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RESEARCH NOTE

Dispersal of land snails by sea storms

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No facts seem to me so difficult as those connected with the dispersal of land Mollusca.
Charles Darwin, letter to J. D. Dana, 29 September 1856
(Darwin Correspondence Database)

Cepaea nemoralis (Linnaeus, 1758), a land snail (shell diameter 18–25 mm) native to Western Europe, occupies a range of habitats including coastal dunes, deciduous woods, meadows and anthropogenic habitats such as hedgerows, gardens and open urban areas (Kerney, Cameron & Jungbluth, 1983). At the eastern and northern extremities of its range, most recorded populations come from anthropogenic habitats (Fig. 1). These can be attributed to accidental human transport followed by local dispersal (Dvořák & Honěk, 2004; Cameron *et al.*, 2011), although deliberate introductions outside the natural range are known in North America (Örstan & Cameron, 2015) and Europe (Ożgo, 2005). However, populations recorded from coastal habitats along the southern and eastern shores of the Baltic Sea are an exception to this restriction to anthropogenic habitats (Riedel, 1988). These populations, many of which were first recorded in the 19th century, have been present longer than those recorded from urban areas inland. Their origins have so far not been explained.

On 13 February 2011, 3 d after a storm, we found nine *Cepaea nemoralis* with shells still closed with an epiphragm (air temperature, approximately 0 °C) in the debris deposited by waves on a sandy beach in the Polish part of the southern Baltic coast near the village of Poddąbie (54.62°N, 16.97°E) (Supplementary Material Fig. S1). On this occasion, the debris brought by the waves did not reach the woods behind the beach. Therefore, the snails in the debris could not have originated from the woods. Two adults and one juvenile revived in the laboratory, survived till spring and were released. This finding suggests a possible mechanism for the dispersal of the species along the southern Baltic coast and could explain its puzzling distribution in eastern Europe.

The Baltic, with an average depth of 52 m, occupies an erosion basin formed during the last ice ages. The coastline stabilized at the end of the Holocene climatic optimum, around 5000 BP (Uścinowicz *et al.*, 2000). In surface-water salinity ranges from 8.5 ppt in the south to 3 ppt in the north. The dominant water circulation is anticlockwise (Fig. 1); eastward currents in the southern Baltic are reinforced by the predominant northwesterly and westerly winds causing inflows of large quantities of water through the straits (Biuro Hydrograficzne Marynarki Wojennej, 2009). Storms in the Baltic are sudden and violent with winds of 60–90 km/h, increasing up to 130 km/h and usually lasting only 1 d (Łomniewski, 1962). They are related to the rapid movement of low-pressure areas from the west and occur mainly in autumn and winter. During storms waves are usually 3–5 m high, but can reach over 12 m (Biuro Hydrograficzne Marynarki Wojennej, 2009). The passage of deep low-pressure areas can cause rapid movements of locally raised sea level, with recorded low-pressure-induced domes of water moving about 300 km along the coast in just 7 h (Wiśniewski & Wolski, 2009). During storm surges, the sea level can rise within a few hours to 1–1.5 m above the norm. Storm-related landslides of escarpments can reach several dozen metres inland, while low-lying areas are subject to storm floods (Uścinowicz *et al.*, 2004).

Field experiments have shown that lotic waters can carry live land snails over long distances. For example, *Arianta arbustorum*, a snail similar in size to *C. nemoralis*, rafting on plant material on the Elbe River covered 20.8 km in 5.5 h; free-floating *Helix pomatia* covered 19.8 km in less than 4.5 h (Tenzer, 2003). Marine dispersal, either by free-floating or rafting on objects, has also been inferred, without direct observations, as a method of introduction of land snails to remote islands (Pilsbry, 1910; Smith & Djajasasmita, 1988). Transportation of land snails by birds has also been shown to be a feasible dispersal mechanism (e.g. Rees, 1965; Maciorowski, Urbańska & Giersztal, 2012; Wada, Kawakami & Chiba, 2012).

On the Polish Baltic coast, *C. nemoralis* occupies dunes and meadows on the escarpment and is liable to be carried away in storm surges. However, land snails may not survive prolonged contact of their bodies with sea water, mostly because of lack of hypo-osmotic regulation (Machin, 1975). Nevertheless, during dormancy, shells can be sealed with an epiphragm, posing a barrier to water. Experiments show that inactive land snails can indeed survive in sea water for days. Probably the most famous is the experiment of Darwin (1859: 397) in which hibernating *H. pomatia* recovered after 20 d of being immersed in sea water. Inspired by Darwin, Aucapitaine kept 100 land snails representing

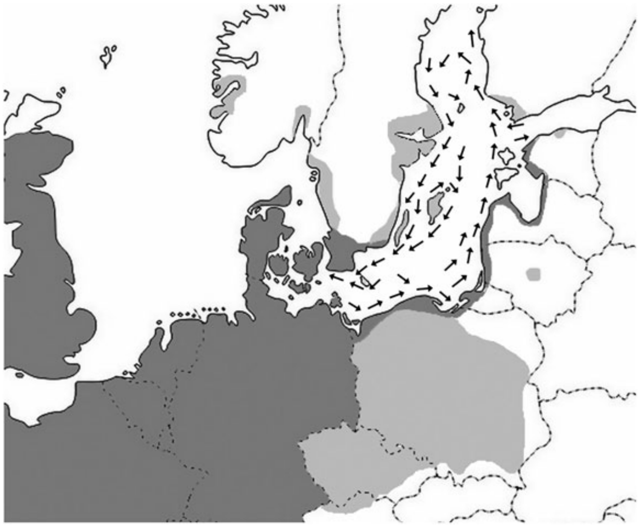

Figure 1. Map showing the northeastern part of the range of *Cepaea nemoralis*. Dark grey areas denote what is believed to be the natural range. The pale grey areas show that part of the range in which populations, mostly recorded recently, are mainly confined to anthropogenic habitats. The boundary between the two is not as sharp as indicated, especially in western Poland. Arrows indicate hydrological flow for the surface water in the Baltic (according to Håkanson, 1991).

10 species in a box with holes immersed in sea water for 14 d (calculated to be about half the time required for a floating object to cross the Atlantic) and 27 individuals of six of the species recovered (Aucapitaine, 1864; Örstan, 2012). In similar experiments by Bartsch (1912) and Mayr & Rosen (1956), some individuals of the land snail *Cerion* survived in sea water for up to 5 d. Mayr & Rosen (1956) believed that their findings had some bearing on the dispersal of *Cerion* among islands, presumably by floating either freely or on plant fragments to which the snails attach during dry weather. Likewise, in a laboratory experiment *Succinea caduca* survived a 12-h immersion in water with a salinity of 35 ppt (Holland & Cowie, 2007). However, none of the 30 non-dormant individuals of the Florida tree snail *Liguus* exposed to sea water for 2 h on a piece of plywood floating on calm water survived (Tuskes, 1981).

To test the survival of *C. nemoralis* in sea water, we placed 20 active adult snails for 12 h in water (salinity 7 ppt at 8 °C) from the Baltic where storm deposited snails were collected. Nineteen snails survived the treatment and remained alive for 2 weeks afterwards, before being released. We did two additional experiments in which two groups of adult *C. nemoralis* were exposed to a solution of 8 ppt NaCl at 21 °C for 11 h. In the first experiment, four snails were floated on a piece of tree bark in the NaCl solution. The snails remained in contact with the solution for the duration of the experiment and were observed to submerge their bodies in it on several occasions. In the second experiment, six snails were confined in a shallow container of the NaCl solution and forced to remain partially submerged. All 10 snails survived and were alive 20 d later when they were released.

Our observation and experiments show that *C. nemoralis*, even when active and not protected by an epiphragm, may survive in the Baltic seawater for the extent of time sufficient for being transported by storm waves from one location along the coast to another. The fact that storms occur predominantly in winter, when the shells of hibernating snails are sealed with epiphragms, and that they usually last for only 1 d, increase the probability of snail survival. Along the southern Baltic coast, suitable *Cepaea* habitats, such as deciduous woods or meadows, are often adjacent to beaches; storm waves carrying snails can bring them close to or directly onto a suitable habitat. The mode of reproduction and the high potential for colonizing novel habitats (Murray, 1964; Ożgo, 2011) suggest that settlement and colonization also have a fair chance of success. *Cepaea nemoralis* is a hermaphroditic obligatory outcrosser. The snails mate several times during a season, and can store sperm for more than a year. Therefore, a single fertilized individual can start a population that may then become the source for further eastward expansion of the species in a stepping-stone mode of dispersal. Genetic constitutions of *C. nemoralis* populations suggest that rare cases of long-distance passive dispersal could explain some of the patterns revealed (Cook, 1998). Our findings indicate that such dispersals are not restricted to overland or aerial transport routes and that marine transport is also feasible.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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