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SHORT COMMUNICATIONS

Estimating the Impact of Ungulates on Holocene Steppe Ecosystems by Analyzing Repaired Injuries in Land Snail Shells

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Reconstructions of environmental conditions of the past epochs inevitably involves certain difficulties. Paleoecologists in their research have to rely on indicators indirectly characterizing the effects of factor of different nature in the past. In this study we propose a method for estimating the impact of ungulates on Holocene steppe ecosystems by analyzing repaired injuries in fossil shells of the land snail *Helicopsis striata* Müller. This species belongs to the Mediterranean group of relict xerophilic mollusks (Nikolaev, 1973; Snegin, 202). Its present-day range includes western and central Europe and the southern part of eastern Europe to th Don River (Shileiko, 1978).

Or studies were performed in the south of the Central Russian Plain, where these snails live on sun-warmed slopes of ravines with chalk soils and often concentrate in relict plant communities. They have a slightly compressed turbinate shell of medium size. In the study region, its large diameter reaches 12–15 mm, and height, 8–11 mm (Snegin, 2004; Snegin and Sychev, 2011). Empty shells of dead snails accumulate in their habitats over many years, which makes it possible to collect representative samples for analyzing variation in conchological traits. Moreover, these shells are well preserved in soil deposits and therefore can be used to reconstruct paleoecological conditions in the European Pleistocene and Holocene ecosystems (Sparks, 1953; Lozek, 1964; Markovic et al., 2007).

In 2012, a soil pit was excavated at the mouth of Veshnyaki ravine in the Yamskaya Step site of the Belogorie State Nature Reserve ((51°10′31.26″ N, 37°37′30.28″ E). In the course of integrated analysis of paleosols, fragments of snail shells were collected, which concentrated in the 230- to 250-см horizon. Radiocarbon dating of soil humus in the Kiev Radiocarbon Laboratory (Ukraine) showed that the age of this horizon is 3290 ± 90 years (Ki-17953), which corresponds to the late Subboreal period of the Holocene. A total of 34 *H. striata* shells were collected from 191.35 kg of soil. They included specimens with intravital injuries that the mollusk could repair and continue growing (Sychev, 2013). In particular, these were cracks resulting from accidental mechanical impact (compression). Such shells were characterized by different orientation of riblet sculpture before and after injury and deviations from the initial geometry and growth direction. Similar injuries and disturbances were also noted in recent shells.

In steppe ecosystems, ungulates are most likely to be responsible for such injuries. The point is that the shell of *H. striata* is thick-walled and fairly durable, and cracks in it probably appeared after a blow with a hard object, such as a hoof. According to available data, injuries inflicted by small birds have a different pattern, looking like local shearing cuts.[1]

Predatory beetles and rodents feeding on snails leave specific traces of gnawing through the shell from the apertural side, which are sometimes difficult to distinguish from accidental mechanical damage after the death of the snail[2] (Fig. 3). Moreover, the probability of snail survival and shell repair after a targeted attack by a predator is low.

Recent forest–steppe ecosystems of the study region are permanently inhabited only by two wild ungulate species, roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). However, some areas populated by *H. striata*, are used for cattle grazing, and the impact of cattle on herbaceous vegetation is similar to

[1] Large birds usually ingest such snails together with the shell.

[2] The recent entomofauna of the study region includes one snail-eating ground beetle species, *Licinus cassideus* Fabricius, 1792 (Carabidae), which lives mainly in steppificated biotopes and xerophilic meadows. This beetle gnaws through the shell with the jaws, starting from the apertural side and reaching snail's soft tissues, but it can only cope with relatively thin shells of young snails. However, it cannot be excluded that steppe ecosystems in the past were inhabited by beetles of other species that could overcome adult snails.

Table 1. Description of biotopes, samples sizes, and proportions of damaged *H. striata* shells

Sampling site	Coordinates	Biotope, economic activities	Number of *H. striata* shells	Proportion of damaged cells, %
1. Gubkin	51°17′49.64″ N, 37°32′14.56″ E	Feather grass steppe traveled by people and used for walking pets; no grazing	850	3.1
2. Telshovka	51°02′24.04″ N, 37°17′01.77″ E	Mixed grass steppe regularly grazed by cattle (about 500 head)	569	22.0
3. Protection zone	51°10′40.39″ N, 37°36′15.59″ E	Mixed grass steppe in the protection zone of Yamskaya Step reserve near abandoned summer cattle barn; no grazing since 2006 2006 г.	147	7.5
4. Veshnyaki	51°10′36.10″ N, 37°37'32.62″ E	Feather grass steppe in Yamskaya Step reserve, no grazing	25	0.0
5. Soil layer, age 3290 ± 90 years	51°10′31.26″ N 37°37′30.28″ E	Veshnyaki ravine in Yamskaya Step area of Belogorie reserve, soil pit	34	14.7

Samples were taken without regard to sampling area, and population density differed between the sites.

that of wild ungulates in the past. Therefore, we also estimated the frequency of intravitally damaged and repaired shells in snails living in areas currently (or until recently) used for cattle grazing (Table 1, biotopes 2 and 3) and in areas not exposed to this impact (biotopes 1 and 4).

Comparisons of populations with respect to the frequencies of shells with repaired injuries was performed using Fisher's test (phi method) (Plokhinskii, 1970).

As follows from the results (Tables 1, 2), the frequency of snails with repaired shells proved to be significantly higher ($p < 0.05$) in biotope 2 (regularly grazed) and biotope 3 (grazed until recently) than in ungrazed biotopes 1 and 4. Comparison of populations from biotopes 2 and 3 with th fossil group from biotope 5 revealed no significant differences, which may be regarded as evidence for a high grazing load on the steppe ecosystems of the study region in the late Subboreal period. According to historical data (Smirnova et al., 2001), the region during that period was inhabited by the tarpan (*Equus ferus*), onager (*Equus hemionus*), European bison (*Bison bonasus*), aurochs (*Bos primigenius*), and saiga antelope (*Saiga tatarica*).

It should also be taken into account that tribes of the Timber-grave, Bondarikhino, and Scythian cultures were living in the southern forest–steppe zone of the Central Russian Plain (including the study region)

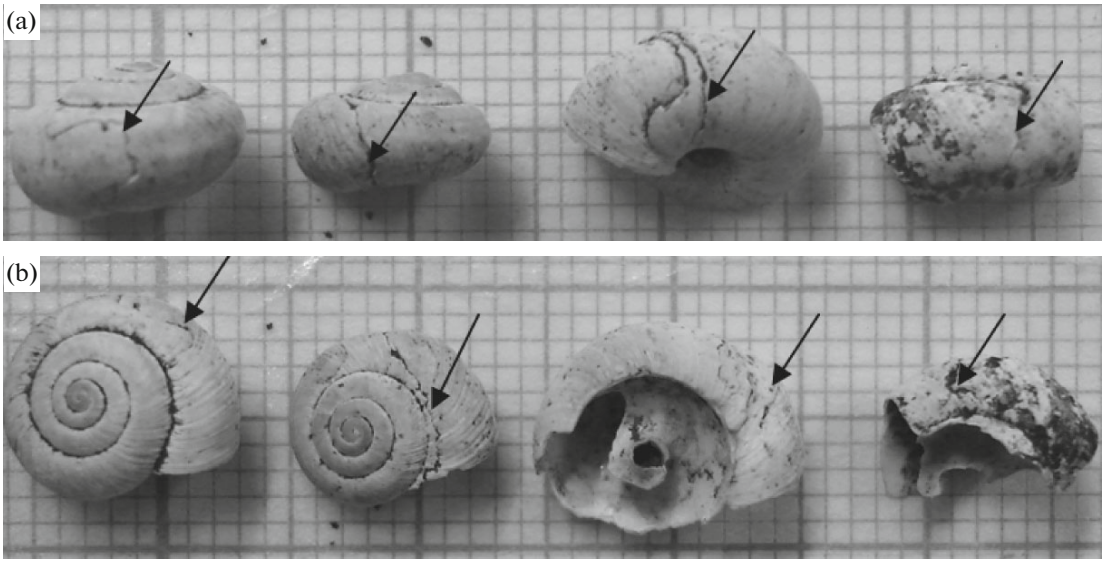

Fig. 1. Fossil *H. striata* shells from horizon 230–250 cm with repaired injuries (arrows): (a) side view, (b) top view.

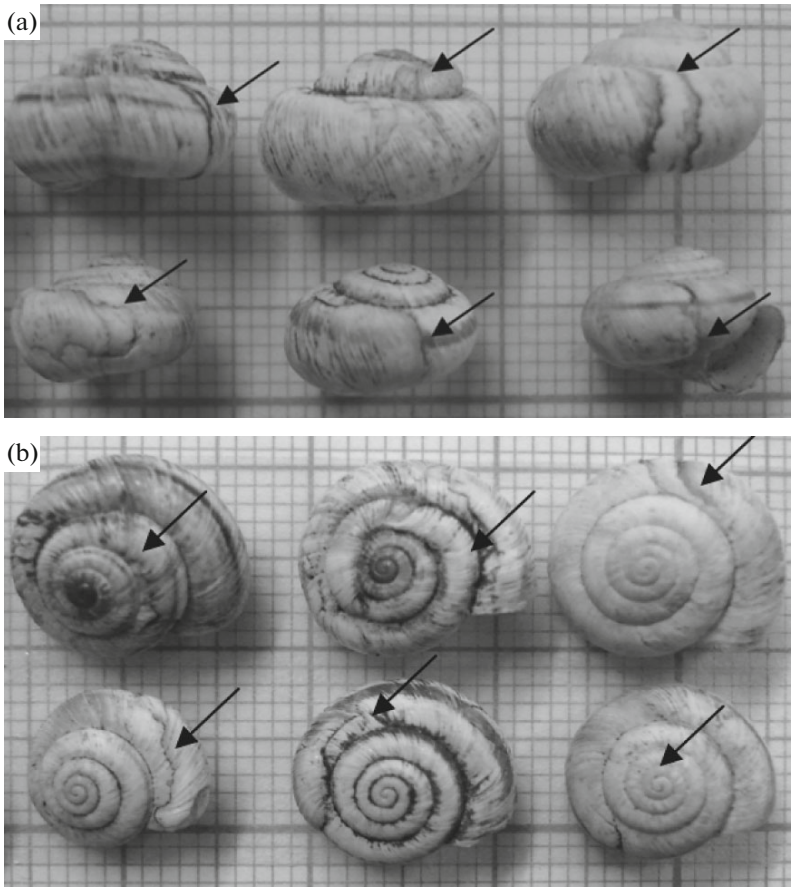

Fig. 2. Recent *H. striata* shells from Teleshovka population with repaired injuries (arrows): (a) side view, (b) top view.

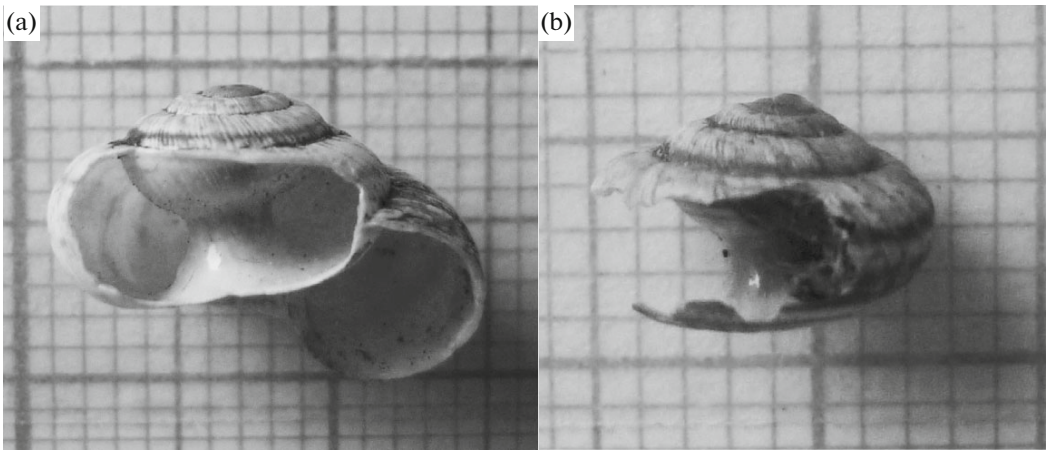

Fig. 3. Shells of *H. striata* damaged by (a) a bird and (a) a ground beetle.

and the turn of the 2nd and 1st millennia BP, and livestock breeding was a major form of their economic activity (Shramko, 1962). Therefore, both wild and domesticated ungulates could account for the high proportion of damaged *H. striata* shells in that period, with grazing impact leading to the formation of short-grass landscapes with sparse ground layer (Chendeev et al., 2014).

Because of the long period of accumulation of empty shells and low rate of their decomposition in carbonate environment, this method can be used for assessing population dynamics (changes in activity) of ungulates only on a long time scale. Using it for revealing relatively fast changes in grazing load during in the past epochs will be incorrect, because the shells separated in time by several decades can form mixed aggre-

Table 2. Values of Fisher test obtained in comparison of population frequencies of *H. striata* shells with repaired injuries. Underlined values are statistically significant at $p < 0.05$)

Population	1	2	3	4	5
1					
2	131.9				
3	5.0	20.8			
4	3.0	22.8	15.7		
5	5.9	1.2	1.4	8.7	

gated on the soil surface or in upper soil horizons. Short-term changes in the abundance of ungulates can also be studied by analyzing repaired injuries on the shells of living *H. striata* snails.

Thus, the results presented above show that the proposed method can be used to reconstruct paleoecological conditions and evaluate grazing load on steppe ecosystems. To test this method more thoroughly, it appears expedient to increase the number of test areas and broaden their geographic range.

It should also be noted that the ability to quickly repair injuries in the shell can be regarded as an adaptation to life in xerophilic communities and is also characteristic of other steppe snails similar to *H. striata* in size, namely, *Xeropicta krynickii*, *X. derbentina*, *Hellicela candicans*, other species of this genus. Apparently, their shells can also be used in studies on reconstructing paleoecological conditions in the steppe ecosystems of Eurasia,

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