Long-distance dispersal of molluscs: ‘Their distribution at first perplexed me much

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COMMENTARY

Long-distance dispersal of molluscs: 'Their distribution at first perplexed me much'

Snails and slugs are notoriously slow animals, with only a single foot to move sluggishly forward. They are surprisingly widespread, however. At least a few species are known from even the most remote oceanic islands. How did they ever get there? Obviously, gastropods should have other means than crawling for dispersal. As Darwin (1859, p. 385) put it, while referring to freshwater snails: 'Their distribution at first perplexed me much'. The 'much' was omitted in the sixth edition of his *Origin of Species*, but the problem remained.

The most important, relatively recent source of information on assisted dispersal of molluscs was published by Rees (1965). In his presidential address to the Malacological Society of London, W.J. Rees dealt with 'The aerial dispersal of Mollusca'. He emphasized that wind-borne and insect-borne dispersal should not be neglected, but in conformity with all previous authors, including Darwin, he regarded dispersal by birds as the most effective mechanism for snails to reach otherwise inaccessible places.

Some of the oldest notes on molluscan transport by birds remained largely buried in obscurity, perhaps because of linguistic problems. Even Rees (1965) seems to have overlooked Kobelt (1871) and Pascal (1891). Kobelt (1871) stated that he considered it not unlikely at all that small bivalves and even operculate freshwater snails, when eaten alive, might pass through the gut unharmed, so that they could still reproduce later on ('… durchaus nicht unwahrscheinlich, dass kleine Muscheln und selbst gedeckelte Wasserschnecken mitunter, wenn lebendig verschluckt, den Darmcanal unverdaut passiren und so verpflanzt werden können'). Kobelt apparently realized that among the molluscs, bivalves can protect themselves best, by simply closing their valves, whereas snails need special structures to protect the open aperture of their shells. Snails that can close the aperture with an operculum, such as most prosobranchs (or Caenogastropoda, as systematists prefer to call them these days), are supposed to be protected better than snails without that door-like structure. The calcareous shell is usually covered by a periostracum, containing conchyoline, which is also present in the operculum. It is a substance that makes the snail less vulnerable in an acid environment, but because it is missing on the inside of the shell, the snail's destruction may still start there. Pascal (1891) suggested that freshwater snails may reach isolated ponds because their egg capsules might pass the digestive tract of swans '... sans altération, a travers leurs intestins [… without change, through their intestine]'.

Rees (1965) also mentioned the possibility of molluscs 'surviving transit through the alimentary canal', adding that he did not know any records of that ever happening. In the same period, Malone (1965) experimentally fed birds of two species, mallard (*Anas platyrhynchos*) and killdeer (*Charadrius vociferus*), with snails and snails' egg masses, but he failed to demonstrate that these survived a regular passage through the intestinal tract. Malone concluded that only specimens that have not yet entered the alimentary system beyond the bird's crop, and were vomited from there, could be transported alive. Rees (1965) reached the same conclusion, adding that living snails or eggs could also 'be scattered after a snail eating bird has been torn to pieces by a bird of prey'.

In a significant article (in Dutch), Cadée (1988) mentioned the finding of living small marine, operculate mud-snails (*Hydrobia ulvae*: shell height mostly 2–5 mm) in the faeces of shelducks (*Tadorna tadorna*), thereby showing that Kobelt's (1871) hypothesis was right. In a more easily accessible article, the same author (Cadée, 2011) described that those snails will often not pass through the digestive tract undamaged. In cases of survival, they may repair their shells afterwards. Kawakami *et al.* (2008) added similar data on remains of snails in bird faeces, although without demonstrating that in their research material (p. 170) 'snail dispersal by passage through the bird gut' indeed took place.

Most recently, Wada *et al.* (2011) have now demonstrated convincingly, both experimentally and by field observations, that even the presence of an operculum is not crucial for snails to survive for some time in a bird's gut. Specimens of *Tornatellides boeningi*, a small pulmonate snail (shell height 2.5 mm), that are preyed upon by the Japanese white-eye (*Zosterops japonicus*) and the brown-eared bulbul (*Hypsipetes amaurotis*), made this clear. It remains unknown whether an epiphragm or only the secretion of mucus took over the protecting role of an operculum. An epiphragm is formed only while at rest and the authors did not indicate whether, during their experiment, the snails were eaten while crawling actively around or at rest.

Taking account of the above, it is now obvious that small bivalves, operculate snails and even pulmonate snails without an operculum may occasionally survive in the digestive tract of a bird, before the calcareous shell is dissolved in the acid environment and the animal is killed. All authors that have reported on this agree, however, that there must be a time limit to survival. For long-distance dispersal of molluscs, where even birds need some time, internal transport is still generally considered a very unlikely explanation, and external transport by birds the most likely mechanism (as suggested already by Lyell, 1832, p. 109). On the basis of only distributional patterns, Wesselingh *et al.* (1999), for example, have argued that avian dispersal of aquatic snails should have been an important mechanism in the geological past. The risk of desiccation is usually considered of major importance, but that is clearly not insuperable. The pulmonate land snail *Balea* even managed to travel over thousands of kilometres of open ocean, from Europe to the Azores and the Tristan da Cunha islands, and back again (Gittenberger *et al.*, 2006).

Long-distance dispersal implies a series of unlikely events. However, time is available and a single snail may be sufficient for a successful range extension, whether it is a hermaphroditic pulmonate, which may be

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capable of selfing, or a parthenogenetically reproducing prosobranch.

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