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Right-handed snakes: convergent evolution of asymmetry for functional specialization

Masaki Hoso[1,*], Takahiro Asami[2,3] and Michio Hori[1]

[1]*Graduate School of Science, Kyoto University, Kyoto 606-8502, Japan*
[2]*Department of Biology, Shinshu University, Matsumoto 390-8621, Japan*
[3]*PRESTO, Japan Science and Technology Agency, Kawaguchi 332-0012, Japan*
**Author for correspondence* (*hoso@terra.zool.kyoto-u.ac.jp*).

External asymmetry found in diverse animals bears critical functions to fulfil ecological requirements. Some snail-eating arthropods exhibit directional asymmetry in their feeding apparatus for foraging efficiency because dextral (clockwise) species are overwhelmingly predominant in snails. Here, we show convergence of directional asymmetry in the dentition of snail-eating vertebrates. We found that snakes in the subfamily Pareatinae, except for non-snail-eating specialists, have more teeth on the right mandible than the left. In feeding experiments, a snail-eating specialist *Pareas iwasakii* completed extracting a dextral soft body faster with fewer mandible retractions than a sinistral body. The snakes failed in holding and dropped sinistral snails more often owing to behavioural asymmetry when striking. Our results demonstrate that symmetry break in dentition is a key innovation that has opened a unique ecological niche for snake predators.

Keywords: handedness; laterality; parallel evolution; molluscivore; land snails

1. INTRODUCTION

Bilateral symmetry is a pervasive feature in external body plans of free-living animals. Thus, derived asymmetry found in external organs implies some functional advantages. For example, marked asymmetry in feeding apparatus plays critical roles for foraging success and/or efficiency in some predators (Hori 1993; Benkman 1996; Shigemiya 2003).

Several snail-eating specialists exhibit asymmetry in their feeding apparatus in the same direction within species (Shoup 1968; Snyder & Snyder 1969; Ng & Tan 1985; Inoda *et al.* 2003). Because snail species are predominantly dextral (clockwise) regardless of habitat (Vermeij 1975), foraging specialization in dextral snails would be selectively advantageous for snail-eating specialists. However, directional asymmetry of the snail-feeding apparatus has only been documented in aquatic arthropods. Here, we show an example of convergent directional asymmetry in dentition of terrestrial snail-eating vertebrates.

Southeast Asian snakes in the subfamily Pareatinae are considered to be dietary specialists, mostly preying on terrestrial snails and slugs (Cundall & Greene 2000). Due to the mechanical lack of effective biting force, snakes cannot crush the hard shell of prey. Instead, they extract the snail soft body from the shell by alternately retracting the left and the right mandibles (Cundall & Greene 2000; Gotz 2002; figure 1*a* and video A of electronic supplementary material). Because snails are asymmetric in whole-body structure, the snake predators may improve the efficiency of soft-body extraction by differential action of the left and the right mandibles. Thus, we expected an adaptation with respect to morphological differentiation between the two mandibles of the snakes for the predation of dextral snails.

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2. MATERIAL AND METHODS

(a) *Measurements*

Using soft X-ray photography, we counted the tooth numbers in the left and the right mandibles of 297 preserved specimens of pareatine snakes (table 1 in electronic supplementary material). To quantify the degree of asymmetry in mandibular dentition, we employed an asymmetry index, calculated for each specimen as $(R-L)\times 100/(R+L)$, where R and L are the tooth numbers on the right and the left mandibles, respectively.

(b) *Experiments*

For prey snails, we used dextral and sinistral strains of *Bradybaena similaris* (both 11–16 mm shell diameter). For predator snakes, we used four snakes of *Pareas iwasakii*, which is a snail-eating specialist (Hoso & Hori 2006; three were from Ishigaki Island and one from Iriomote Island in the Ryukyu Archipelago, Japan; snout–vent length: 400–580 mm; head width: 7.6–8.9 mm). The relatively limited sample size of snakes was due to difficulty in collecting *P. iwasakii*, which is rare and endangered (Ota 2000).

We conducted feeding experiments between November 2004 and January 2006. We recorded predation behaviour using an infrared digital video camera (SONY DCR-PC300). In each observation, we placed a snake behind a snail on a horizontal wooden bar (600 mm length, 15 mm width, 3 mm thickness) 300 mm above the bottom of the cage (600×300×360 mm) in a dim room kept at 25°C, simulating natural foraging conditions for an arboreal, nocturnal snake (Sengoku 1996). Each snake attempted predation on 10–18 sinistrals and 8–15 dextrals of *B. similaris* (65 and 47 trials in total on sinistrals and dextrals, respectively). In every trial, the snake successfully grabbed the snail with its jaws regardless of snail handedness. Successful predation was defined as completion of swallowing the soft body. A snail's successful escape from predation was defined as survival for at least one week after a predation attempt. To examine the efficiency of extracting the soft body after striking success, we measured the handling time and the number of mandible movements, both of which indicate feeding performance in snakes (Pough & Groves 1983), from the moment of orientating the upper jaw on the outer surface of the shell to the moment of dropping the empty shell. We counted a sequence of single alternate retractions of the left and right mandibles as one mandible retraction. Each snake was kept from prey for at least for 5 h before each trial.

(c) *Statistical analyses*

We used JMP (SAS Institute Inc., release 6.02, 2005) for statistical analyses. The effects of coiling direction and shell diameter on predation success, handling time and the number of mandibular retractions were tested using general linear mixed models (GLMMs), which allow both fixed and random terms to be fitted to the models, with random terms controlling for repeated measures within snake individuals. JMP uses the restricted maximum-likelihood model (RMLM) to decompose the variances and to derive parameter estimates. The models were adequately fit ($R^2=0.2$ for predation success, $R^2=0.47$ for handling time and $R^2=0.31$ for the number of mandibular movements). The effects of shell diameter were not significant ($p=0.264$ for predation success, $p=0.113$ for handling time and $p=0.173$ for the number of mandibular movements).

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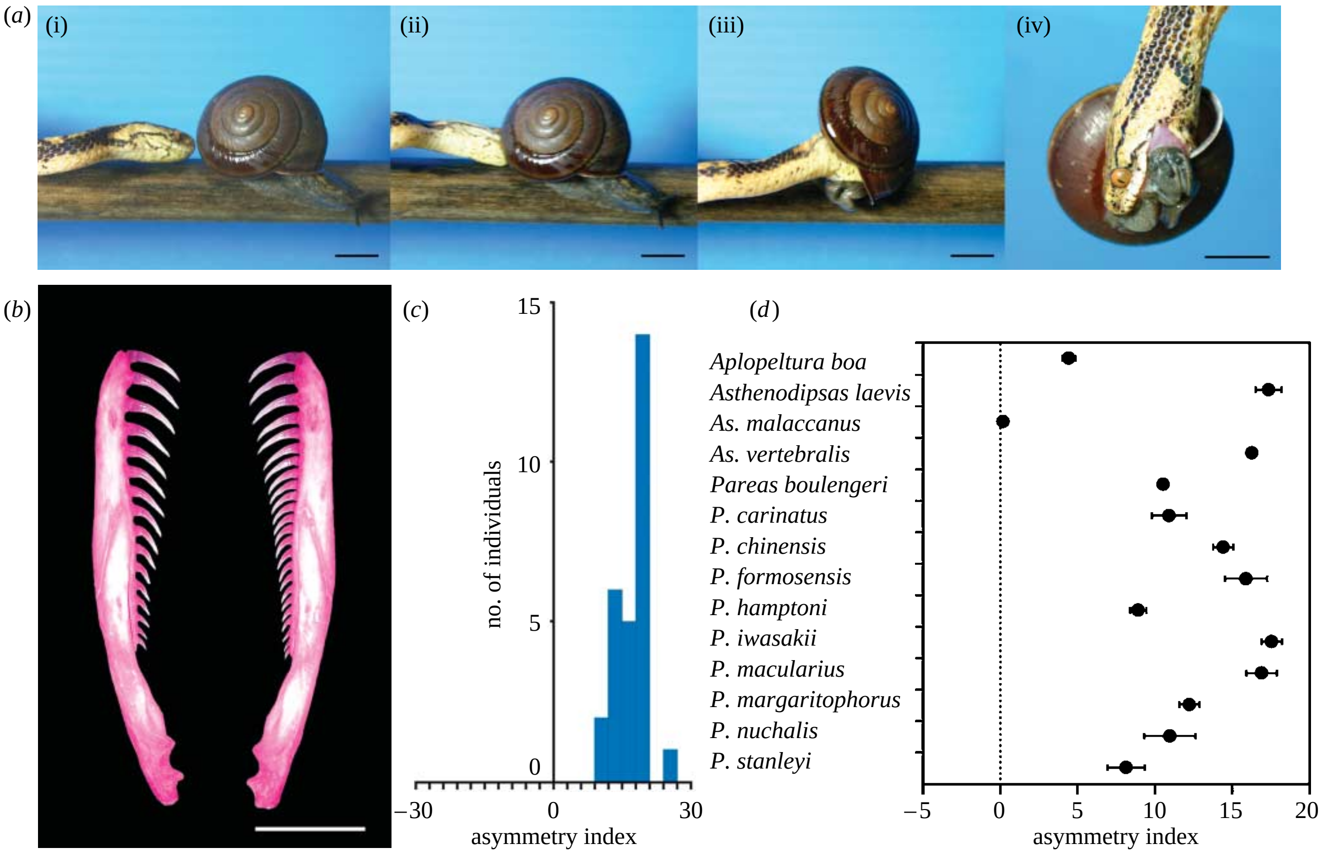

Figure 1. Feeding behaviour and morphology of dentition asymmetry of pareatine snakes. (*a*) The foraging sequence of *Pareas iwasakii* on a dextral snail (i)-(iv). *Pareas iwasakii* approaches a snail from behind following the snail's mucus track. The snake tilts the head leftward (i), grabs the basal foot near the aperture (ii) and (iii) and swallows by pulling the snail body out of the shell with alternate retraction of left and right mandibles (iv). Scale bars, 10 mm. (*b*) Lateral view of the left and the right mandibles of *P. iwasakii*, left and right in the figure, respectively. This specimen (KUZ 28134) shows 16 left teeth and 24 right teeth, stained with alizarin red. Scale bar, 5 mm. (*c*) Distribution of asymmetry index of tooth number in 28 individuals of *P. iwasakii*. (*d*) Variation in the asymmetry index of mandibular tooth count in 14 pareatine species (means ± s.e.). *Aplopeltura boa* reportedly feeds on small lizards in addition to molluscs and *Asthenodipsas malaccanus* exclusively feeds on slugs (Stuebing & Inger 1999). The broken line indicates symmetry.

3. RESULTS AND DISCUSSION

We found marked directional asymmetry in mandibular tooth number (left: 17.5 ± 1.1, right: 24.9 ± 1.1, $n=28$; figure 1*b*,*c*) of a snail-eating specialist *P. iwasakii*. This was established before hatching (left: 18, right: 26, $n=1$) and showed no correlation with snout–vent length (Kendall's $\tau=0.154$, $p=0.306$, $n=24$). Thus, dentition asymmetry does not change through the ageing processes. The mandibles were clearly asymmetric in 12 out of 14 pareatine species examined (figure 1*d*). However, the two species which are known to be non-snail-eating specialists (Stuebing & Inger 1999) showed symmetry. Thus, the dentition asymmetry probably reflects dietary specialization on snails.

To determine whether the dentition asymmetry of *P. iwasakii* has been adapted specifically for the predation of dextral snails, we conducted feeding experiments using the dextral wild-type and sinistral variant of a land snail *B. similaris*. We found that the sinistral morph required significantly longer handling time than the dextral (four wild-captured snakes; REML GLMM, $F_{1,84.4}=41.3$, $p<0.0001$; figure 2*a*) and more mandible retractions to complete soft-body extraction ($F_{1,68.8}=34.0$, $p<0.0001$; figure 2*b*). The dentition asymmetry should, therefore, be an adaptation for improved performance in the extraction of the dextral soft body.

Pareas iwasakii failed in the predation of sinistral snails more frequently than in the predation of dextrals ($F=1$, $p=0.0006$). The snakes showed obvious difficulties in holding sinistral prey because the upper jaws barely reached the outer shell surface on which the jaws need to anchor (video B of electronic supplementary material). This is the physically natural outcome of behavioural asymmetry when striking (figure 1*a*). They did not adjust striking behaviour for sinistral prey or recognize the direction of asymmetry of prey.

According to the phylogeny of the three pareatine genera (Rao & Yang 1992), the dentition asymmetry is ancestral and the symmetry of slug eaters is secondarily derived. The symmetry break of snake dentition may have been a key innovation that initiated the adaptive radiation of pareatine snakes throughout Southeast Asia as dextral-snail eaters. Solid reconstruction of pareatine phylogeny is, however, necessary to validate this example against the general derivation of asymmetry from symmetry in animals (Palmer 1996, 2004).

In addition, our experiments demonstrate a defensive function of sinistrality for snails against snake

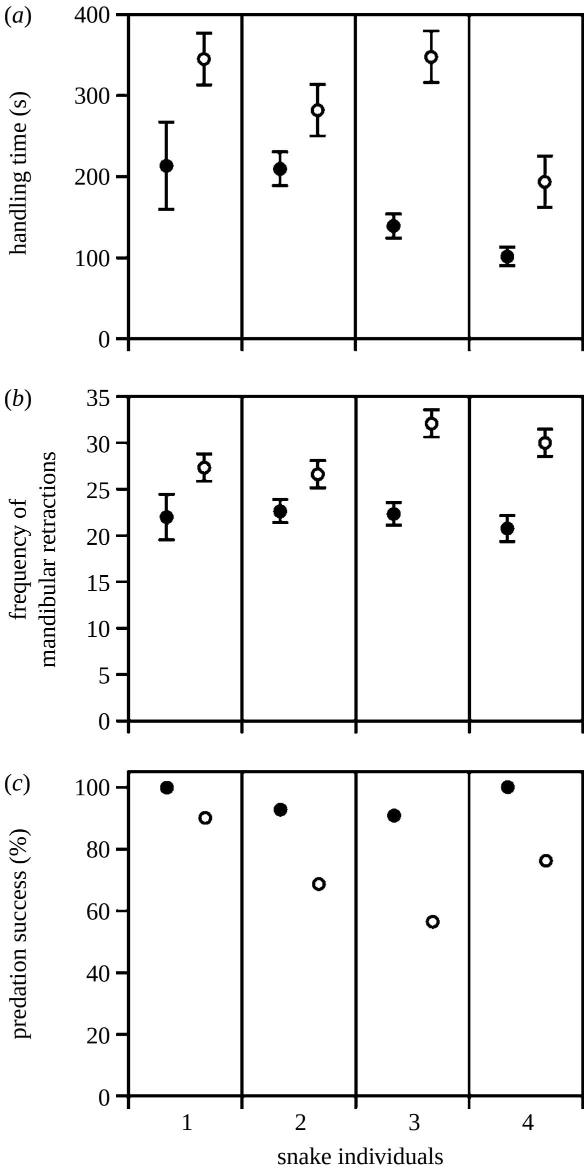

Figure 2. Feeding performance and success on dextral (filled circles) and sinistral (open circles) morphs of *Bradybaena similaris* by the four snakes of *Pareas iwasakii*. (*a*) Handling times, (*b*) the number of mandibular retractions for soft-body extraction (means ± s.e.) and (*c*) predation success.

predators. Sinistral variants have been generally considered to suffer selective disadvantages on account of the overwhelming predominance of dextrals (Vermeij 1975, 2002; Johnson 1982; Gould *et al.* 1985; Asami *et al.* 1998; but see Dietl & Hendricks 2006). However, sinistrals should enjoy a selective advantage over dextrals under chirally biased predation by snakes. The remarkable diversity of sinistral snails in Southeast Asia (Vermeij 1975; Hoso *et al.* 2006, unpublished data) may be attributable to 'right-handed predation' by the snakes.

Predation of land snails by soft-body extraction has been independently employed at least by three groups of colubrid snakes (Cundall & Greene 2000). Among them, neotropical snail-eating snakes of the subtribe Dipsadini (genera *Dipsas*, *Sibon* and *Sibynomorphus*) closely resemble pareatines in several character complexes including cranial morphology (Savitzky 1983) and soft-body extracting behaviour by alternate mandible retraction (Sazima 1989; Gotz 2002). Their similarities may also suggest convergence of morphology and behaviour for the predation of dextral snails between tropic and neotropic snail-eating snakes.

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Policy on animal testing. This research adhered to the Association for the Study of Animal Behaviour/Animal Behavior Society Guidelines for the Use of Animals in Research (published on the Animal Behaviour website), the legal requirements of the country in which the work was carried out and all institutional guidelines.

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NOTICE OF CORRECTION

Figure 1 is now presented in the correct form.

26 February 2007