2. Climatic context of Santander, Cantabria (northern Spain). (A) Temperature and precipitation between 1971 and 2000 (data taken from www.aemet.es). (B) Mean relative humidity (RH) between 1971 and 2000 (data taken from www.aemet.es) and weighted mean monthly rain δ^{18} O values between 2000 and 2006 (data taken from www.iaea.org). (C) Relationship between weighted mean rain δ^{18} O and air temperature. (D) Relationship between weighted mean rain δ^{18} O and precipitation amount.

specimens exhibited a shell length and width of 18.53 ± 1.04 and 25.41 ± 0.89 mm, respectively. Early- to mid-Holocene shells were 18.03 ± 2.26 mm in length and 24.04 ± 3.72 mm in width. Late-glacial to earliest-Holocene individuals exhibited a length of 20.63 ± 1.04 mm and a width of 27.11 ± 1.69 mm (Appendix S1). Late-glacial and earliest-Holocene shells were significantly larger than early- to mid-Holocene and modern specimens (Table 3; Figs. 3C–D). PC1 and log-transformed geometric mean of shell length exhibited equivalent results: i.e., late-glacial to earliest-Holocene shells showed the largest body size values and declined to values of early- to mid-Holocene and modern individuals (Table 3; Figs. 4C–D).

Table 2
Taphonomic condition of Cepaea nemoralis shells recovered from archeological sites located
in northern Spain.

Sample ID	Age (cal)	n	# broken shells	# shells with Corrasion	# shells with carbonate coating	# shells with color loss	Average TTG	
MO	Modern		12	0	4	0	0	$0.3 \pm 0.5 $
AR	6380	± 70	30	3	30	0	28	2.0 ± 0.4
CR3	6580	± 60	22	10	22	12	22	3.0 ± 0.8
CR6	7520	± 50	30	15	30	16	30	3.0 ± 0.6
EM	8440	± 30	30	13	30	0	6	1.6 ± 0.7
LF	10,930	± 200	30	1	30	0	30	2.0 ± 0.2
EP	12,100	± 280	30	1	30	0	30	2.0 ± 0.2

n = number of shells; TTG = total taphonomic grade.

Carbon isotopic composition of the shell

Twelve modern shells displayed δ^{13} C values from -13.1% to -8.5%(Table 4; Appendix S2; Fig. 4A). The δ^{13} C values obtained from aliquots sampled subsequently along ontogeny from a single modern individual varied from -12.0% to -7.2% (n = 43), showing thus a guite large Δ^{13} C value of ~5‰ (Table 5; Appendix S3; Fig. 5A). The intrashell δ^{13} C values were higher at early ontogenetic stages and declined throughout organism life history, reaching the minimum value in the lip (=oldest growth episode). The δ^{13} C values of ~8.4–6.3 ka shells (n = 36) ranged from -13.4% to -5.0%(Table 4; Appendix S2; Fig. 4A). The intrashell $\delta^{13}\text{C}$ values of a ~6.3 ka individual (n=40) from Arenillas site varied between -10.5%to -8.5%, with a Δ^{13} C value of 2.1% (Table 5; Appendix S3; Fig. 5B). Sample aliquots from early ontogenetic stages were higher in δ^{13} C values than those collected at older phases (Fig. 5B). The $\delta^{13}\text{C}$ values of ~12.1–10.9 ka shells (n=21) ranged from -11.7% to -4.9%(Table 4; Appendix S2; Fig. 4A). Intrashell δ^{13} C values of a ~12.1 ka shell from El Piélago site (n=47) varied between -8.2% and -5.6% $(\Delta^{13}C = 2.6\%)$ (Table 5; Appendix S3; Fig. 5C). The $\delta^{13}C$ values from the early life were higher than those deposited during the older ontogenetic stages. Whole-shell δ^{13} C values did not correlate with snail body size (Figs. 6A–B).

Oxygen isotopic composition of the shell

The shell δ^{18} O values of modern specimens varied from -2.9% to -0.3% (Table 4; Appendix S2; Fig. 4B). The intrashell δ^{18} O values of a modern shell varied from -1.3% to +0.1% (Δ^{18} O = 1.3\%) (Table 5; Appendix S3; Fig. 5D). The δ^{18} O values of ~8.4–6.3 ka shells (n = 36)



Figure 3. Shell taphonomy and morphometrics of late-glacial to Holocene *Cepaea nemoralis* shells from northern Spain. (A) Frequency distribution of the total taphonomic grade (TTG). (B) Proportion of shells damaged by different taphonomic indexes used in this study. (C) Relationship between maximum shell length and width (mm). (D) Relationship between aperture height and width (mm).

showed a range of values from -3.6% to +0.1% (Table 5; Appendix S2; Fig. 4B). Intrashell δ^{18} O values of a ~6.3 ka individual varied between -1.1% and +0.9%, with a Δ^{18} O value of 1.9% (Table 5; Appendix S3; Fig. 5E). The δ^{18} O values of ~12.1–10.9 ka shells (n=21) ranged from -1.9% to +1.0% (Table 4; Appendix S2; Fig. 4B). Intrashell δ^{18} O values of ~12.1 ka specimen varied between -2.2% and +1.3%, with a Δ^{18} O value of 3.5% (Table 5; Appendix S3; Fig. 5F). The intrashell values of a late-glacial individual exhibited considerably more marked seasonal cycles than a middle-Holocene and a live-collected specimen (Figs. 5D–F). Entire-shell δ^{18} O values correlated significantly with shell size (Figs. 6C–D).

Discussion

Modern analog: living C. nemoralis

Modern shell δ^{13} C values ($-10.3 \pm 1.1\%$) indicate *Cepaea* consumed exclusively C₃ plants, considering that the shell is enriched in ¹³C by ~8–22‰ with respect to diet (e.g., McConnaughey and Gillikin, 2008; Metref et al., 2003; Stott, 2002; Yanes et al., 2008b, 2009). This is consistent with the dominance of C₃ plants in natural landscapes from northern Spain. *Cepaea* is a generalized herbivorous and feeds mostly on decayed plant material, but at dry conditions,

Table 3	
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Sample ID	mple ID Age (cal yr BP) n A			В		С	C D			Е		F		PC 1		Geometric			
																		mean	
																		log(le	ngth)
MO	Modern		12	18.53	± 1.04	25.41	± 0.89	15.97	± 0.64	12.77	± 0.41	10.22	± 0.57	12.32	± 0.49	0.01	± 0.03	1.27	± 0.02
AR	6380	± 70	30	17.65	± 1.66	23.88	± 2.85	15.35	± 1.34	12.25	± 0.92	9.76	± 0.70	10.81	± 1.18	-0.06	± 0.10	1.24	± 0.04
CR3	6580	± 60	22	18.87	± 2.07	26.01	± 2.94	15.99	± 1.56	13.14	± 1.14	9.98	± 0.89	11.51	± 1.43	0.00	± 0.11	1.27	± 0.05
CR6	7520	± 50	30	17.91	± 2.43	23.69	± 4.20	15.48	± 1.95	12.81	± 1.55	10.02	± 1.36	11.02	± 1.77	-0.05	± 0.15	1.25	± 0.06
EM	8440	± 30	22	19.08	± 1.44	24.44	± 3.16	16.53	± 1.19	12.99	± 0.74	10.39	± 0.66	11.52	± 1.26	0.00	± 0.08	1.28	± 0.04
LF	10,930	± 200	30	20.39	± 1.05	26.73	± 1.38	17.30	± 0.92	13.40	± 0.70	10.77	± 0.59	12.36	± 0.67	0.07	± 0.05	1.31	± 0.02
EP	12,100	± 280	30	20.87	± 0.98	27.49	± 1.90	17.41	± 0.76	13.66	± 0.66	10.77	± 0.60	12.04	± 0.85	0.08	± 0.05	1.32	± 0.02

n = number of shells; A = maximum shell length; B = maximum shell width; C = height of two last spires; D = height of last spire; E = aperture height; F = aperture width; PC1 = principal component 1.



Figure 4. Isotopic composition and body size of modern and archeological *Cepaea nemoralis* snails from northern Spain. (A) Carbon stable isotope values of the shell. (B) Oxygen stable isotope values of the shell. (C) Mean PC1 of log-transformed morphometric data. (D) Geometric mean of log-transformed shell length. Symbols represent mean values whereas whiskers represent the standard deviation of the data. Horizontal dashed lines represent mean values for live-collected snails. YD = Younger Dryas stadial (~12.1 cal ka BP in this study).

Cepaea tends to ingest higher proportion of living plants to compensate water loss through evaporation (Mensink and Henry, 2011). *Cepaea* may also consume variable amounts of limestone as a source

Table 4

Oxygen and carbon stable isotope values of entire *Cepaea nemoralis* shells from archeological sites located in northern Spain.

Sample ID	Age (cal y	n	δ ¹⁸ 0‰(PDB)	δ^{13} C‰(PDB)		
MO	Modern		12	- 1.1	± 0.7	-10.3	± 1.1
AR	6380	± 70	10	-1.4	± 0.9	-9.6	± 2.2
CR3	6580	± 60	8	-0.8	± 1.0	-6.4	± 1.5
CR6	7520	± 50	7	-0.8	± 0.7	-6.4	± 0.9
EM	8440	± 30	11	-0.6	± 0.4	-9.5	± 2.0
LF	10,930	± 200	10	0.0	± 1.0	-8.5	± 1.2
EP	12,100	± 280	11	-0.2	± 0.4	-6.1	± 0.7

n = number of shells.

of calcium to build their shells. This unknown proportion of limestone intake complicates the use of shell δ^{13} C values as a quantitative paleovegetation proxy (e.g., Goodfriend and Hood, 1983; Yanes et al., 2008b). Considerably higher δ^{13} C values during the younger ontogenetic stages of a living individual (Fig. 5A) may be explained by more intense limestone ingestion during the juvenile period to enhance growth rates. This agrees with higher radiocarbon age anomalies during the early life of the bulimulid *Rabdotus alternatus* (Say, 1830) from Texas (Fig. 2: Goodfriend et al., 1999), interpreted as higher calcium intake while snails are juveniles. Alternatively, higher intrashell δ^{13} C values may reflect larger consumption of 13 C-enriched C_3 plants as a consequence of stronger water stressed conditions (e.g., Dawson et al., 2002; Farquhar et al., 1989). This is consistent with the idea that snail breeding tend to occur during the warmest seasons (e.g., Cowie, 1984), and therefore, newly hatched snails record higher δ^{13} C values in the juvenile parts of their shells. Although higher calcium intake and/or summer breeding may explain the observed patterns here, such hypotheses remain to be tested empirically for the study area.

Active periods of snails are controlled by climate. Snails are mostly active during an optimum range of temperature and humidity, where feeding and consequently, calcification is enhanced. In the study area, temperature varies between ~9.5 and 19.9°C, rain falls throughout the year and average RH is always above 73% (Fig. 2). Under such environmental setting, modern *Cepaea* may be active almost year round, but during summer and winter months shell growth may be minimized (e.g., Iglesias et al., 1996). If most shell growth occurs primarily during the fall (September-November) and spring (March-May), as observed for the helicid Cornu aspersum (Müller, 1774) from northwestern Spain (Iglesias et al., 1996), modern Cepaea deposits shell at air temperatures of ~14°C and δ^{18} O values of rain near -6% (SMOW). Adopting this environmental scenario and using measured shell δ^{18} O values and the flux-balance model by Balakrishnan and Yapp (2004), RH conditions during calcification can be predicted. Model calculations suggest that modern snails precipitated shell when RH was ~91%, on average (Fig. 7A). This predicted value is consistent with maximum RH values observed at night or during rain events in the study area at the soil surface. Hence, the model predicts plausibly well RH conditions during calcification and may be used to propose paleoatmospheric conditions in northern Spain.

In a recent study on clumped isotopes, Zaarur et al. (2011) observed that snails deposit carbonate at body temperatures higher than those in the environment. The temperature offset between clumped-isotope temperatures and air temperatures vary considerably across localities and species, but tend to be larger at colder sites (Zaarur et al., 2011). At higher latitudes, snails may deposit shell during the daytime under the sunlight, which may increase the temperature of the snail body with respect to environmental temperature. In this study, we assumed that ambient temperatures during snail activity represent probably well the temperature of calcification. However, in future paleoclimatic studies may be useful to combine clumped isotopes and δ^{18} O measurements of shells.

Table 5
Summary of the intrashell carbon and oxygen stable isotope values of three Cepaea nemoralis individuals from northern Spain

Specimen ID	Age (cal yr BP)	n	$Mean \; \delta^{13}C$		$Max \; \delta^{13}C$	$Min \ \delta^{13}C$	$\Delta^{13}C$	Mean δ^1	$Mean \ \delta^{18}O$		$Min \; \delta^{18}O$	$\Delta^{18}O$
MO-intra-1 AR-intra-1 EP-intra-1	$\begin{array}{c} Modern \\ 6380 \pm 40 \\ 12100 \pm 280 \end{array}$	43 40 47	-9.6 -9.4 -7.2	$_{\pm 0.6}^{\pm 0.8}$	- 7.2 - 8.5 - 5.6	-12.0 -10.5 -8.2	4.8 2.1 2.6	$-0.7 \\ -0.3 \\ +0.2$	${\scriptstyle\pm0.3\ \pm0.4\ \pm0.7}$	+0.1 +0.9 +1.3	- 1.3 - 1.1 - 2.2	1.3 1.9 3.5

n = number of samples analyzed within a single shell.

Modern shells are enriched in ¹⁸O by ~4.9‰, on average, with respect to unmodified rain water. Such isotopic offset between rain and shell is explained by water loss from the hemolymph through evaporation (Balakrishnan and Yapp, 2004; Goodfriend et al., 1989; Yapp, 1979; Zaarur et al., 2011) and is consistent with published field studies on living specimens (e.g., Balakrishnan et al., 2005a,b; Baldini et al., 2007; Lécolle, 1985; Yanes et al., 2008b, 2009; Zanchetta et al., 2005).

The small range of intrashell δ^{18} O values (shell Δ^{18} O = 1.3‰) of a modern shell along ontogeny (Fig. 5D) indicates smoothed seasonal cycles. The range of δ^{18} O values within a single shell is smaller than the seasonal range of rainfall δ^{18} O values (rain Δ^{18} O = 3.6‰). This is explained because snails record rain and water vapor δ^{18} O values from the season and the part of the day when they are active. Although snails restrict their growth to times when climatic factors are favorable (i.e., warmer/wetter seasons), some seasonal environmental information may be inferred from intrashell isotopic analyses. Higher δ^{18} O values of the shell are likely associated with drier conditions whereas lower values are often linked to a wetter context (e.g., Lécolle, 1985; Yanes et al., 2009; Zanchetta et al., 2005). Accordingly, the studied individual likely grew throughout two subsequent spring/summer seasons and one fall/winter season (Fig. 5D), reflecting a biannual lifespan, in agreement with the biological cycle known for Cepaea. Hence, valid seasonal environmental information may be deduced from intrashell δ^{18} O profiles of land snails.

Paleoclimatic inferences: ancient C. nemoralis

Paleovegetation

The δ^{13} C values of shells fluctuated through time. Late-glacial and earliest Holocene shells (~12.1 - 10.9 cal ka BP), as well as some middle Holocene shells (~6.6 – 7.5 cal ka BP), exhibited higher δ^{13} C values than modern individuals (Fig. 4A). This may be caused by (1) water stress during drier conditions in the past than today; (2) higher ingestion of limestone in the past than at present; and/or (3) lower atmospheric CO₂ concentration in the past than now. During the last glacial-interglacial transition in the northern Hemisphere climatic conditions shifted from drier/cooler to wetter/warmer (e.g., Beaulieu et al., 1994). Such climatic shift may have caused water stress which affected the isotopic signature of the C₃ vegetation. Under water stress, C₃ plants become enriched in ¹³C because stomatal pores are longer closed to prevent water loss (e.g., Dawson et al., 2002; Farquhar et al., 1989). Such ¹³C-enriched tissues of plants may be tracked in the shell. Instead, snails may have ingested more intensively limestone in the past than at present, which would result in higher shell δ^{13} C values (e.g., Yanes et al., 2008b). Finally, atmospheric CO₂ concentrations fluctuated significantly during the last deglaciation (e.g., Cole and Monger, 1994; Fischer et al., 1999; Huybers and Langmuir, 2009). Lower CO₂ levels during the deglaciation may have caused higher plant δ^{13} C values, which in turn, were recorded in the shells. Some or all these hypotheses may explain the higher δ^{13} C values observed in late glacial and some Holocene shells (Fig. 4A). The shell δ^{13} C values from this study combined with other European and Mediterranean snail published records (Bonadonna and Leone, 1995; Colonese et al., 2007, 2010a,b, 2011; Yanes et al., 2011b, 2012; Yates et al., 2002; Zanchetta et al., 1999) indicate no evident late-glacial to Holocene shifts in the δ^{13} C values of the vegetation (Fig. 8A). However, snail proxies from different localities also differ in species. Different species potentially exhibit diverse ecological habits, which could have, in part, masked variations in plant δ^{13} C values through time.

Intrashell δ^{13} C values of a late glacial (Fig. 5C) and a mid-Holocene (Fig. 5B) shell were noticeably subdued compared to the modern specimen (Fig. 5A). This may reflect a wider seasonal range of plant δ^{13} C values in modern ecosystems, perhaps explained by recent anthropogenic influence (e.g., eutrophication). Interestingly, δ^{13} C values were always higher during the juvenile stage whereas δ^{13} C values declined progressively reaching the minimum values at the oldest growth episode (Figs. 5A–C). This may reflect higher limestone consumption during the early life of the snail to acquire the amount of calcium necessary for rapid shell growth. This hypothesis may be tested in future studies by subsequent radiocarbon dating along shell growth direction (Goodfriend et al., 1999).

Ancient atmospheres

The δ^{18} O values of ~12.1–10.9 ka shells were, on average, ~1% higher than ~8.4-6.3 ka shells and modern individuals, pointing to different atmospheric conditions between glacial and interglacial times. The late-glacial period here, dated at ~12.1 cal ka BP, matches with the Younger Dryas event (YD) of the northern Hemisphere (~13.0–11.5 cal ka BP; Rasmussen et al., 2011). Three late glacial scenarios are proposed in the context of the model by Balakrishnan and Yapp (2004). (1) If rain δ^{18} O values and temperatures during the YD were comparable to current values (Fig. 7B), then glacial shells with a δ^{18} O value of ~0.2‰ precipitated when RH was ~88%. Subsequently, RH increased to present values of ~91%. (2) Sea-surface temperature (SST) estimates from alkenone proxies off the Iberian Peninsula (37°N) suggest that temperatures around the YD were ~4°C cooler than today (Bard, 2002). Moreover, rain δ^{18} O values decrease ~0.58‰ every ~1°C of temperature decrease (e.g., Rozanski et al., 1993). If these conditions dominated in the study area around the YD stadial, then snails possibly deposited shell at temperatures of ~10°C, rain δ^{18} O values of -8.3% (SMOW), and RH values of ~85%. From there, temperature, rain δ^{18} O values, and RH increased to present values of 14° C, -6% (SMOW) and ~91\%, respectively (Fig. 7C). (3) Finally, ocean waters were ~1‰ higher during the YD than the Holocene globally, as suggested by benthic foraminifera data (Zachos et al., 2001). If rain δ^{18} O values experienced a similar modification, then, shells precipitated when rain δ^{18} O values were ~-7.3% (SMOW), temperature was ~10°C and RH was ~87%. Thereafter, conditions fluctuated to present values (Fig. 7D). The three proposed paleoscenarios suggest that calcification around the YD occurred at appreciably drier conditions than today. This finding agrees with paleoclimatic proxies from the North Hemisphere which documented drier conditions, cooler temperatures and lower δ^{18} O values of meteoric waters during the late glacial period, including the YD (e.g., Dansgaard et al., 1989, 1993; G.R.I.P. Members, 1993; Grootes et al., 1993; Johnsen et al., 1997; Rasmussen et al., 2007, 2011; Verbruggen et al., 2010). Other regional proxies, such as mountain lake sediment cores from Cantabria (Moreno et al., 2011) and marine deep-sea cores from the Iberian margin (e.g., Eynaud et al., 2009) and the Mediterranean (e.g., Dormoy et al., 2009), have confirmed that the YD stadial was a cold/dry episode.

The late glacial ¹⁸O-enriched shells here are coherent with the observed higher δ^{18} O values of late glacial land-snail shells from other



Figure 5. Intrashell isotopic profiles of *Cepaea nemoralis* shells from northern Spain. (A) Carbon isotope values of a live-collected specimen. (B) Carbon isotope values of a ~6.3 ka individual. (C) Carbon isotope values of a ~12.1 ka shell. (D) Oxygen isotope values of a isotope values of a ~12.1 ka shell. (F) Oxygen isotope values of a ~12.1 ka shell. (D) Carbon isotope values of a ~12.1 ka shell. (D) Oxygen isotope values of a ~12.1 ka shell. (D) Oxygen isotope values of a ~12.1 ka shell. (E) Oxygen isotope values of a ~12.1 ka shell. (E) Oxygen isotope values of a ~12.1 ka shell. (D) Oxygen isotope values of a ~12.1 ka shell. (E) Oxygen isotope values of a ~12.1 ka shel



Figure 6. Relationships between the average isotopic composition of the shell and snail body size. (A) Relationship between carbon isotope values and PC1. (B) Relationship between carbon isotope values and geometric mean. (C) Relationship between oxygen isotope values and PC1. (D) Relationship between oxygen isotope values and geometric mean.

European and Mediterranean paleontological and archeological sites (Bonadonna and Leone, 1995; Colonese et al., 2007, 2010a,b, 2011; Yanes et al., 2011b, 2012; Yates et al., 2002; Zanchetta et al., 1999). Land-snail shells from the same age interval exhibit a substantial isotopic scatter of several per mil (Figs. 8A-B), which reflects climatic variations at microhabitat scale (=daily and seasonal variations within the microhabitat where snails live). This stresses the significance of analyzing numerous specimens to calculate a meaningful average value representative of the studied period or locale (e.g., Balakrishnan et al., 2005b; Yanes et al., 2011c). European and Mediterranean snail published records indicate that shells exhibit higher δ^{18} O values during the late glacial period associated with overall drier conditions (e.g., reduced rainfalls), whereas early- to middle-Holocene shells generally record lower δ^{18} O values, linked to a wetter scenario associated with enhanced precipitations (Fig. 8B). Such overall decline in shell δ^{18} O values from the late-glacial period to interglacial times should probably reflect the combined effects of (1) a progressive increase in RH, possibly associated with enhanced rainfall, (2) a continued increase in air temperatures, and (3) a gradual increase in rain δ^{18} O values possibly linked to the increase in temperature. Hence, European and Mediterranean land-snail entire shells appear to record convincingly well the local, regional and even global atmospheric conditions in their isotope codes.

Intrashell δ^{18} O profiles of three specimens corroborate that *Cepaea* exhibits a short lifespan (annual to biannual) based on the few identified cycles (Figs. 5D–F). Higher δ^{18} O values often represent drier seasons, linked to somewhat lower RH values and/or higher rain δ^{18} O values, whereas lower values may represent wetter months (e.g., Balakrishnan et al., 2005a; Yanes et al., 2009; Yapp, 1979; Zanchetta et al., 2005). The late-glacial snail experienced a more prominent climatic seasonality than interglacial specimens (Figs. 5D–F). Likely, glacial snails experienced

longer hibernation periods due to cooler temperatures. Despite larger dormant phases, intrashell δ^{18} O values suggest that seasonality was more marked during the YD than at the mid-Holocene and today (Fig. 5F). This is consistent with the contention that the YD stadial was characterized by a change in the seasonality of precipitation compared to the Holocene. The summer precipitation tends to be greater during the cooling phases than in interglacial times (e.g., Bordon et al., 2009). Ferguson et al. (2011) also documented an increase in the magnitude of seasonality in the SST from southern Spain during the late-glacial period as a result of a greater winter cooling. All in all, although calcification of snails is restricted to favorable (warmer and wetter) seasons, the present study illustrates that the approximate snail lifespan and the magnitude of seasonality may be identified by studying intrashell oxygen isotope profiles along ontogeny.

Relationship between shell size and climate

Whereas *Cepaea* size proxies (PC1 and geometric mean) did not show a relationship with δ^{13} C values (Figs. 6A–B), they strongly correlated with δ^{18} O values (Figs. 6C–D). Shells with larger sizes tracked higher δ^{18} O values while smaller individuals yielded lower δ^{18} O values. This relationship suggests that *Cepaea* size was in part influenced by local and regional climate. Ecological (predation pressure, density of individuals, interspecific competition, etc.) and environmental (humidity, temperature, calcium amount, contamination, etc.) factors affect snail size in different manners (e.g., Huntley et al., 2008; Olson and Hearty, 2010; Pfenninger, 2004). One of the best studied environmental variables recognized as a snail-size driver is humidity. Unfortunately, the published literature shows controversial results on the magnitude and direction to which humidity influences snail dimension. In localities where water is a limiting factor, snails reach larger sizes to prevent



Figure 7. Calculated shell δ^{18} O values as a function of relative humidity (RH) using the evaporative steady-state flux-balance model by Balakrishnan and Yapp (2004). (A) Modern shells. Gray area represents the measured range of shell δ^{18} O values of live-collected *Cepaea nemoralis* from Cantabria whereas black dot represents the average value. (B) Paleoclimatic scenario since the Younger Dryas stadial (YD) to modern conditions assuming invariant temperature and rain δ^{18} O values. The arrow shows a hypothetical trajectory of decreasing shell δ^{18} O values as a response of increasing RH. (C) Paleoclimatic scenario since the YD to modern conditions assuming that during the YD temperatures were ~4°C lower than today and rain δ^{18} O values were ~2.3% lower than at present (see text). The arrow illustrates a theoretical trajectory of decreasing shell δ^{18} O values as a consequence of the combined effect of increasing RH, temperature and rain δ^{18} O values. (D) Paleoclimatic scenario since the YD period to the present, assuming that the YD was portrayed by temperatures 4°C lower than today and rain δ^{18} O values 1.3‰ lower than at present (see text). The arrow displays a possible trajectory of decreasing shell δ^{18} O values in response to increasing RH, temperature and rain δ^{18} O values. (B) Paleoclimatic scenario since the YD period to the present, assuming that the YD was portrayed by temperatures 4°C lower than today and rain δ^{18} O values 1.3‰ lower than at present (see text). The arrow displays a possible trajectory of decreasing shell δ^{18} O values in response to increasing RH, temperature and rain δ^{18} O values.

water loss due to their lower surface-to-volume ratio (Nevo et al., 1983), i.e., larger snails exhibit greater survivorship in drier locales (e.g., Nevo et al., 1983; Hausdorf, 2006, and references therein). In contrast, other studies observed that snail size increased with increasing humidity (see review in Goodfriend, 1986). Alternatively, the relationship between size and humidity may not be linear, but each species has an optimum humidity level above and below of which size is reduced (e.g., Hausdorf, 2006, and references therein). Other studies observed no significant relationship between size and climate (e.g., Hausdorf, 2006; Welter-Schultes, 2001). Contradictory results mirror multiple forces operating jointly at different directions and scales (Hausdorf, 2006). On one hand, wetter conditions will permit longer periods of food intake and shell growth. But larger snails exhibit less risk of desiccation than small specimens (Nevo et al., 1983). Concurrently, land-snail size may not be employed easily as a paleohumidity proxy. In the present study, shells exhibited larger dimensions during the late-glacial to earliest Holocene period, and decreased toward early-mid-Holocene and today (Figs. 4C-D). This is consistent with snails from Bermuda which showed larger sizes during glacial rather than interglacial cycles (Olson and Hearty, 2010). The shell-size trend here (Figs. 4C–D) exhibits a similar fashion than shell δ^{18} O values (Fig. 4B), which is interpreted as a progressive increase in RH, temperature and rain δ^{18} O values (Figs. 7B– D). Consequently, *Cepaea* may reach larger sizes under somewhat drier conditions. As far as we know, no modern analog exists to verify this hypothesis empirically for the study area and the target species. However, this intriguing significant relationship between size and shell δ^{18} O values suggests that the dimension of *Cepaea nemoralis* from northern Spain may respond, at least partially, to climate change.

Conclusions

The multifaceted approach used in the present study demonstrates that *C. nemoralis* shells recovered from archeological sites from Cantabria and Asturias, northern Spain, are credible retrospective archives of late glacial-Holocene atmospheres. X-ray diffraction evaluations indicate shells were unmodified diagenetically despite their differences in macroscopic taphonomic alteration. Taphonomic data suggest that Holocene shells resided longer in the taphonomic active zone whereas glacial shells appear to have been buried quicker. Whole-shell δ^{13} C values



Figure 8. Comparison of the isotopic composition of land snail shells from the Mediterranean and European regions (latitude: ~37–54°N) during the late glacial-Holocene transition. (A) Carbon stable isotope values. (B) Oxygen stable isotope values. Note that whereas carbon isotope values do not show a clear trend through time, oxygen isotope values clearly declined from glacial toward interglacial conditions.

indicate snails consumed C₃ plants with variable water-stress conditions alongside unknown amounts of limestone. Intrashell δ^{13} C profiles indicate snails exhibited higher values during their early life. This is interpreted hypothetically as a higher consumption of limestone during the younger ontogenetic stages to encourage calcification, and may be tested empirically by radiocarbon dating in future studies. The δ^{18} O values of entire shells were on average ~1% higher during the late glacial period (~12.1 cal ka BP) and the earliest Holocene (~10.9 cal ka BP) pointing to drier conditions than during the early to middle Holocene (~8.4-6.3 cal ka BP) and the present. A snail flux-balance model suggests that during the late glacial RH was ~85-88% and increased gradually to present values of ~91%. Intrashell δ^{18} O profiles indicated that C. nemoralis is short-lived (annual to biannual) and that seasonality was more marked during glacial than interglacial times. Snail body size (PC1 and geometric mean) was considerably larger at ~12.1-10.9 cal ka BP than at ~8.4–6.3 cal ka BP and the present. This suggests that Cepaea may reach larger dimensions under drier conditions, in support of the hypothesis which postulates that larger snails exhibit higher survivorship against dry conditions due to their lower risk of desiccation. This hypothesis remains to be tested for modern Cepaea along environmental gradients in the study area. Overall, this study shows that relevant average (annual to biannual) and seasonal paleoenvironmental information can be deduced from the study of land snail assemblages preserved in archeological sites.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.yqres.2012.06.008.

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