Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Oxygen stable isotopic disparities among sympatric small land snail species from northwest Minnesota, USA

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ARTICLE INFO

Article history:
Received 1 May 2017
Received in revised form 18 July 2017
Accepted 24 July 2017
Available online xxxx

Keywords:
Small land snails
Stable isotopes
Ecology
Quaternary
Minnesota
USA

ABSTRACT

The oxygen isotopic composition ($\delta^{18}O$) of land snail shells can be a valuable paleoenvironmental archive if the climatic parameters that influence the isotopic system are fully understood. Previous calibration studies have examined a limited number of species or individuals, and most have focused on larger (>10 mm) taxa, which do not represent the dominant shell material in the Quaternary fossil record. In this study, we evaluate the $\delta^{18}O$ values of small land snails (<10 mm), which are common in modern settings and are often preserved in a wide array of Quaternary geologic and archeologic deposits. Our primary goal was to determine if coexisting species record equivalent isotopic information in their shells, regardless of differences in their ecology, dietary habits, behavior, and/or body size. We collected and analyzed 265 individuals of 11 species from 12 sites in northwest Minnesota (USA), which exhibits extremely abundant and diverse terrestrial malacofauna in North America. We did not observe significant correlations between shell $\delta^{18}O$ values and the type of ecosystem (forest/grassland) or hydrologic setting (upland/lowland). However, the majority of species differed significantly in shell $\delta^{18}O$ values. Larger taxa (*Catinella*, *Succinea*, *Discus*) consistently yielded higher $\delta^{18}O$ values than smaller taxa (*Euconulus*, *Gastrocopta*, *Hawaiia*, *Vallonia*), by up to ~3‰. These isotopic offsets among sympatric taxa could be attributed to a number of physical, behavioral, and/or evolutionary traits, including the ability of larger species to tolerate drier conditions better than their smaller counterparts, differences in their preferred microhabitats or phylogentic non-independence. Regardless of the reason, our results imply that researchers should not combine isotopic data from different types of land snails without first investigating modern specimens to determine if it is appropriate. Moreover, our data suggest that combining instrumental climate data, a snail flux-balance model, and shell $\delta^{18}O$ values can help us to better understand the ecology of land snails.

1. Introduction

More than 1200 species of land snails have been identified and described in North America (see recent review by Nekola, 2014a). Over 40% of these species have shells that are categorized as small (~5–10 mm), minute (~2–5 mm), or micro (<2 mm) (Nekola, 2005; hereafter we refer to them collectively as "small"). Small land snails are present in a wide variety of ecosystems, ranging from the tropics to the high Arctic (Nekola and Coles, 2010; Nekola, 2014a,b), and their shells are frequently preserved in archeological, lacustrine, fluvial, wetland, loess, alluvial, and colluvial deposits (Yapp, 1979; Goodfriend and Ellis, 2000; Balakrishnan et al., 2005a; Paul and Mauldin, 2013). Even though small snail shells are abundant–often accounting for 90% or more of regional faunas (Nekola, 2014b), accessible, and are a potential source of paleoenvironmental and paleoecological information, their scientific study in North America has been mostly limited to radiocarbon dating (Pigati et al., 2004, 2010, 2013, 2015; Rakovan et al., 2010; Rech et al., 2012). Thus far, relatively few studies have used them to evaluate or reconstruct past environmental conditions in North America (Yapp, 1979; Goodfriend and Ellis, 2000; Balakrishnan et al., 2005a; Paul and Mauldin, 2013).

Fossilized shells of small land snails are excellent candidates for use in paleoenvironmental studies because (1) they exhibit a broad latitudinal/spatial coverage within the continental realm, spanning a wide variety of habitats ranging from rainforests to deserts, (2) they are highly sensitive to climate/environmental change, (3) they are plentiful and well preserved throughout the Quaternary geologic and archeologic records, (4) they are composed entirely of aragonite, so the presence of contaminants in fossil shells (typically in the form of calcite) can be detected using standard x-ray diffraction techniques, and (5) most Quaternary species are extant, so direct comparisons and calibrations using living counterparts are usually possible.

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http://dx.doi.org/10.1016/j.palaeo.2017.07.029
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The oxygen isotopic composition ($\delta^{18}O$) of small fossil shells holds particular promise as a paleoenvironmental proxy. Yapp's pioneering study (1979) was the first to exploit the relation between climate and oxygen isotopes in land snail shells, and inspired several dozen studies aimed at reconstructing various climate parameters. However, shell $\delta^{18}O$ values are affected by multiple atmospheric variables that are often difficult to discriminate, including rainwater $\delta^{18}O$, water vapor $\delta^{18}O$, relative humidity, and temperature (Balakrishnan and Yapp, 2004). Thus, proper interpretation of $\delta^{18}O$ values of land snail shells remains challenging.

Calibration studies using modern specimens from areas with well-constrained climate data can improve the interpretation of fossil shell $\delta^{18}O$ data. In North America, only a handful of field studies have carried out calibration assessments using modern land snails (Yapp, 1979; Sharpe et al., 1994; Goodfriend and Ellis, 2002; Balakrishnan et al., 2005b; Yanes, 2015). In general, these studies have examined a limited number of species or individuals, and most have focused on larger (>10 mm) taxa, which do not represent the most abundant shell material found in the Quaternary fossil record.

Another uncertainty when evaluating land snail isotopic data is whether or not different coexisting (sympatric) species record equivalent environmental information in their shells, regardless of potential differences in their ecology, dietary habits, behavior, and/or body size. Many land snail isotope studies have focused on a single species (e.g., Yanes et al., 2008; Colonese et al., 2010, 2011; Prendergast et al., 2015, 2016), which minimizes problems associated with potential variations resulting from differing snail ecologies or species-specific biological fractionations (i.e., vital effects). In other studies, however, researchers have combined isotopic data derived from multiple species (e.g., Yapp, 1979; Balakrishnan et al., 2005a,b; Zanchetta et al., 2005). In some instances, species that overlap in space and time appear to track equivalent isotopic information (e.g., Zanchetta et al., 2005; Yanes et al., 2009, 2011, 2013; Yanes and Romanek, 2013; Yanes, 2015), but this is not always the case (Balakrishnan et al., 2005b; Yanes et al., 2013). This issue is particularly relevant for studies with a broad spatio-temporal scope because land snail assemblages can vary tremendously over both space and time, making it difficult or impossible to use a single taxon for all analyses.

In this study, we evaluate the oxygen isotopic composition of multiple key species of small land snails collected from forest and grassland ecosystems in northwest Minnesota. The study sites are located in a mid-latitude region (46–48°N) at the transition between taiga, deciduous forest, and grassland biomes (Fig. 1), and contains a rich and diverse assemblage of land snails (Nekola, 2003). Moreover, relevant climate data from this sampling region is readily accessible for comparison with snail shell $\delta^{18}O$ values. This study tests the hypothesis that multiple species of small land snails collected from the same region record equivalent $\delta^{18}O$ values in their shells, regardless of differences in the local ecosystem (forest or grassland), hydrologic setting (upland or lowland),[1] and physical properties (shell size, morphology, etc.). The $\delta^{18}O$ data are then compared to climate data from the region and examined using an evaporative steady-state flux balance-mixing model for land snails developed by Balakrishnan and Yapp (2004). The results from this work will serve as a much-needed methodological reference for investigators working on fossil land snails in the geologic and archeologic records of North America and elsewhere.

2. Material and methods

2.1. Geographic and climatic setting

We collected live snails from a total of twelve localities in northwest Minnesota, including (from north to south) Beaches WMA, Halma Roadside, Halma Swamp, Strathcona, Old Mill SP, Oak Ridge, Huot Forest, Eastlund, Waubun SE, Callaway N, Bluestem Prairie, and Barnesville WMA (Fig. 1; Table 1; Supplementary Table S1). These localities were chosen because they have similar climates, are positioned at approximately the same elevation (~330–567 m a.s.l.), exhibit comparable and relatively pristine woodland and grassland areas, and contain a diverse and abundant assemblage of small land snails (Nekola, 2003). In addition, air temperature and other climate data for the area are readily accessible through the National Oceanic and Atmospheric Administration's National Centers for Environmental Information (https://www.ncdc.noaa.gov). We selected time-series climate data for the recording period between 2010 and 2017 from the northwest Minnesota region. Monthly average air temperatures in northwest Minnesota range from −13.7 °C to +20.9 °C, with an average annual temperature of ~4.8 °C. The total annual precipitation amount is ~596 mm, with summer months being the wettest. In addition, the weighted average annual $\delta^{18}O$ value of precipitation is −12 ± 1‰ (relative to Standard Mean Ocean Water; SMOW), ranging from ~−7‰ to ~−20.5‰ (SMOW) (Henderson et al., 2010).

2.2. Land snail field collection strategy

Documentation of terrestrial gastropods from each site was accomplished by hand collection of larger shells and litter sampling for smaller taxa from representative 100–1000 m^2 areas (Nekola, 2003). Soil litter sampling was primarily used as it provides the most complete assessment of site faunas (Oggier et al., 1998). As suggested by Emberton et al. (1996), collections were made at places of high micromollusc density, with a constant volume of soil litter of ~4 l being gathered at each site. For woodland sites, sampling was concentrated along the base of rocks or trees, on soil-covered bedrock ledges, and/or at places found to have an abundance of shells. For grassland sites, samples consisted of small blocks (~125 cm^3) of turf, loose soil and leaf litter accumulations under or adjacent to shrubs, cobbles, boulders, and/or hummocks, and other locations observed to have an abundance of shells.

2.3. Land snail species

The malacofauna of northwest Minnesota include at least 41 different extant species (Hubricht, 1985; Nekola, 2003). Eleven species were selected for the present study including: *Catinella avara* (Say, 1824), *Catinella exile* (Leonard, 1972), *Discus catskillensis* (Pilsbry, 1896), *Discus cronkhitei* (Newcomb, 1865) [aka *D. whitneyi* (Newcomb, 1865)], *Euconulus* c.f. *alderi* (Gray, 1840), *Euconulus fulvus* (Müller, 1774), *Gastrocopta contracta* (Say, 1822), *Gastrocopta tappaniana* (Adams, 1842), *Hawaiia minuscula* (Binney, 1841), *Succinea* (*Novisuccinea*) *ovalis* (Say, 1817), and *Vallonia gracilicosta* (Reinhardt, 1883). Species were identified to species level based on shell features, geographic distribution, published descriptions, and anatomic comparisons with the mollusk collection at the University of New Mexico curated by one of us (JCN). We selected these species because they have high abundance in both modern settings and Quaternary sites across North America. We note that although the Succineidae (e.g., *Catinella* and *Succinea*) are usually medium to large in shell size (>10 mm), the results of previous work by our research group indicate they are similar to many smaller shells in terms of isotopic systematics (Pigati et al., 2010). Succineidae shells are also among the most common Pleistocene to Holocene land snail fossils, and thus we have included them in the present analysis.

Land snail physiology, ecology, and behavior suggest that survival and environmental depends on their ability to maintain adequate levels of internal body water across a wide variation of air temperatures and relative humidity (Wilbur and Yonge, 1964; Cook, 2001; Pearce and Örstan, 2006). During periods of activity, snails secrete mucus, which is mostly made of water, and high levels of relative humidity reduce the risk of desiccation via evaporation. To accommodate these needs,

[1] The term “uplands” is used to denote areas that are positioned well above the local water table, whereas “lowlands” refers to areas where groundwater is at or near the surface.