Predation by *Gecarcoidea lalandii* (Crustacea, Gecarcinidae) on dextral and sinistral *Amphidromus inversus* (Gastropoda, Pulmonata, Camaenidae)

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ABSTRACT

The tropical tree snails of the subgenus *Amphidromus* s.str. receive much attention from researchers because populations consist of roughly equal proportions of dextral and sinistral individuals. Studies indicate that this stable genetic antisymmetry is maintained because of disassortative mating. Deviations of the theoretically expected 50:50 proportion have, however, been frequently reported. An explanation for this deviation could be modulation by chirally biased predation. On the island of Kapas, Malaysia, seventeen individuals of *Gecarcoidea lalandii*, a nocturnal terrestrial crab, were caught and housed with live *Amphidromus inversus*. A low level of predation by the crab on the snails was found. However, there is no reason to assume that predation by *G. lalandii* is chirally biased.

INTRODUCTION

Gastropods are well known for their coiled body form. Their shell and body are asymmetric and twist clockwise (dextral) or anticlockwise (sinistral) when viewed from the shell apex. Both forms (dextral and sinistral) are each other's mirror image (Fig. 1). Over 90% of snail taxa are dextral, and in most species, reverse-coiled mutants are usually exceedingly rare (Palmer, 2004; Gittenberger et al., 2012). In terrestrial snails, these rare mirror-image mutants will normally experience positive frequency-dependent selection, because a dextral individual and a sinistral individual are normally unable to mate with each other (Asami et al., 1998; Schilthuizen & Davison, 2005).

Sometimes, however, a sinistral population may become established within the range of a dextral species due to random genetic drift. Observations in the field and also computer simulations confirm this (Van Batenburg & Gittenberger, 1996; Stone & Björklund, 2002). However, until recently, cases of persistent chiral dimorphism in natural populations remained unexplained. Understanding such exceptions can have important implications for the study of evolution, genetics and development (Gigord et al., 2001; Seehausen & van Alphen, 1998).

The South-East Asian tree snail subgenus *Amphidromus* s.str. is such a dimorphic exception (Palmer, 1996; Schilthuizen & Davison, 2005; Schilthuizen et al., 2005; Sutcharit et al., 2006). For the past 10 years, this subgenus has been intensively studied with the aim of understanding how chiral dimorphisms in this group are maintained. Observations on several of these species suggest that dextral and sinistral individuals usually occur in roughly equal proportions within local populations (Solem, 1983; Craze et al., 2006; Sutcharit et al., 2006; Sutcharit & Panha, 2006). Eventually, Schilthuizen and co-workers showed that a snail's tendency to mate with the opposite coiling morph is likely to have arisen as a result of the concomitant increase in fecundity (Schilthuizen et al., 2007), and that this type of sexual selection maintains dimorphism.

Fig. 1. A sinistral (left) and a dextral (right) *Amphidromus inversus* (O.F. Müller, 1774) from Pulau Kapas, Malaysia (shell height ca. 40 mm). Colln. Universiti Malaysia Sabah. Figure derived from Schilthuizen et al. (2014).

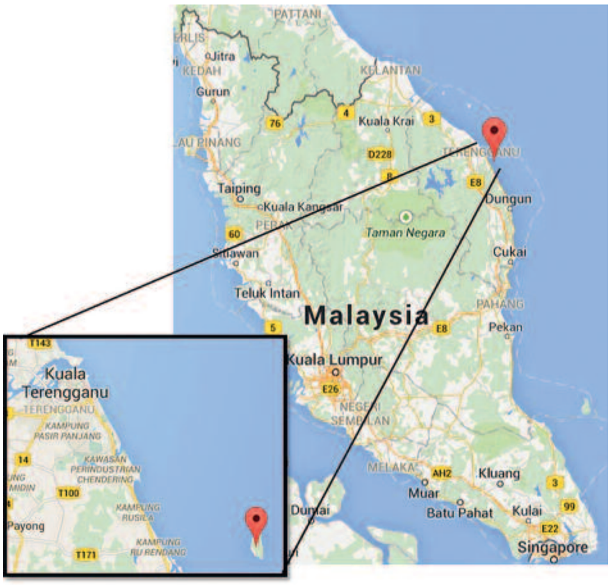

Fig. 2. The location of the island of Kapas, Malaysia.

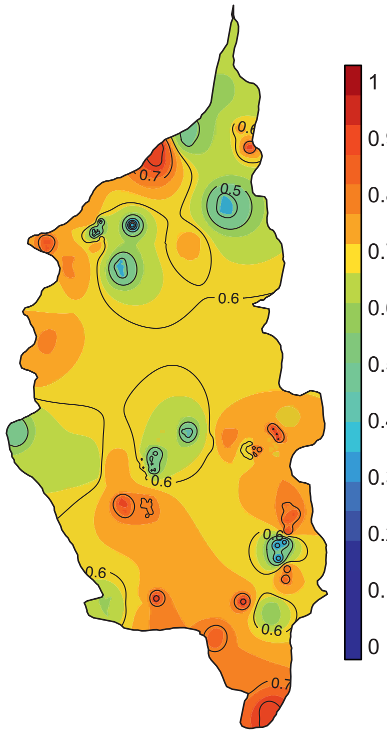

Fig. 3. Map showing the weighted distribution of proportion of sinistrals of *Amphidromus inversus* on Pulau Kapas. Figure derived from Schilthuizen et al. (2014).

Deviations from 50:50 proportions in *Amphidromus* species have often been reported by different researchers (Schilthuizen et al., 2005, 2007, 2014; Craze et al., 2006; Sutcharit et al., 2006). Craze (2009) showed that such deviations may be the result of enhanced drift of the recessive allele in isolated subpopulations. Schilthuizen et al. (2014) attempted to test this in *Amphidromus inversus* (O.F. Müller, 1774). On the island of Kapas (Malaysia, Terengganu; Fig. 2), the proportions of sinistrals vs. dextrals in this species is roughly 65% vs. 35%. Schilthuizen et al. (2014) mapped the microgeographic variation in chiral proportions on Kapas (Fig. 3). Expecting, under the hypothesis of Craze (2009), that the deviations from equal proportions would be stronger in areas with more fragmented vegetation, they also mapped vegetation parameters and snail population density. Furthermore, they looked at predation rates. The results of this study did not support the hypothesis that deviation from 50:50 proportions is due to genetic drift. However, they did find a weak negative correlation between the proportion of sinistrals and relative predation on dextrals.

In this study, I will further investigate predation on *A. inversus* on the island of Kapas. Sutcharit et al. (2006) also proposed that this is a subject that needs to be investigated further. Two predators are currently known or suspected: rodents (who break off top whorls of their prey) and crustaceans (who peel off whorl walls) (Schilthuizen et al., 2007, 2014). Earlier research has been done on predation by rats on *Amphidromus*, and this work showed that rodent predation is not frequency-dependent (Craze et al., 2006; Schilthuizen et al., 2007). Predation by crabs, however, has not yet been studied in detail.

Carnivorous crabs are known to eat snails (Magalhaes, 1948; Dietl, 2003), and circumstantial evidence that on Pulau Kapas *Amphidromus* is being eaten by crabs is available, as broken shells were found scattered around *Ocypode* crab burrows (Fig. 4). However, preliminary work (data not shown) revealed that it is not *Ocypode*, but *Gecarcoidea lalandii* H. Milne Edwards, 1837 is the culprit in this case.

Gecarcoidea lalandii is a fully terrestrial crab and is active at night outside of its burrow. The habitat of this crab and that of *Amphidromus inversus* overlap and it is known that the sister species *G. natalis* (Pocock, 1888), preys on *Achatina fulica* (Férussac, 1821), an invasive land snail (Lake & O'Dowd, 1991). *Gecarcoidea lalandii* have asymmetrical chelae which could work in their advantage when opening snails. This has already been studied in other asymmetrical crabs: *Eriphia smithii* MacLeay, 1838, *Calappa philargius* (Linnaeus, 1758), *Lydia annulipes* (H. Milne Edwards, 1834), *Epixanthus dentatus* (White, 1848), *E. frontalis* (H. Milne Edwards, 1834), *Thalamita spinimana* Dana, 1852, *Charybdis feriata* (Linnaeus, 1758), and *Portunus sanguinolentus* (Herbst, 1783) which have an advantage when opening a dextral snail shell because they have the larger crushing claw on the right side of their body (Ng & Tan, 1985; Shigemiya, 2003). In this study, therefore, I aimed to investigate whether claw asymmetry in *G. lalandii* might also bias predation of dextral vs. sinistral prey.

Fig. 4. Empty shells of *Amphidromus inversus* with possible crab predation marks near an entrance of an *Ocypode* crab burrow. Photo M. Schilthuizen.

Fig. 5. Shells of *Amphidromus inversus* offered to one *Gecarcoidea lalandii* crab. Three shells (on left) are not damaged and three other shells are broken in three different ways by one *G. lalandii* individual.

METHODS

Fieldwork on Kapas

The fieldwork on the island of Kapas took place from February 11th 2015 till April 8th 2015. The coast line on the west side of the island is divided into different sandy beaches, separated by rocky outcrops. Each beach was considered separately.

Observations on *Amphidromus inversus*

A narrow strip of forest adjacent to the coast line of the island of Kapas was thoroughly searched for *A. inversus* shells. For every shell found on the ground, a picture was taken, chiral morph was noted, and damage (if any) was described. This was conducted during the day between 09:30 a.m. and 12:00 noon and between 04:00 p.m. and 06:00 p.m. A Pearson's Chi-squared test with Yates' continuity correction was used to check for a significant difference between predation rates on dextral and sinistral *A. inversus*. Difference in proportions of S/D shells and expected S/D (65%/35%) shells was also calculated with a Chi-squared test.

Experiment *Gecarcoidea lalandii*

On two locations on the island of Kapas, on different days, 17 individuals of *G. lalandii* were caught using a net. Each individual was placed into a storage box (AppleLady, 50 × 41 × 30 cm l × b × d), for five nights. In the storage box were stones, wood and leaf litter to match their natural environment, three sinistral and three dextral live *A. inversus* individuals, matched for size. During the five nights, the *G. lalandii* crabs were given no other food. The boxes were opened at 10.00 a.m., 04.00 p.m., and 10.00 p.m. to refresh the air. The experiment started on March 15th (crab nrs. 2 and 3), March 18th (crab nr. 4), March 22th (crab nrs. 5 and 6), March 23th (crab nrs. 7 and 8), March 24th (crab nr. 9), March 27th (crab nr. 10), March 30th (crab nrs. 11 and 12), April 1st (crab nrs. 13, 14, and 15), April 2nd (crab nr. 16), and April 3th (crab nrs. 17 and 18). Crab nr. 1 was not used. After an experiment was stopped the crab was given a purple drop of nail polish on its carapace and was released on the site where is had been caught. The number of eaten snails and the damage to the shell (if any) were recorded.

RESULTS

Amphidromus inversus

There was no difference in predation rate between sinistrals (37 damaged shells versus 88 undamaged shells) and dextrals (17 damaged shells versus 35 undamaged shells); N = 178 (chi-squared = 0.15886, df = 1, p-value = 0.6902). In total, 125 sinistral individuals and 53 dextral individuals were found. These numbers do not differ from the expected 65% vs. 35% proportions (N = 178, chi-squared = 2.135, df = 1, p-value = 0.1440).

Gecarcoidea lalandii

Nine crabs were clearly left handed, two individuals were right handed, and six individuals showed no discernibly larger cheliped on one side. These assessments were done visually, because the crabs were too scared of aggressive to measure with measuring tape or calliper.

Four male individuals of *G. lalandii* damaged one or more *Amphidromus* shells and ate the occupants. In total, five dextral shells and two sinistral shells were broken. The shells had been opened in different ways (Fig. 5). The top whorl may be broken off, the side of the shell may be peeled off, or the whole shell may be crushed into pieces.

DISCUSSION

Gecarcoidea lalandii does indeed prey on *A. inversus*. Four different male crabs were found to break one or more shells of *A. inversus* and eat the occupants in an experimental setting. It seems that *A. inversus* is not a preferred prey item, since the majority of the subjects did not prey on the snails. The observation that only male crabs broke *A. inversus* shells does raise some questions. Is this a relevant difference? Are males more aggressive and/or resourceful when hungry? Further research with a larger dataset needs to be done to answer these questions.

Amphidromus shells were broken in different ways by *G. lalandii*. Schilthuizen et al. (2014), made the wrong assumption when stating that crabs break open a snail only by peeling of the aperture. The results of my research are, however, in line with Zipser & Vermeij (1978), who showed that "… *Carpilius maculatus* (L.), *C. convexus* (Forskål), and *Eriphia sebana* (Shaw & Nodder), and the parthenopid *Daldorfia horrida* (L.), typically sever the spire of their prey, or make a gash in the body whorl. They tend to employ sustained pressure on the prey shell and, except for *Eriphia*, rarely attack the outer lip...". Their paper described research on marine crabs, and the result of a land crab opening a shell in a similar manner is a new addition to the knowledge of crab-snail interactions.

Along the coast of Kapas, there is no difference in predation rate on dextral versus sinistral *A. inversus*. With the current knowledge that *G. lalandii* could open an *A. inversus* in different ways, it is impossible to distinguish between predation marks of rats and crabs. However, overall, it appears not likely that predation by rodents and crustaceans combined is chirally biased (Craze et al., 2006; Schilthuizen et al., 2007; this study).

It can be concluded that *G. lalandii* is a predator of *A. inversus*, but it is most likely that rats are still the most important predator. At this point, there is no reason to assume that *G. lalandii* has an influence on the chiral proportions of *A. inversus.*

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