biology letters

Animal behaviour

Hitchhiking behaviour in the obligatory upstream migration of amphidromous snails

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Migratory animals endure high stress during long-distance travel in order to benefit from spatio-temporally fluctuating resources, including food and shelter or from colonization of unoccupied habitats. Along with some fishes and shrimps, nerite snails in tropical to temperate freshwater systems are examples of amphidromous animals that migrate upstream for growth and reproduction after a marine larval phase. Here I report, to my knowledge, the first example of 'hitchhiking' behaviour in the obligatory migration of animals: the nerite snail *Neritina asperulata* appears to travel several kilometres as minute juveniles by firmly attaching to the shells of congeneric, subadult snails in streams of Melanesian Islands, presumably to increase the success rate of migration.

Keywords: amphidromy; growth lines; hitchhike; home scar; Neritidae; migration

1. INTRODUCTION

Many animals such as birds, insects and fishes customarily travel long distances in response to spatio-temporally fluctuating resources, including food and shelter, or to ensure reproductive success (Dingle & Drake 2007). A less-known but remarkable example of migration is found in small aquatic snails with apparently limited mobility. Freshwater nerites of the gastropod families Neritidae and Neritiliidae are examples of amphidromous animals that undergo a marine phase when their larvae are swept downstream to the sea (Kano *et al.* 2002; McDowall 2007). Metamorphosed juveniles settle at river mouths and then migrate (often over 10 km) upstream where they spend the rest of their life. The upstream migration of settled juveniles has been observed in several nerite species, sometimes in large aggregations (Schneider & Lyons 1993; Kobayashi & Iwasaki 2002). The energy cost of migration is compensated by lower predation pressure in the upper reaches of streams and by the increased upstream availability of food for these animals, all of which graze on microalgae (Schneider & Lyons 1993; McDowall 2007).

Here I demonstrate that small juveniles of *Neritina asperulata*, an amphidromous species of Neritidae,

migrate great distances by clinging to the shells of congeneric, subadult snails in streams in the Melanesian Islands. To my knowledge, this is the first reported case of 'hitchhiking' behaviour that shifts the cost of migration onto other organisms while reaping the benefit. This case is, I believe, unique, not only among diadromous animals with marine and freshwater periods, but also among other forms of obligatory migration.

2. MATERIAL AND METHODS

Field observations were made and samples taken in streams and rivers on Guadalcanal (Solomon Islands) and Santo (Republic of Vanuatu). Juvenile nerites attached to the shells of other snails were collected, measured and preserved, along with adults and free-living juveniles. DNA sequencing was performed using standard protocols for a wide range of *Neritina* snails from the Indo-Pacific, including the hitchhiking individuals, to assign the juveniles to species and to understand the evolution of the hitchhiking behaviour. Bayesian and likelihood phylogenies were reconstructed using 658 bp sequences of the mitochondrial cytochrome oxidase subset I (COI) gene (DDBJ/EMBL/GenBank accession numbers AB477472–AB477514; see electronic supplementary material for details). Opercula of the juvenile shells were observed under a scanning electron microscope to identify the species and to infer the presence or absence of a planktotrophic larval period (figure S1, electronic supplementary material).

The preference of juveniles for the attached mode of life was evaluated in a simple field experiment. Eleven hitchhiking juveniles were separated from a subadult snail of *N. pulligera* and randomly placed in a plastic container ($21 \times 15 \times 8$ cm) half-filled with freshwater, together with the previous host, another subadult individual, an empty shell of *N. pulligera* and a stone of the same size (all from the same river environment). The positions of the juveniles were recorded after 6 h; two replicas were made with the same individuals.

3. RESULTS

Small juveniles of *N. asperulata* (< 5 mm in maximum shell length, MSL) were found almost exclusively (98.6%) on the shells of *N. pulligera*, an abundant, large-sized congeneric species with upstream migration behaviour (figure 1*b,c*; Kano 2006). Seventy-one juveniles occurred on 11 subadult individuals of *N. pulligera* from five rivers and streams (1–16 juveniles on a host). Collection sites were located at distances of 1.0–6.7 km from the river mouths and 0.5–4.0 km from the upper limits of tidal influence. The MSL of the host snails and of the hitchhiking juveniles was 21.5 ± 4.4 mm (range: 17.7–29.0) and 3.4 ± 0.5 mm (2.3–4.3), respectively. The juveniles aggregated densely at the posterior side of the creeping host, where they had attached firmly to the shell surface. The shells of most juveniles had irregularly spaced growth lines and an interiorly thickened outer lip of the aperture; some shells had an extensively eroded apex (figure 2*b,c*).

The hitchhiking juveniles were abundant at Mataniko waterfalls, Santo (6.5 km upstream from the mouth and 4.0 km from the tidal reach), where the riverbed and other hard substrates were covered with a thick layer of tufa (figure 1*a*). The shell of *N. pulligera* was also covered with this calcareous layer, while its posterior, juvenile-bearing surface had circular etchings, each with a shallower surrounding depression (figure 1*d,e*). Larger, free-living juveniles and adults of *N. asperulata* collected here (MSL of 5.0–24.6 mm) uniformly had a clear inflection point of shell growth at an MSL of 3.4 ± 0.4 mm (2.9–4.3). After the inflection point, the shell shape became wider and flatter with a more rapidly expanding aperture than the previous
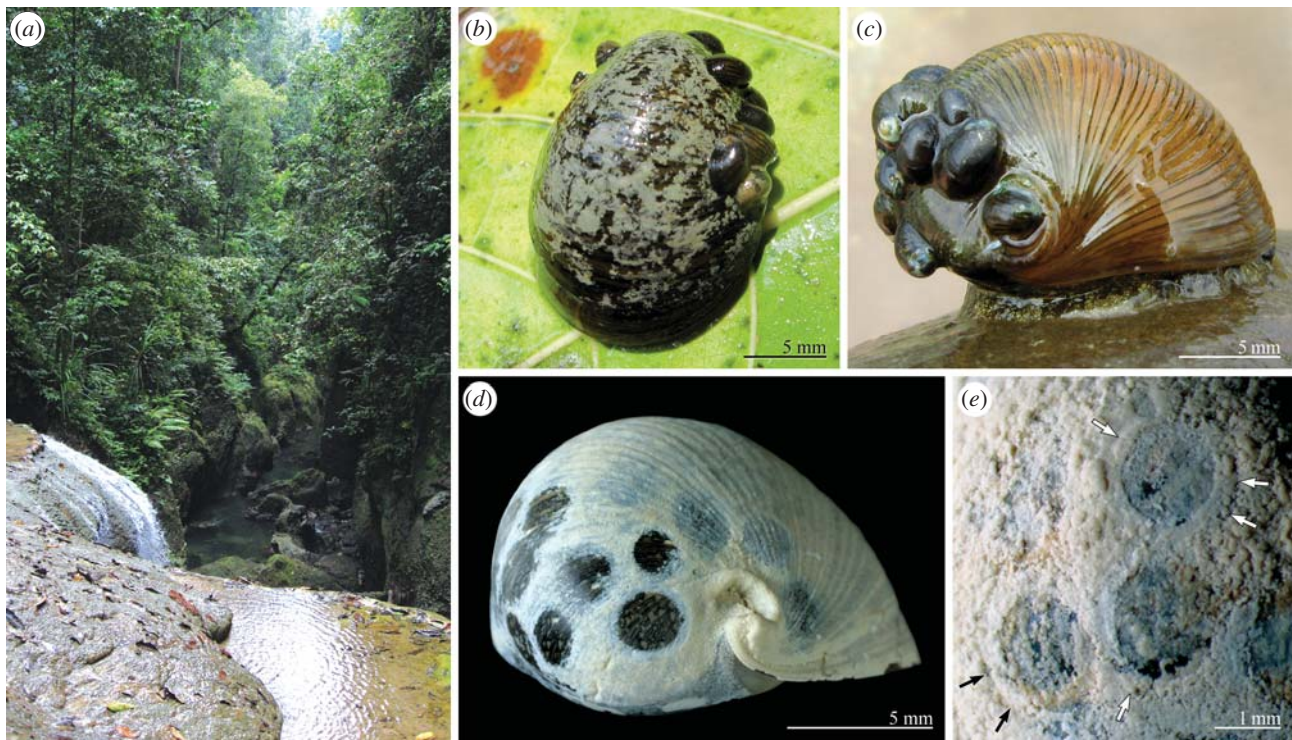
Figure 1. (*a*) Mataniko waterfalls (Solomon Islands) from top, where hitchhiking snails were most abundant. Image courtesy of K. Jörger, copyright © 2007. (*b*,*c*) Hitchhiking juveniles of *N. asperulata* on subadult *N. pulligera* at Mataniko (*b*) and Lungga, Solomons (*c*); note calcareous tufa deposit on shells of host and some juveniles at Mataniko. Snails were removed from water for photography. (*d*,*e*) Home scars in calcareous layers on host shells, beneath the foot of hitchhiking juveniles at Mataniko. Arrows point to shallower, surrounding depressions that correspond to the mantle margin.

whorls, and the shell surface was smooth without growth lines (figure 2*d*,*e*).

In the experiment, a total of 22 juveniles were found on either the previous host (13) or another snail (9), and none on an empty shell or a stone, or wandering in the container after 6 h. This indicates a strong preference of the juvenile *N. asperulata* for attaching to living snails ($p < 0.00001$, binomial test), but not necessarily to an accustomed individual ($p > 0.05$). Hitchhiking juveniles did not make a noticeable etching on the calcareous layer of the hosts in a 24 h period after the experiment.

The juveniles of two more congeneric species were found exclusively on the host shells of *N. pulligera*, although far fewer cases were observed (figure 2*f*).

4. DISCUSSION

The juveniles of the amphidromous neritid *N. asperulata* attach to the shells of another amphidromous species *N. pulligera* and create circular etchings composed of two concentric levels in the tufa deposit of the host shell (figure 1). Territorial limpets on rocky shores form similar but larger 'home scars' on calcareous substrata by acidic mucopolysaccharides and/or carbonic anhydrase from the foot and mantle in months or years (Bromley & Heinberg 2006 and references therein). The time required by the hitchhiking juveniles to form the etchings is unknown, but it seems to be at least several days or even weeks. This prolonged period in the same position and their determinate growth (discussed subsequently) suggest that the function of the attaching behaviour is better explained as hitchhiking for the purpose of upstream migration rather than in terms of other benefits, for example grazing on microalgae that might be present on the host shell.

The adults of *N. asperulata* have been found exclusively in rapid streams (e.g. Haynes 2000), and their upstream migration seems to be obligatory. In fact, all individuals of this species hitchhike in rivers with long lower reaches through which they migrate to reproduce. They always have a clear flexion point of shell growth that visibly records the transition from an attached to a free-living mode of life (figure 2*d*,*e*). The shell size at the flexion point was, on average, the same as that of the hitchhiking juveniles, suggesting a determinate size in the hitchhiking period. To my knowledge, *N. asperulata* has always occurred together with *N. pulligera* in the same rivers and streams; this might possibly be a coincidence, because the former is a much rarer species than the latter.

The hitchhiking juveniles are found too far away from the sea if we assume that they grow and migrate (by themselves) as fast as other neritids do. Even if pelagic larvae settle at the uppermost part of the estuary, they still need to travel 4 km to Mataniko waterfalls while increasing their size by 3 mm from the larval shells of 0.4 mm (Kano 2006). However, no single juvenile of a comparable size was found at locations more than 2 km above the tide in population studies of two congeneric species without the hitchhiking behaviour (Schneider & Lyons 1993; Pyron & Covich 2003). Based on their reported growth rates of 0.030–0.035 mm d^{-1}, an estimate can be inferred that the hitchhiking juveniles at Mataniko spent 86–100 days travelling 4 km. Meanwhile, mark-recapture experiments
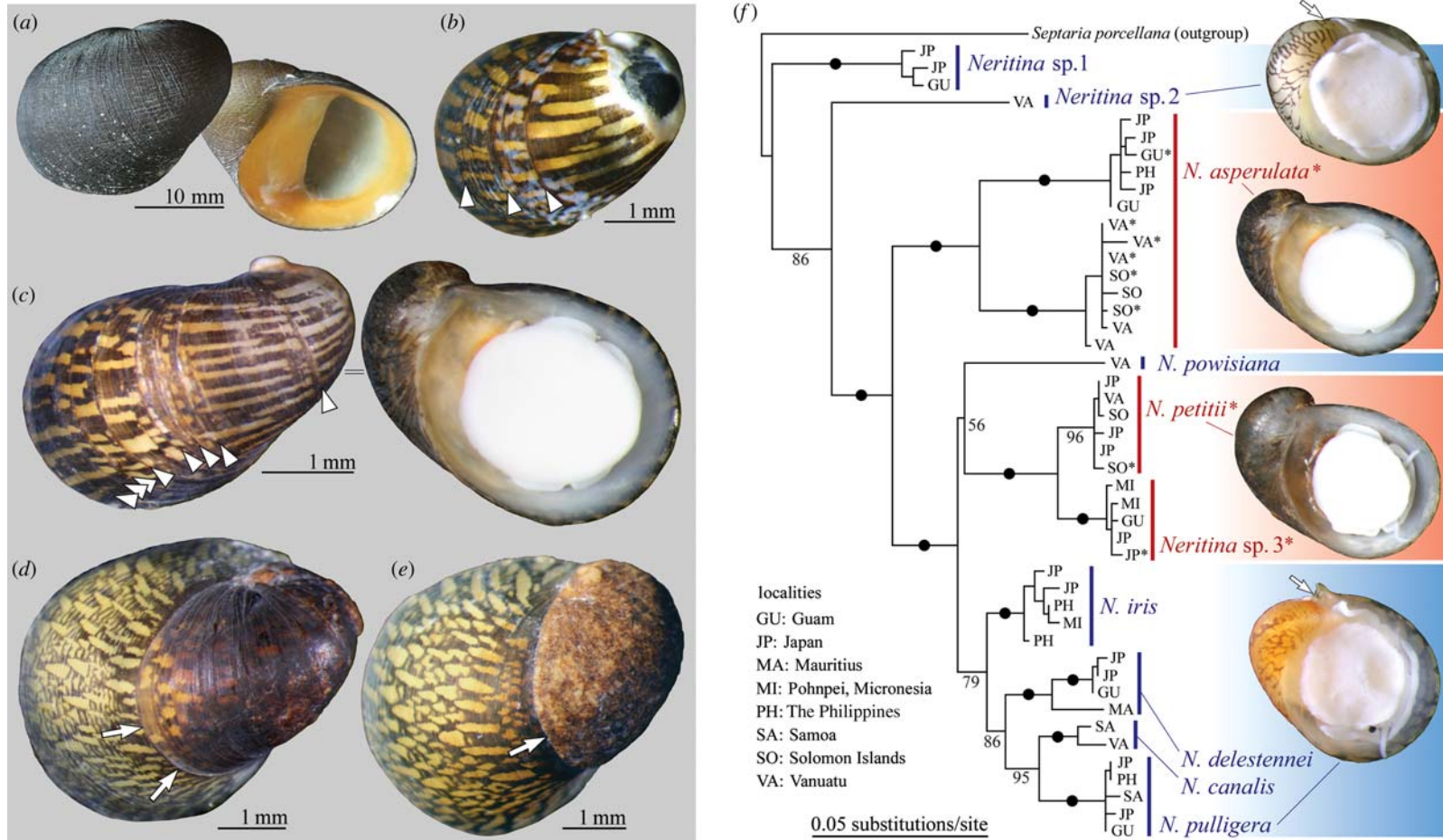
Figure 2. (a−e) Hitchhiking snail N. asperulata. (a) Adult shell from Santo. (b) Attached juvenile with an eroded apex and growth lines on shell (arrowheads). (c) Attached juvenile showing sole of foot and continuous rim of shell aperture. (d,e) Free-living juveniles from Mataniko waterfalls with a flexion point of shell growth (arrows), which records transition from attached mode of life. Note that shells are smooth after flexion point. Initial part in (e) is covered with a tufaceous deposit, suggesting determinate growth of hitchhiking juveniles. (f) Bayesian COI phylogeny of Indo-Pacific Neritina, with posterior probabilities shown below branches (dots: 100%). Asterisks indicate hitchhiking individuals/species. Genetic homogeneity among individuals from remote localities suggests amphidromy for hitchhiking species, as does their opercular nuclei (electronic supplementary material). Hitchhiking species (red) were recovered as non-monophyletic, while their juveniles share the same shell features for attached mode of life. Species in blue letters are free-living throughout life, with an uneven and interrupted apertural rim (arrows).

of *N. punctulata* revealed the greatest mean movement rate of 7.3 m d^{-1} in upstream migration (Pyron & Covich 2003), which translates to 548 days to travel a distance of 4 km. The distinct growth lines, thickened aperture and eroded apex in the attached shells (figure 2b,c), which are all very rare in the juvenile shells of other neritids, suggest their exceptionally slow and sporadic growth (Vermeij 1993), and hence their migration to the waterfalls at an ordinary speed on the host shells in a year or two. This delayed growth may be compensated by the long lifespan of amphidromous nerites (>20 years; Kano 2006).

The shell aperture of the hitchhiking juveniles is in one plane with a continuous rim and may have evolved for secure attachment. This clearly contrasts with the juvenile shells of non-attaching species of *Neritina*; their uneven and interrupted aperture prevents them from lying flat on a planar surface (figure 2f). The apparently determinate growth of the hitchhiking juveniles may also be adaptive, because if too large, the juveniles may risk dislodgement of themselves or the host. The hitchhiking behaviour and associated morphology, however, might have evolved independently in multiple clades of *Neritina*.

Larger nerites are more capable of creeping upstream through rapids than smaller ones (Schneider & Lyons 1993). The hitchhiking of *N. asperulata* therefore seems to be beneficial in shifting the cost of migration onto the larger congener, thereby increasing the success rate of migration. Another plausible benefit of the hitchhiking behaviour is protection from predators. Living on other shells is a known way of avoiding predators (Vermeij 1993) and may also contribute to successful migration of the juveniles. Potential predators of snails observed were fishes, crabs and prawns in the study rivers and streams.

Juveniles attaching to the shells of larger snails are commonly observed in migrating gastropods, including several other nerites (e.g. Schneider & Lyons 1993; Hau 2007). However, in such examples, the attaching behaviour does not seem to be obligate, and many more free-living juveniles of the same size class were found than these opportunists. Diverse groups of limpets attach to the shells of other molluscs for various reasons including parasitism, filter feeding, grazing, substratum requirement or protection from predators, but not for migration (Bromley & Heinberg 2006). Among other animal groups, hitchhiking travel has been suggested for a wide variety of parasites in birds, fishes and other migrating animals (Hellgren *et al.* 2007). However, none of the parasites is obliged to travel for the completion of its life cycle; rather, their travels are unintentional and not necessarily advantageous. The glochidial larvae of unionoid bivalves in streams may be the only example of some relevance. These obligate ectoparasites effectively avoid being swept away downstream and 'migrate against flow' by attaching to their fish hosts (Kat 1984). In conclusion, the present finding of obligatory hitchhiking to facilitate travel upstream by using another species that is migrating upstream suggests a novel and intricate example in animal evolution.

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