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# The ecology of shell shape difference in chirally dimorphic snails

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## Abstract

The Southeast-Asian tree snail subgenus *Amphidromus s. str.* (Gastropoda Pulmonata: Camaenidae) is unusual among all gastropods for its genetic antisymmetry: populations consist of stable mixtures of individuals with clockwise (dextral) and counterclockwise (sinistral) coiling directions. Although previous studies in *A. inversus* suggest that this genetic dimorphism is maintained by sexual selection, it cannot be ruled out that environmental factors also play a role. Adult shell shapes in *A. inversus* are known to show subtle differences between both coiling morphs, and it is known that in snails in general, shell shape is under environmental selection, thus creating the possibility that micro-niche use of both coiling morphs differs. In this paper, we first confirm that hatchlings also differ in shell shape. We then proceed with field studies to compare dextral and sinistral juveniles and adults for (i) direction and rate of dispersal within the vegetation and (ii) micro-niche occupation. However, we failed to detect any difference in both ecological traits. In addition to earlier data that show that there is no clustering of morphs in the field and that both morphs suffer identical predation pressure, these new data do not provide any evidence for a role for environmental factors in maintaining the coil dimorphism in this species.

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## Introduction

Despite their name, many animals classified with the Bilateria have secondarily evolved outwardly asymmetric body plans. The Mollusca are a good case in point. The Pleistomollusca (composed of the two most diverse classes, Gastropoda and Bivalvia; Kocot *et al*., 2011) have (at least as adults) highly asymmetric bodies, which may be partly permitted by the fact that they are (almost) sessile, and the need for balancing forces on both sides of the body axis is less than in animals that either move fast themselves or live in a fast-flowing medium. In gastropods, the asymmetry is visible most easily in the fact that the visceral mass, and the shell that envelops it, is helically coiled. As with all asymmetric three-dimensional shapes, snails are chiral. That is, they can potentially exist in two mirror image forms (or enantiomorphs): clockwise (dextral) coiling or anticlockwise (sinistral) coiling (Gittenberger, 1988; Palmer, 2004). However, almost all gastropod species are directionally asymmetric, *i.e*., the entire species consists either of dextral or of sinistral individuals (Schilthuizen and Davison, 2005). Only a small number of taxa are known to be composed of dextral and sinistral individuals mixed in similar proportions.

The best-known of such chirally dimorphic taxa is the subgenus *Amphidromus* Albers, 1850 (Camaenidae). Of its 36 known species, all of which are large-bodied tree snails from Southeast-Asia (Sutcharit and Panha, 2006a), at least 28 are composed of populations that consist of appreciable frequencies of dextral and sinistral individuals (Schilthuizen *et al*., 2005). For one widespread species, *A. inversus* (Müller, 1774), it was previously documented (Schilthuizen *et al*., 2007) that: (i) coiling direction, like in

other pulmonate gastropods, appears to be determined by a single factor with delayed maternal inheritance; (ii) unlike other gastropods (Asami *et al*., 1998), dextral and sinistral individuals do not experience interchiral mating difficulties; and (iii) sperm transfer in interchiral copulation may be more effective, given the chiral shapes of the spermatophore and the female spermatophore-receiving organ. Using computer simulation it was shown that, under such conditions, chiral dimorphism is likely to be stably maintained.

At the same time, however, evidence exists that shell shape in *Amphidromus* (like in, *e.g*., *Lymnaea* [Utsuno *et al*., 2011] and *Partula* [Davison *et al*., 2009]) shows slight differences depending on the coiling direction. In mixed populations, adults of one morph often have shells that are basally or medially squatter or narrower than the other morph, although which coiling direction is thus affected differs among species and sometimes also among populations (Schilthuizen and Haase, 2010; Nakadera *et al*., 2010). Since shell height : width proportions and aperture angle are strongly related to the geometry of a snail's micro-niche, in particular the inclination of the surface on which it lives (Goodfriend, 1986; Okajima and Chiba, 2009, 2011), it is not inconceivable that, in addition to sexual selection, environmental selection also plays a role in maintaining the coiling dimorphism. To elaborate on this: Rather than being genetically determined, ecological differences could be the by-product of shell shape differences which, in turn, are caused by the coiling direction. Coil polymorphism could thus allow the species to occupy two distinct micro-niches within the same habitat.

In previous papers, we already showed that dextrals and sinistrals in *A. martensi* and *A. inversus* are spatially mixed down to the level of individual trees (Schilthuizen *et al*., 2005; Craze *et al*., 2006). For the latter species, we also showed that predation pressure on both morphs is equally strong for those predators that crack the shell (Schilthuizen *et al*., 2007). However, it remained to be investigated whether the two coiling morphs may select distinct micro-niches. Also, in studies of dispersal (Schilthuizen *et al*., 2005) only inter-tree dispersal has been investigated over short (one week) and long (one year) time periods, but following individual snails within trees over durations of many weeks has not yet been done. (Similar studies in *e.g*., the polymorphic snail *Cepaea nemoralis* showed that different colour morphs have different migration tendencies (Wolda, 1963) and the same might apply to coiling morphs in *A. inversus*.). Finally, although shape differences among adult shells are well documented (Schilthuizen and Haase, 2010; Nakadera *et al*., 2010), juvenile *Amphidromus* snails have not yet been studied for shape differences.

In this paper, therefore, we attempt to fill these three gaps in our knowledge. We report on two field studies that aim to compare both coiling morphs in *A. inversus* for micro-ecological characteristics, and a biometric study on shape differences between dextral and sinistral hatchlings.

## Material and methods

### *Study species and population*

*Amphidromus inversus* (Müller, 1774) is a widespread, chirally dimorphic species, occurring throughout Southeast Asia. It has a whitish shell that is *c*. four cm

*Fig. 1*. A juvenile sinistral *Amphidromus inversus*, Pulau Kapas (Malaysia). Photo: Angela Schmitz-Ornés.

tall and two cm wide (Fig. 1). As in all Camaenidae, the shell peristome folds like a lip upon reaching sexual maturity. During surveys in 1989 and 1997, one of us (M.S.) found a dense population of this species in primary and secondary forest on the two-km-long island of Kapas, off the east coast of Peninsular Malaysia (approximately 103°16'E 5°12'N). The shell coloration in this population is quite monomorphic and somewhat lighter than in other populations of *A. inversus*, which has led Sutcharit & Panha (2006b) to describe it as a separate subspecies, a taxonomic decision which we shall not adopt. The dispersal and niche field studies reported on below were carried out in this population. The morphometric study was conducted with a laboratory culture derived from this population, and maintained in Leiden since 2007.

*Lab culture*

In the lab, snails were maintained at 27°C, 80% RH, 12h:12h light:dark in Plexiglas tanks of 20 cm high, 20 cm wide, and 40 cm long, with a 3 cm thick layer of coarse sand on the bottom and a few large chunks of decaying wood. Tanks were inhabited by roughly equal numbers of dextral and sinistral adults and large juveniles, up to a maximum of 35 individuals per tank. These were mixtures of animals that had been collected in Kapas in 2008 and 2010, and animals born in captivity. The snails were fed with twigs covered in algae. *Sepia* shells were always present as a source of calcium, and the cultures were sprayed with demineralised water several times per week. Once a week, each tank was cleaned, and fresh egg batches were placed in separate petri dishes where they were also given food and *Sepia* shell until they reached a size of at least 1.5 cm shell height. Hatchlings that died in the petri dish were cleaned and stored. The juvenile shells used for the morphometrics (see below) were randomly selected from among these stored shells.

*Geometric morphometrics in hatchlings*

A total of 183 dextral and 211 sinistral shells of hatchling snails (all of similar size, 1.75 - 2.5 whorls) were taken from the Leiden lab culture. These individuals, which had died immediately after hatching, were collected over a period of three years and preserved. For this study, all these shells were photographed and measured as described in Schilthuizen and Haase (2010). Briefly, the shells were placed in such a way that the line of view was perpendicular to both the columella and the horizontal axis of the apertural plane. Photographs of sinistral shells were mirrored in Adobe Photoshop. Images were transformed into a tps format using tpsUtil (Rohlf, 2004a) and landmarks were defined in tpsDig 2.0 (Rohlf, 2004b). Using auxiliary lines parallel and perpendicular to the columella, a set of landmarks was placed on the image, consisting of four points on the intersections of the auxiliary lines, four on the outer sides of the shell where it touches the auxiliary lines, two on both sides of the first whorl, one in the corner of the parietal and columellar wall and two more points on the outer and inner corner of the parietal and palatal wall (see Fig. 2). Analyses were performed with programs from the IMP suite of programs (http://www3.cansius.edu/~sheets/morphsoft.html). Procrustes superimpositions were generated in CoordGen6h. TwoGroup6h was used to compare coiling morphs pair-wise and graphical representations of differences between means as vectors of landmark displacement on thin-plate splines were generated. Data were analyzed using programs from the IMP suite as well. Goodall's F-tests were used to explore shape difference between chiral morphs.

*Field study on dispersal*

This study was carried out by one of us (S.L.) within three forest plots of 50 × 50 m each, between 18 May and 6 July, 2008. The areas are named S1 (5°13'03.15"N, 103°15'49.3"E), S2 (5°13'04.70"N, 103°16'02.00"E), and S3 (5°12'50.4"N, 103°15'52.55"E), with S1 and S3 located within the coastal vegetation of "site 2" of Schilthuizen *et al*. (2007). S2 was located in the interior of the island, in tall forest. Each was mapped for borders, logs and other landmarks, and snail-containing trees, vines, shrubs, and saplings. During the study period, each site was visited 12 times for durations of 150 min. each. Visits were spaced over time as evenly as possible, and alternated between the morning and the afternoon. During each visit, the plot was searched intensively, and each living snail found was given a unique pencil mark. Where possible, this was done without lifting the snail. In cases where it was unavoidable to pick up a snail, it was returned to the spot where it had been found. Age (juvenile / adult) and coiling direction were recorded, as well as the location where the animal was found (mapped plant, plant type/species, microhabitat, height above the ground). Upon recapture, distance to previous location was measured via the shortest available route, and converted to dispersal distance per day by dividing by the number of days since the previous record.

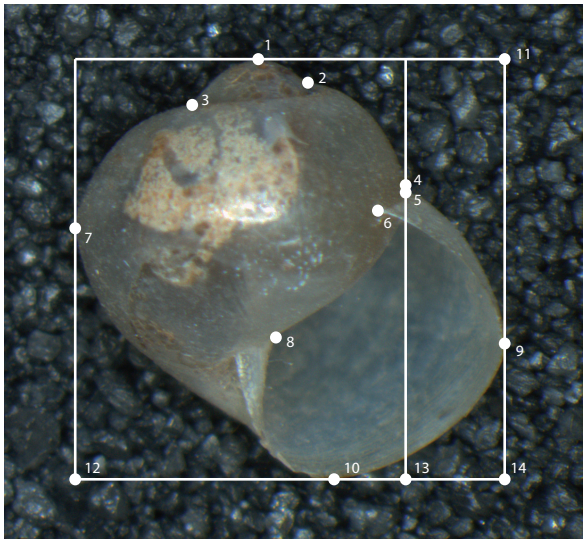


*Fig. 2*. Landmarks and reference points superimposed on an image of an *A. inversus* hatchling, as used in the geometric morphometric analysis.

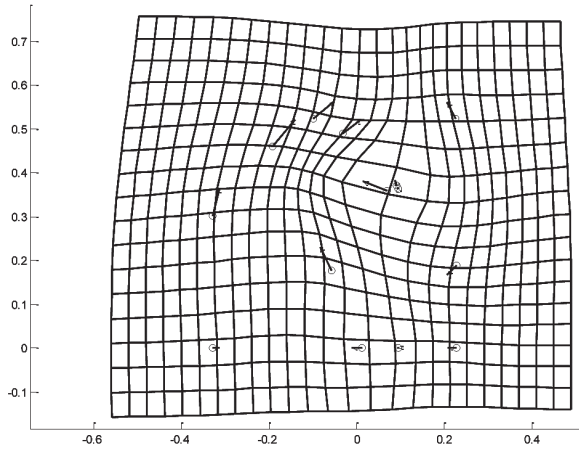


*Fig. 3*. Deformation grids with vectors indicating landmark transformations from the mean sinistral to the mean dextral shell (exaggeration five times).

*Field study on micro-niches*

This study was carried out by two of us (M.H. and M.S.) from 26 to 30 July, 2010, at Site 2 of Schilthuizen *et al*. (2007), a strip of coastal forest on flat sandy soil of approximately 150 × 30 m. We traversed the site, collecting 200 live, active individuals of all ages at random. Then, we collected a further 101 individuals, but focusing on dextrals and juveniles, so that our representation of ages and coiling morphs would be more even (since dextral is the rare of the two morphs here; Schilthuizen *et al*., 2005). For each collected individual, we recorded the following six micro-environmental parameters: HEI, height above the ground (upper values limited by the highest snails that we could reach from the ground). DIA, diameter of the branch or stem on which the snail was. ANG, angle of the branch or stem relative to vertical (ranging from 0° for horizontal to 90° for vertical). CIR, position on branch or stem circumference (ranging between 0°–lowest possible position and 180°–highest possible position). ROU, surface roughness (ranging from 0, smooth to 5, rough). POS, the angle of the snail's columella relative to the longitudinal axis of the stem or branch. In some cases, snails were found in positions that rendered one or more of these parameters irrelevant. For example, if ANG was 90°, CIR could not be determined, and for snails on leaves (which yielded PLD, proportion of leaf dwellers), only HEI and ROU could be determined. ANG and CIR were combined into an additional parameter, PLA, the angle of the plane on which the snail was sitting, relative to vertical, as: PLA = ANG + ((90 - ANG) × *sin* (CIR)).

## Results

*Geometric morphometrics in hatchlings*

In our analysis with the Twogrouph6h software, significant shape differences were revealed, as confirmed by Goodall's *F*-test ($P < 0.001$; F = 20.35; df = 24; distance between means = 0.0263). The deformation grid (Fig. 3) shows that the shape differences between dextral and sinistral hatchlings particularly involve landmarks 6, 8, and 9 (see Fig. 2 for the positions of these landmarks).

*Field study on dispersal*

In sites S1, S2, and S3, we found 280, 73, and 262 live snails, respectively (D:S proportions were 108:171, 42:31 and 84:178, respectively). Accumulation curves over all 13 visits showed levelling off only at S1, for which the total population size could be estimated at *c*. 175 individuals; accumulation curves at S2 and S3 increased linearly and were incompletely sampled. Despite the large number of marked live individuals, 495 of these 615 snails (81%) were seen only once and not

encountered again. Consequently, our dispersal data are based on the 142 movements recorded for the 120 snails seen more than once. Table 1 shows the mean dispersal distances per day, combined for all three sites, and separated by age and chiral morph. Distance moved per day was 25.3 ±27.1 cm (mean ± SD). There were no significant differences (Kruskal-Wallis test: all *P*-values > 0.05) in dispersal rate between dextrals and sinistrals, either pooled or separated into juveniles and adults (Fig. 4).

*Field study on micro-niches*

Our sampling yielded 146 (81 adults, 65 juveniles) dextral and 155 (67 adults, 88 juveniles) sinistral individuals. Table 2 shows the values for the environmental parameters for all four groups. None of the variables were different between dextrals and sinistrals.

## Discussion

The connection between land snail shell shape and niche preferences is established for several shape traits (see Introduction). The shape differences we previously recorded (Schilthuizen and Haase, 2010) for dextral and sinistral *Amphidromus inversus*, however, are very subtle (which is expected since they share a single gene-pool), and it was uncertain whether these would be associated with measureable differences in niche-use between the two chiral morphs in the field.

We first conducted a conchometric study to investigate whether shape differences are also present in juveniles. This was confirmed: as Fig. 3 shows, sinistral hatchlings had a slightly wider parietal side of the aperture compared with dextral ones. This corresponds with a similar shape difference found in adults (Schilthuizen and Haase, 2010). In addition, the vectors on the deformation grid appear to show that the hatchlings also have a slightly taller body whorl. However, since all these vectors are perpendicular to the centre of the shell, these results may be explained by a systematic error in the positioning of dextral and sinistral shells by the experimenter (such experimenter bias has been shown before; see Schilthuizen and Haase, 2010). It is less likely that the apertural shape change is caused by experimenter bias because the vectors leading away from the apertural landmarks have directions that are different from each other and from those of the body whorl landmarks. Another reason to view these hatchling results with some caution is that they were derived from a laboratory colony. Thus, the hatchling shell shapes may not reflect those found under natural conditions. Moreover, as the lab colony has a mixed genetic background, the shape differences are likely to be different from those found in the field, since population-level disparity is known to exist in the response of shell shape to coiling direction (Schilthuizen and Haase, 2010; Nakadera *et al*., 2010). Nevertheless, the new data do suggest that the conchological ontogenies of dextral and sinistral individuals are not exact mirror images of one another.

These differences in shell shape, however, do not appear to translate to ecological differences that can be measured with the techniques we have used so far. Previously (Schilthuizen *et al*., 2007), we already showed that predation (presumably by rats) was identical in both morphs, and (Schilthuizen *et al*., 2005) that both morphs occur randomly mixed at the level of individual trees. Here, we investigated whether ecological differences exist at a smaller spatial scale. Firstly, we were unable to detect any differences between morphs in individual migration behaviour. Distance moved per day amounted to an average of 0.3 m for both morphs, although the frequency distribution was highly skewed, with a small number of individuals migrating longer distances, of up to 1.2 m. This pattern of dispersal is similar to those found in other land snails (*e.g*., Schilthuizen and Lombaerts, 1994; Kleewein, 1999; Giokas and Mylonas, 2004), and also corresponds with larger-scale studies of the *A. inversus* population structure (Schilthuizen *et al*., 2005). We also did not detect any micro-environmental differences in the places on a tree where individuals of both morphs were present: dextral and sinistral individuals did not differ for the various parameters we measured.

The data presented here do not rule out the possibility that sinistrals and dextrals differ in their response to other, yet uncharted, aspects of the environment. For example, our micro-environmental investigations were limited to the lower 2.5 m of the vegetation. Since these tree snails use the entire vertical range of the vegetation (including the canopy) as their habitat, differences may only be apparent at higher strata (as is the case in, *e.g*., certain colour morphs of *Cepaea nemoralis*; Wolda, 1963). Also, we have not yet investigated any preference in the morphs for particular tree species. However, given that dextrals and sinistrals occur as mixed populations in each individual tree (Schilthuizen *et al*., 2005), this is rather unlikely.

In conclusion, although differences in the ecology of dextrals versus sinistrals may exist in yet unstudied

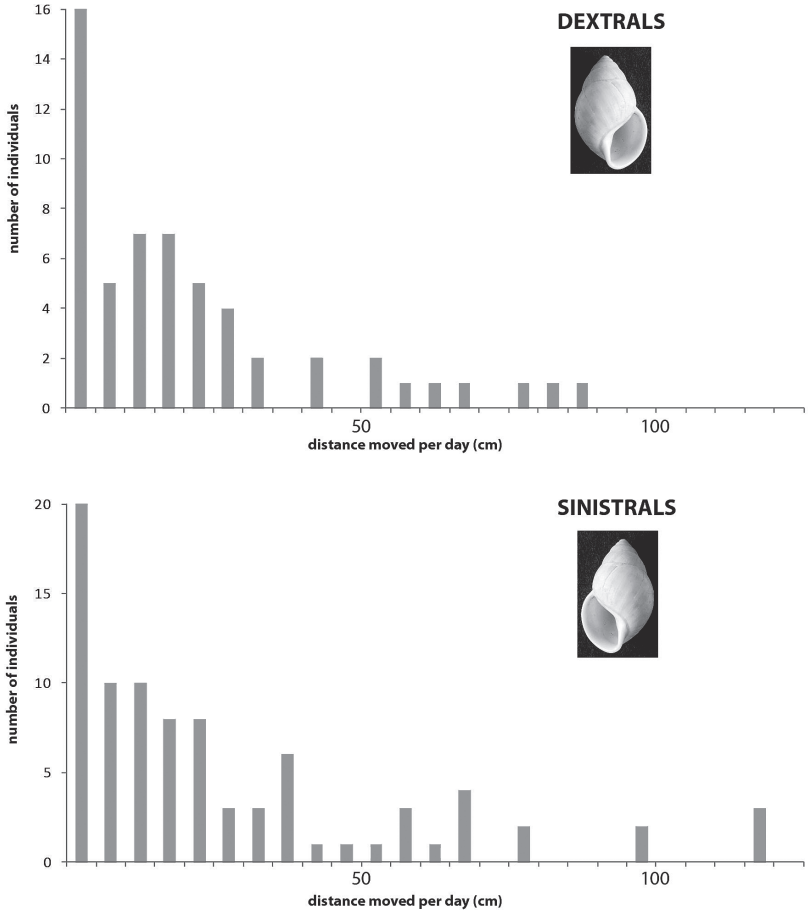


*Fig. 4*. Daily dispersal distances for 142 movements by dextral (top) and sinistral (bottom) snails, combined for all three study sites.

*Table 1*. Daily dispersal distances in the field for dextral and sinistral, marked individuals, separated into juveniles and adults (bottom) and pooled (top).

| | |
|---|---|
| dextral (total) | sinistral (total) |
| 21.7 ±22.7 cm (mean ±SD; n=56) | 27.7 ±29.5 cm (mean ±SD; n=86) |
| dextral (ad.) | dextral (juv.) |
| 17.6 ±19.3 cm (mean ±SD; n=18) | 26.7 cm (±29.9; n=62) |
| sinistral (ad.) | sinistral (juv.) |
| 23.6 ±24.2 cm (mean ±SD; n=38) | 30.3 ±28.9 cm (mean ±SD; n=24) |

*Table 2*. Values (mean ± SD) for dextrals and sinistrals, for each of the environmental parameters (see text for explanations of the abbreviations).

| | dextral (ad.) | dextral (juv.) | sinistral (ad.) | sinistral (juv.) |
|---|---|---|---|---|
| HEI | 196 cm (±96; n=81) | 201 cm (±85; n=65) | 174 cm (±68; n=67) | 170 cm (±65; n=88) |
| ANG | 59° (±27; n=74) | 51° (±29; n=54) | 65° (±21; n=66) | 64° (±23; n=80) |
| CIR | 55° (±52; n=66) | 30° (±39; n=53) | 53° (±47; n=62) | 53° (±54; n=72) |
| ROU | 1.3 (±1.2; n=81) | 1.5 (±1.6; n=65) | 1.3 (±1.1; n=67) | 1.7 (±1.5; n=88) |
| DIA | 20 cm (±35; n=74) | 12 cm (±9; n=54) | 17 cm (±9; n=66) | 20 cm (±34; n=80) |
| POS | 28° (±23; n=74) | 39° (±24; n=54) | 28° (±23; n=66) | 31° (±23; n=80) |
| PLA | 73° (±22; n=74) | 64° (±25; n=54) | 77° (±18; n=66) | 76° (±17; n=80) |
| PLD | 0.09 | 0.17 | 0.01 | 0.09 |

aspects of the environment, the results presented here make it increasingly unlikely that chiral dimorphism in *Amphidromus inversus* is maintained by environmental selection, implicating sexual selection (Schilthuizen *et al*., 2007) as the major factor.

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