ปฏิสัมพันธ์แบบผู้ล่าและเหยื่อระหว่างงูกินทาก *Pareas carinatus* และหอยทากบกในประเทศไทย

นางสาวพัชร ดนัยสวัสดิ์

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรดุษฎีบัณฑิต
สาขาวิชาวิทยาศาสตร์ชีวภาพ
คณะวิทยาศาสตร์ จุฬาลงกรณ์มหาวิทยาลัย
ปีการศึกษา 2558

PREDATOR-PREY INTERACTION BETWEEN SNAIL-EATING SNAKE *Pareas carinatus* AND TERRESTRIAL SNAILS IN THAILAND

Miss Patchara Danaisawat

A Dissertation Submitted in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy Program in Biological Sciences
Faculty of Science
Chulalongkorn University
Academic Year 2015

Thesis Title	PREDATOR-PREY INTERACTION BETWEEN SNAIL-EATING SNAKE *Pareas carinatus* AND TERRESTRIAL SNAILS IN THAILAND
By	Miss Patchara Danaisawat
Field of Study	Biological Sciences
Thesis Advisor	Professor Somsak Panha, Ph.D.
Thesis Co-Advisor	Professor Takahiro Asami, Ph.D.

Accepted by the Faculty of Science, Chulalongkorn University in Partial Fulfillment of the Requirements for the Doctoral Degree

....Dean of the Faculty of Science
(Associate Professor Polkit Sangvanich, Ph.D.)

THESIS COMMITTEE

....Chairman
(Noppadon Kitana, Ph.D.)

....Thesis Advisor
(Professor Somsak Panha, Ph.D.)

....Thesis Co-Advisor
(Professor Takahiro Asami, Ph.D.)

....Examiner
(Associate Professor Kumthorn Thirakhupt, Ph.D.)

....Examiner
(Assistant Professor Tosak Seelanan, Ph.D.)

....Examiner
(Assistant Professor Chirasak Sutcharit, Ph.D.)

....External Examiner
(Professor Hidetoshi Ota, Ph.D.)

พัชร ดนัยสวัสดิ์ : ปฏิสัมพันธ์แบบผู้ล่าและเหยื่อระหว่างงูกินทาก *Pareas carinatus* และหอยทากบกในประเทศไทย (PREDATOR-PREY INTERACTION BETWEEN SNAIL-EATING SNAKE *Pareas carinatus* AND TERRESTRIAL SNAILS IN THAILAND) อ.ที่ปรึกษาวิทยานิพนธ์หลัก: ศ. ดร.สมศักดิ์ ปัญหา, อ.ที่ปรึกษาวิทยานิพนธ์ร่วม: ศ. ดร.ทากาฮิโร่ อาซามิ, 95 หน้า.

ปฏิสัมพันธ์เชิงนิเวศระหว่างผู้ล่าและเหยื่อมีส่วนขับเคลื่อนการเกิดวิวัฒนาการร่วมกันของสิ่งมีชีวิตทั้งสองทั้งในเชิงสัณฐานวิทยาและพฤติกรรม การศึกษาก่อนหน้าในงูกินทากชนิด *Pareas iwasakii* ซึ่งมีพื้นที่การกระจายอยู่ในเอเชียตะวันออกแสดงให้เห็นว่าความอสมมาตรของพฤติกรรมการล่าและจำนวนฟันที่ขากรรไกรช่วยให้งูมีความจำเพาะเจาะจงต่อเหยื่อที่เป็นหอยเวียนขวา อย่างไรก็ตามพฤติกรรมการล่าเหยื่อของงูในกลุ่มนี้ยังไม่ค่อยมีการศึกษามากนัก การศึกษาในครั้งนี้ได้นำเสนอพฤติกรรมและประสิทธิภาพในการกินเหยื่อของงูกินทากชนิด *P. carinatus* ซึ่งเป็นชนิดที่มีขอบเขตการกระจายกว้างที่สุดในกลุ่มงูสกุลเดียวกัน อีกทั้งยังมีหอยทากบกทั้งแบบเวียนซ้ายและเวียนขวากระจายร่วมอยู่ในพื้นที่ จากการศึกษาพฤติกรรมพบว่าการล่าเหยื่อของงูกินทากชนิด *P. carinatus* สามารถแบ่งได้เป็นสามช่วงเวลาย่อย ได้แก่ ช่วงเวลาก่อนกินเหยื่อ ระหว่างการกิน และ ภายหลังการกิน ซึ่งพฤติกรรมที่เกิดขึ้นระหว่างช่วงเวลาดังกล่าว สามารถแบ่งย่อยได้เป็น 9 กลุ่มพฤติกรรมหลัก และ 15 พฤติกรรมย่อย ผลจากการศึกษาเชิงสัณฐานวิทยาและการปรับพฤติกรรมบางประการพบว่า ในงูชนิดนี้ความอสมมาตรของฟันขากรรไกรและพฤติกรรมการเอียงหัวทางซ้ายและขวาที่เกิดขึ้น ไม่มีผลต่อความสำเร็จในการล่าเหยื่อเหมือนอย่างที่เคยทราบกันมา ช่วงเวลาก่อนที่งูจะเข้าไปงับเหยื่อ งูมีการเลือกขนาดของเหยื่อโดยใช้สายตาเป็นหลัก โดยมากแล้วงูมักจะหลีกเลี่ยงการกินหอยเวียนซ้ายขนาดใหญ่ (23.64 ± 0.87 mm) ในขณะที่ขนาดของหอยเวียนขวาไม่มีผลต่อการเลือกกินเหยื่อของงู และการเลือกเหยื่อแบบนี้ก็เกิดขึ้นทั้งที่มีและไม่มีการแลบลิ้น จากหอยเวียนซ้ายชนิด *Dyakia salangana* ที่ใช้ในการทดลอง งูเลือกที่จะเข้าหาเหยื่อเพียง 17 จาก 29 ครั้ง ซึ่งหอยที่งูแสดงความสนใจมีขนาด 14.6 ± 1.6 มิลลิเมตร และหลังจากเคลื่อนที่เข้าหาเหยื่อ งูเลือกที่จะกินหอยเพียง 10 ตัวซึ่งมีขนาด 11.3 ± 1.6 มิลลิเมตร และเลี่ยงที่จะกินหอยเวียนซ้ายที่มีขนาดเฉลี่ยที่ 22.1 ± 1.1 มิลลิเมตร การเลือกเหยื่อของงูที่เกิดขึ้นนี้ไม่ได้เป็นผลมาจากกลิ่นที่แตกต่างกันของหอยต่างชนิด ซึ่งนั่นหมายถึงงูสามารถจดจำการเวียนของเปลือกได้โดยที่ไม่ต้องรับกลิ่นผ่านการแลบลิ้น เมื่อหอยที่ถูกกินมีขนาดมากกว่า 12 มิลลิเมตร ประสิทธิภาพในการกินต่อหอยเวียนขวาจะเพิ่มขึ้นเหนือหอยเวียนซ้ายในเชิงของน้ำหนักที่กินได้ต่อการดึงด้วยขากรรไกรหนึ่งครั้ง ($F_{1,47} = 66, p = 0.024$) และน้ำหนักที่กินได้ต่อหน่วยเวลาเพิ่มขึ้น ($F_{1,47} = 57, p = 0.001$) การกินหอยเวียนซ้ายจะยากขึ้นตามขนาดของเหยื่อ แต่ขนาดกลับไม่มีผลต่อประสิทธิภาพในการกินหอยเวียนขวา ซึ่งสอดคล้องกับการเลือกเหยื่อที่งูจะหลีกเลี่ยงกินหอยเวียนซ้ายที่มีขนาดใหญ่กว่า 12.4 มิลลิเมตร แต่ไม่เลือกขนาดของเหยื่อที่เป็นหอยเวียนขวา จากการเลือกเหยื่อของงูและผลที่ทำให้อยู่รอดของหอยเวียนซ้ายขนาดใหญ่ในการศึกษานี้สนับสนุนสมมุติฐานที่ว่าการเลือกกินหอยเวียนซ้ายในขนาดที่เหมาะสมเป็นสิ่งที่ถูกขับเคลื่อนโดยวิวัฒนาการระหว่างการจดจำการเวียนของเปลือกในงู และขนาดที่เหมาะสมที่จะหลีกเลี่ยงจากผู้ล่าในหอยโดยเฉพาะหอยเวียนซ้าย งูกินทากชนิด *P. carinatus* เป็นงูที่หากินบนต้นไม้ซึ่งมีหอยต้นไม้ทั้งแบบเวียนซ้ายและเวียนขวากระจายร่วมในพื้นที่ ในหอยต้นไม้ที่กระจายร่วมกับงูกินทากชนิดนี้มีถึง 17.3 % จาก 900 ชนิดที่เป็นหอยเวียนซ้าย ขณะที่ในพื้นที่การกระจายของ *P. iwasakii* ในเอเชียตะวันออกนั้นแทบจะไม่พบหอยเวียนซ้ายเลยคือมีเพียงแค่หนึ่งจาก 23 ชนิดเท่านั้น การที่หอยเวียนซ้ายมีจำนวนน้อยในพื้นที่ ทำให้งูไม่สามารถแยกแยะการเวียนของเปลือกได้เมื่อพบเหยื่อที่เป็นหอยเวียนซ้ายและทำให้เกิดความผิดพลาดเมื่อ *P. iwasakii* ต้องล่าเวียนซ้ายในขณะที่งู *P. carinatus* ที่สามารถจดจำการเวียนของเปลือกได้ เลี่ยงที่จะไม่กินหอยเวียนซ้ายซึ่งกินได้ยากกว่าและประสบความสำเร็จทุกครั้งที่มีการล่า อย่างไรก็ตามการศึกษาครั้งนี้ไม่ได้สนับสนุนวิวัฒนาการร่วมกันของแต่ละฝ่าย แต่อาจกล่าวได้ว่างูสามารถปรับตัวเพื่อหลีกเลี่ยงการกินหอยเวียนซ้ายที่ให้ประสิทธิภาพในการกินน้อยกว่าไปกินหอยเวียนขวาซึ่งมีอยู่มากในพื้นที่ การที่ผู้ล่าสามารถจดจำการเวียนของเปลือกได้นั้นก็เป็นประโยชน์กับทั้งผู้ล่าและเหยื่อโดยผู้ล่าจะหลีกเลี่ยงการกินเหยื่อที่ให้ประสิทธิผลต่ำ และสำหรับเหยื่อกระบวนการนี้อาจไปเร่งการเกิดชนิดใหม่โดยผ่านยีนที่เกี่ยวข้องกับการเวียนของเปลือกได้ในอนาคต

สาขาวิชา วิทยาศาสตร์ชีวภาพ	ลายมือชื่อนิสิต ....
ปีการศึกษา 2558	ลายมือชื่อ อ.ที่ปรึกษาหลัก ....
	ลายมือชื่อ อ.ที่ปรึกษาร่วม ....

5373815923 : MAJOR BIOLOGICAL SCIENCES

KEYWORDS: PREDATION / HANDEDNESS / DENTITION / PREY-SELECTION / COILING DIRECTION

PATCHARA DANAISAWAT: PREDATOR-PREY INTERACTION BETWEEN SNAIL-EATING SNAKE *Pareas carinatus* AND TERRESTRIAL SNAILS IN THAILAND. ADVISOR: PROF. SOMSAK PANHA, Ph.D., CO-ADVISOR: PROF. TAKAHIRO ASAMI, Ph.D., 95 pp.

Ecological interactions between predator and prey can drive their dynamic coevolution in morphology and behavior. Previous studies on East Asian snail-eating specialists, *Pareas iwasakii* suggested directional asymmetries in striking behavior and dentition function for specialized predation on dextral snails. However their predatory behaviors mostly remain unknown. This study provides predatory behaviors and performances of *P. carinatus*, which most widely occurs in the genus and coexisting with dimorphic snail prey. The result suggested that predatory behaviors of *P. carinatus* can be divided into the pre-capture, feeding and post-feeding phases, in which the snake pursues 9 behaviors which probably differ in function. These behaviors can be identified by 15 different displays. The result of morphological study and some behavioral response demonstrated that the direction of either head-tilt or dentition asymmetry is not functionally crucial for predation success to dimorphic prey by *P. carinatus*. This mean that the specialized handling of asymmetric prey does not require so strong asymmetry in dentition or striking behavior as expected from the previous study. During pre-seizure phase, snakes showed the trend of prey-size selection before predation by relying on visual recognition. The snake frequently avoided approaching or striking at relatively large sinistral prey (23.64 ± 0.87 mm), whereas the size of dextral snail did not affect whether the snake struck. This was also the case when the snake did not flick the tongue. From 29 sinistrals of *Dyakia salangana*, the snake only approached smaller 17 in the mean shell size (14.6 ± 1.6 mm) than the rest (23.7 ± 0.87). After approach, the snake struck at smaller 10 (11.3 ± 1.6) but not at other larger sinistrals (22.1 ± 1.1). These size-dependent decisions for predation on conspecific preys are not ascribable to prey odor differences. Therefore the snake recognizes prey handedness without relying on vomeronasal chemoreception by tongue-flick. The benefit of preying on the dextral instead of the sinistral snails increased with prey size over 12 mm in shell diameter, in term of soft-body mass gained per retraction ($F_{1,47} = 66$, $p = 0.024$) and the gain per time ($F_{1,47} = 57$, $p = 0.001$). This size-dependent increase of cost for preying on a sinistral instead of a dextral explains that the snake preyed on all of the sinistrals smaller than 12.4, and avoided sinistrals that are larger than this size. The presence of this threshold size supports a hypothesis that the size-dependent increase of cost for preying on a sinistral has driven the evolution of prey-handedness recognition and size-dependent avoidance of sinistral-predation. This arboreal snake is frequently active on trees where dimorphic tree snails abundantly co-occur. These tree snails are almost invariably sinistral in 17.3 % of 900 prey species. While, *P. iwasakii* rarely encounter sinistral prey with only one sinistral out of 23 potential prey species. Thus, it would be advantageous to evolve an ability to distinguish between prey enantiomorphs and explains the failure of *P. iwasakii* to capture a given sinistral. In contrast, *P. carinatus* should be advantageous to avoid predation on costly sinistrals. In this case, predator does not evolve to exploit sinistrals by arms race. Instead the snake has shifted to avoid inefficient sinistral because the easier dextral prey still remains abundant. Predator’s recognition of prey handedness, which benefits both the snake predator and sinistral prey, could further accelerate ecological prey speciation by a reversal gene.

Field of Study: Biological Sciences	Student's Signature
Academic Year: 2015	Advisor's Signature
	Co-Advisor's Signature

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to my thesis advisor, Prof. Dr. Somsak Panha for his invaluable help, guidance and encouragement throughout the course of my research. Furthermore I would like to acknowledge with pleasure my co-advisor, Prof. Dr. Takahiro Asami, for his meticulous scrutiny, not only academic research but also for many other methodologies in life.

I would like to express my sincerely grateful to Dr. Noppadon Kitana, Associate Professor Kumthorn Thirakhupt, Assistant Professor Dr. Tosak Seelanan, Assistant Professor Dr. Chirasak Sutcharit for serving on my thesis committees, and giving more important guidance for the improvement of the quality of my thesis. The appreciative thanks to Prof. Dr. Hidetoshi Ota for his inspiration and important suggestion at the initial until accomplish this work.

I wish to express appreciation to the members of Animal Systematics Research Unit, Chulalongkorn University for all kindly helps during field work and laboratory experiments, and also Mr. Chun Ardwichai and Mr. Wichase Chiang-Nuer for all the supports in the field from my master degree study until present time. I would like to thank Dr. Nontivich Tandavanitj and Dr. Josef Harl for their guidance, practical advice and improvement in my writings of this manuscript. I also thanks to Dr. Chattaphas Pongcharoen, Dr. Patai Charoonnart and Miss Pawara Pachit for their kindly help and encouragement throughout my study period, especially during the final lesson.

This study was financially supported by Thailand Research Fund, through the Royal Golden Jubilee PhD Program (PHD/0082/2552) and The 90th Anniversary of Chulalongkorn University Fund (Ratchadaphiseksomphot Endowment Fund).

Finally, I most gratefully acknowledge to my family for their encouragement and all kind of supporting during my life that push me to this achievement.

CONTENTS

Page

Page

List of Figures

List of Tables

Chapter I

Introduction

One of the driving forces of coevolution is interaction between predators and prey. The interactions between predators and their prey is a result of behaviors involved through predator avoidance and prey capture under the effects of diverse biotic and abiotic factors (Domenici et al., 2007; Gvoždík et al., 2013; Krebs, 1985). Their adaptations in behavior and morphology shape their population dynamics and has further consequences in community structure (Dawkins and Krebs, 1979). However, our knowledge on these interactions is limited. Even basic information on predation behavior and prey selection is little known especially in specialist predators. Understanding of complex dynamics of ecology and evolution between predators and their prey requires critical studies of their behavior and morphology that determine survival and reproductive success.

Specialized snail-eaters

Since their origins during the Middle or Late Jurassic to the Early Cretaceous, snakes evolved in many terrestrial habitats and became a diverse group of vertebrates (Allen et al., 2013; Apesteguía and Zaher, 2006; Caldwell et al., 2015; Hsiang et al., 2015). The reduced and combined skull bones and their flexibility of lower jaw characters have driven the snakes' evolution for adaptation to a wide range of diets (Cundall and Greene, 2000; Gans, 1961; Lee et al., 1999). Although all snakes are carnivorous and most of them are generalist predators, some other species, including the snail-eating snakes are known to have unique and specialized dietary habit.

Predation on gastropods have been reported in four snake families: Dipsadidae (Lewis et al., 2013; Mertens, 1952; Ray et al., 2012; Sazima, 1989), Pareidae (Götz, 2002; Hoso et al., 2007), Lamprophiidae (Branch, 1975) and Colubridae (Arnold, 1977; Arnold, 1981). Only the members of the Dipsadidae and Pareidae are known as specialized snail eaters. Although these two families share a suit of external morphological and functional characteristics, their specialized behaviors and morphological characters are known to have evolved independently (Pyron et al., 2013; Sazima, 1989; Vitt and Caldwell, 2009).

The Southeast Asian snail-eating snake family Pareidae consists of 14 species belonging to three genera: *Aplopeltura*, *Asthenodipsas* and *Pareas*. They are dietary specialists and prey on terrestrial snails and slugs (Cundall and Greene, 2000; Greene, 1997; Pough, 1983; Vitt and Caldwell, 2009). They exhibit specific adaptations for arboreal life and feeding on snails, such as long slender bodies, oversize heads, short snouts, moveable eyes and flexible mandibles (Sazima, 1989; Vitt and Caldwell, 2009). In addition, the pareid snakes have mandibular teeth that show varying degree of asymmetry in number and size. Such asymmetries are consider to have evolve to feeding on particular clockwise-coiled snails (Hoso et al., 2007). The feeding behavior of *P. carinatus* from Indonesia was roughly described by Götz (2002). This species reportedly uses both chemical and visual cues to detect snail prey. They prefer to catch the snails from behind and use mandibular movements to extract the prey's soft body from the shell. Götz (2002) suggested that pareid snakes show more frequent mandibular movements and faster extractions than dipsadid snakes.

Interaction between snail-eating snakes and their snail prey

Several more recent authors examined the interactions between snail prey and snail-eating snakes. Hoso et al. (2007), for example, reported that counterclockwise-coiled (sinistral) snails survive predation more frequently from predation by *Pareas iwasakii* than clockwise-coiled (dextral) snails. With respect to the snakes, the right mandibular teeth are smaller, more delicate, slender and greater in number than the mandibular teeth on the left side, ones (24.9 *vs*. 17.5 in mean value). These characters are attributed to feeding adaptation for dextral snails. Moreover, in this study also the numbers of mandibular teeth (asymmetry index) among the 14 Asian snail-eating snake species were compared. The mandibles were more or less asymmetrical in 12 specialized species, whereas the other two species known as non-specialists for the snails showed symmetrical mandibular structures. Hoso and Hori (2008) reported that modifications of shell aperture are a specific impediment to predation by snakes. The survival rate of large sinistrals was higher than that of dextral species. In addition, phylogenetic analyses demonstrated that the sinistral lineages evolved more frequently from dextral lineages within the distribution range of the snail-eating snakes than vice versa (Hoso et al., 2010).

Predators select size-compatible prey, this pattern has led to a hypothesis that adaptation processes through predator-prey interactions may vary among different areas. The frequency of predator-prey interaction depends on ecological factors including prey availability in each area, specificity of predators to prey, and potential predation by different predators in different areas (Thompson, 1999). Thailand shows larger diversity in terrestrial snails than temperate regions (Schilthuizen, 2011). It is possible that pareid snakes in Thailand may have achieved different patterns of adaptations from the previously known examples.

Objectives of this study

Arm race between predator and prey may drive their coevolution. Evolution of either a predator or prey may change the selection pressure on the other, the evolutionary response of which then might also influence the character stage of its counterpart. In natural environments, those interactions are often asymmetrical, and some evidence shows that predator-prey interactions are often characterized by greater responses of prey to predators than vice versa (Abrams, 1986; Vermeij, 1994). This study focuses on basic information between snail-eating snakes and snail prey in term of predation behavior, morphology of feeding apparatus, prey selection and predation success and efficiency.

The objectives of this study are

1. Examination of the predatory behavior of the keeled-scale snail-eating snake *Pareas carinatus*
2. Examination of the effects of prey morphology on the feeding performance of *P. carinatus*
3. Examination of the role of the snake's feeding apparatus to predation success

This study provides crucial information to understand adaptation of keeled-scaled snail-eating snakes, in particular of *Pareas carinatus*, for predation on different types of snail prey.

Chapter II

Literature review

Dietary specialization occurs in various groups of vertebrates. In case of snakes, most of them are generalists which consume a wide variety of animals including invertebrates, and both endotherm and ectotherm vertebrates. However, some particular groups of snakes are referred to as dietary specialists, which consume much limited groups of animals and even at particular life-stages (Zug, 1993). Because of limb degeneration in early stages of their evolution, snakes depend almost entirely on structure of the remaining portions of the body (i.e., jaw apparatus, trunk, etc.), and the way of their use in capturing and subsequent handling of prey (Cundall and Greene, 2000). The snakes that well known as generalists are often exhibited highly variable feeding behavior in response to different morphology and contexts of prey encounter (Mehta, 2003; Mori, 1991). With respect to those specialist snakes, however extent of behavioral flexibility in response to similar but actually more or less differential prey remains to be studied.

Feeding technique of the snail-eating snake

Morphological and behavioral adaptations to extract prey's soft body from the shell prior to swallowing have obviously been independently evolved in two lineages of snakes, the families Pareidae and Dipsadidae, that almost exclusively consume terrestrial molluscs (Cundall and Greene, 2000; Laporta-Ferreira and Salomão, 2004; Mertens, 1952; Ray et al., 2012; Vitt and Caldwell, 2009). Most of these dietary specialists also share a suit of external and functional characteristics, such as long slender body, oversize head relative to the nuchal region, short snout, movable eyes, and flexible mandibles (Sazima, 1989). However, variations in feeding patterns and extent of dietary specializations are poorly understood for either of these families. The snail-eating snakes can consume both shelled and unshelled mollusks. Below feeding techniques of those two snake families were summarized in the following three different ways.

1. Wedge and drag in Dipsadid snakes

This technique was reported from *Sibon nebulosus, Tropidodipsas philippii* and *T. annuliferus*. The snakes grasp snail soft body, and then wedge the shell with substrate and use body muscular contractions to extract the snail soft body by the body musculature (Gans, 1983; Laporta-Ferreira and Salomão, 2004; Sheehy III, 2012).

2. Coiled around and use mandibular transport in Dipsadid snakes

The snake follows mucus tract of prey and exhibit high frequency tongue flicking. The snake coiled and held the shell in its coil. Lower jaw retractions were used to pull out the soft body rather than using body musculature. This technique was reported from *Dipsas indica* (see Sazima (1989)).

3. Hold shell and use mandibular transport in Pareid snakes

This technique was reported from observations on *Pareas carinatus* and *P. iwasakii*. The snake grasped the snail's soft body, lifted the shell up from substrates and inserted the lower jaws into shell opening while the upper jaws are fixed on the shell base. The snail's meat was extracted by alternative moving of the lower jaws (Götz, 2002; Hoso et al., 2007). This process termed the mandibular walk (Cundall and Greene, 2000).

Besides these, the Natricidae (*Storeria dekayi*) that prey mainly on an earthworm and other small invertebrate also feed on a snail. The Natricid snake grasps the snail's soft body before drag and wedged the shell against immovable object. The snake twists their body until the columellar muscle brake. Then snake pulled snail's body typically by using both upper and lower jaws clamped onto the snail body (Rossman and Myer, 1990). In addition, the snail-eating snakes also prey on slugs (unshelled mollusk) with a different feeding technique from preying on snail. Sazima (1989) reported the feeding behavior of *Dipsas indica* (Dipsadidae) on a veronicellid slug (*Sarasinula linguaformis*) by the snake follows a mucus tract of slug about 2 m by flicking its tongue and repeatedly touching the mucus tract by the tongue. When the snake gets closed to the slug, it touched slug with tongue several times and moved its eyes toward the prey. Before strike, snake arched their neck and grasp slug at mid-body, lifts the slug from the substrate with torsion of fore-body and then quickly swallowed the slug from the tail. Usually, the snake swallowed the slug prey more quickly with a small number of jaw retraction compared with the cases of predation on a snails. This may be an adaptation to avoid copious while handling the slug (Bizerra et al., 2005).

For the Asian snail-eating snake family Pareidae, Götz (2002) observed the feeding behavior of captive *Pareas carinatus* on the European ground-dwelling snail, and reported that the behavior was characterized by sole mandibular movements that resulted in the extraction of the snail body. Hoso et al. (2007) described the morphological and behavioral features of the Japanese pareid species and attributed them to an exclusive of those adaptions to feed on terrestrial snails of *Asthenodipsas leavis*. They also highlighted an extreme state of asymmetry in the number of mandibular teeth as indicated by the value of asymmetry index in *Pareas iwasakii*. Their experiment further demonstrated that such extreme asymmetry in jaw dentition is an adaptation to consume the efficiently dextral snails and poorly handles the sinistral snails in term of the efficiency extracting the soft body, or even frequent feeding failure. However, based on an overwhelming predominance of the dextral over the sinistral snails in the snake's natural habitat, Hoso et al. (2007) assumed that the effect of such disadvantage is negligibly small. Furthermore, left-right reversal of prey by one-locus mutation, which results in speciation (Ueshima and Asami, 2003) is subject to positive selection because of survival advantage under predation by pareid snakes (Hoso et al., 2010).

Prey detection and recognition by snakes

The arm race in tactics of detection between predator and their prey has intensely affects the life-history and behavioral strategies of both parties (Dawkins and Krebs, 1979). Living prey generate a sign that predator can exploit to detect the prey. Once potential prey is detected, the predator may benefit to decide whether attacking or ignoring. Most predators apply decision rules according to physical features of prey. Squamates reptiles usually detect moving prey by vision, non-moving prey by chemical cues, moving or non-moving prey by tactile or thermal cues.

Snakes typically recognize potential prey either by chemical cuesand/or visual cues. Vomeronasal chemoreception is known to be the dominant sensory mode used by most snakes to locate their prey (Burghardt, 1967; Chiszar et al., 1990) Visual cues are used to obtain immediate information of prey's physical characters such as size and current motivation (Saviola et al., 2012).

Roles of visual and olfactory cue for prey detection

Visual cue

Visual detection is used by most snake species which are sit-and-wait predators, while it is not apparent inactive-foraging predators (Vincent et al., 2005). Visual stimuli are used for prey capture by both aquatic and terrestrial snakes. Visual cues provide information of prey's physical characters such as shapes and sizes, which are impontant for predation success. The newborn garter snake *Thamnophis sirtalis* recognizes prey movement by vision (Burghardt, 1969). Extensive work also suggested that an ambush snake relies upon visual cues to launch a strike (Chen et al., 2012; Shine and Sun, 2003) whereas chemoreception provides the most critical information of prey items for active predators (Cundall and Greene, 2000).

Chemical cue

Chemical stimuli associated with snake's foraging strategies and their behavioral display. Consequently leads the snake to discriminant prey from non-prey target and indicated individual interests in existing chemical substance. There are two chemical sensing systems occurred in all the snakes: the main system (nasal organ) and the accessory system (vomeronasal organ). Neurons in olfactory and vomeronasal epithelium tissues are unique in being regenerated throughout the lifetime of snakes. However, the degree of development of nasal and vomeronasal sensing organs varies among groups of snakes (Chiszar et al., 1981). The importance of chemical stimuli in detecting and discriminating prey has been documented in many groups of snakes such as a garter snake (*Thamnophis sirtalis*) (Burghardt, 1969; Burghardt and Pruitt, 1975), a western rattlesnake (*Crotalus viridis*) (Chiszar et al., 1990; Cowles and Phelan, 1958), a western diamondback rattlesnake (*Crotalus atrox*) (Cowles and Phelan, 1958), a mojave rattlesnake (*Crotalus scutulatus*) (Cowles and Phelan, 1958), a red diamond rattlesnake (*Crotalus ruber*) (Cowles and Phelan, 1958), a smooth Snake (*Coronella austriaca*) (Amo et al., 2004), a graham's crayfish snake

(*Regina grahamii*) (Gordon, 1968) and a banded water Snake (*Nerodia fasciata*) (Daghfous et al., 2012).

Snakes have the well-developed vomeronasal sensing system, for which they flick the tongue, to perceive odors. The tongue protrudes from the mouth to collect odor molecules from the substrate and to deliver those to the vomeronasal organ (Halpern and Kubie, 1980). Tongue-flicking behavior has been used as an indicator of using olfactory cues and to quantify olfactory responses (Burghardt, 1967; Cowles and Phelan, 1958; Saviola et al., 2012; Weaver and Kardong, 2010).

Sensory cues for snail-eating snake

Snakes, as well as other animals, sensory cue is usually correlated with prey preference and associated with their foraging ecology (Gans, 1983; Kardon and Smith, 1991), however prey detection in snail-eating snake is few documented. A south American snail-eating snake, *Dipsas indica*, detects the prey by chemoreception. This snake points the snout toward the substrate and repeatedly touches the ground by tongue. The snake can follows slug mucus trail for about 2 m without sighting and touches the slug with the tongue when its closed to the prey (Sazima, 1989). However, *Tropidodipsas philippii*, *T. annuliferus* and *Sibon nebulatus* use both visual and chemical cues to locate their prey. These snake initially notice the change of prey’s movement when the prey come into the field by vision and access to prey with tongue flicking behavior (Sheehy III, 2012). Use of olfactory cues was also reported in a slug-eating population of *Thamnophis elegans* (Arnold, 1981). Although possible signals for prey detection by Southeast-Asian snail-eating snake was reported brifely in Götz (2002), relative importance of visual and olfactory sensory systems remain unanswered.

Dentition asymmetry

External bilateral symmetry is a fundamental for the body plan of the Bilateria. They are, however, mostly asymmetric in internal structure such as the arrangement of internal organs resulting from primary asymmetry appearing in early development (Okumura et al., 2008). Some of them have secondarily evolved handedness in behavior and morphology such as flounder's eyes and snail's coil (Utsuno and Asami, 2010). These symmetry breaks are often driven by local environment and generate secondary asymmetry that functions for interaction with the external environment (Benkman, 1996; Dietl and Hendricks, 2006; Govind, 1989; Stewart and Albertson, 2010).

Because predation consumes energy and time and raises the risk of being preyed, predators minimize time consumption for predation and maximize the efficiency of energy intake by predation. Specialist predators exhibit more or less specialized morphology, behavior and physiology to exploit a narrow range of available resources (Ferry-Graham et al., 2002; Pianka, 1976). Many snake species are known as dietary specializations. The snakes usually possess the skull structure, teeth, and cranial musculature, function for prey capture and ingestion (Cundall and Greene, 2000). For example, the quadrate length of piscivorus snake is specialized for reducing swallowing time (Vincent et al., 2009). The egg-eater *Oligodon*, specialize in predation on leathery-shelled eggs, modified their blade-liked teeth for slitting the egg shells before inserting their head and consuming the egg contents inside (Minton, 1963).

Morphological adaptation is also obvious in the snail-eating snake family Pareidae. The pareid snakes are regarded as snail eaters, which evolved specialized techniques for the snail soft-body extraction by using jaw movement from the shell (Cundall and Greene, 2000; Götz, 2002). The experiment by Hoso et al. (2007, 2010) explained the secondary asymmetry found in the predatory behavior and mandibular dentition of *Pareas* as the outcome of specialization for preying on dextral snails. These snakes extract the soft body by using the mandible movement (Götz, 2002). The terrestrial snail species are mostly dextral (Gittenberger et al., 2012), and thus dextral prey is most likely to be predominant in snake habitats. Among the 14 *Pareas* species (Vogel, 2015; Wallach et al., 2014; You et al., 2015), 12 species are supposedly snail eaters and possess more teeth in the right mandible than in the left (Hoso et al., 2007; You et al., 2015). *Pareas iwasakii*, which exhibits the most asymmetric dentition in the genus, tilts the head and strikes at prey consistently leftwards and only poorly performs predation on sinistral snails. The relatively frequent evolution of sinistral lineage in sympatry area with *Pareas* is considered to the result of single-gene speciation by left-right reversal against the right-handed predation by snakes (Hoso et al., 2010; Utsuno and Asami, 2010).

Directional asymmetry in the feeding apparatus, which is not the default state of the Bilateria, has probably repeatedly evolved in predators of snails other than pareid snakes (Bay, 1974; Dietl and Vega, 2008; Inoda et al., 2003; Ng and Tan, 1985; Shigemiya, 2003). These cases suggest but cannot by itself be evidence that a predator's handedness plays a role in the predation of asymmetric prey. It is difficult to know whether it is necessary and how significant for the predator to be as asymmetric as it is. Similarly a little empirical evidence for the functional or mechanical importance of the direction or degree of dentition asymmetry for pareid snakes to extract soft-body of the dextral prey. In the case of the pareid feeding apparatus, the strength of dentition asymmetry seems to vary within and between species (Hoso et al., 2007). This variation in the degree of asymmetry may provide a rarely available opportunity to examine how dependent the efficiency of dextral-prey predation is on the dentition asymmetry.

Feeding efficiency in snakes

Feeding efficiency is influenced by ecological, functional and physiological factors (Vincent and Mori, 2008). Snakes are carnivorous animals that consume larger prey than their head. For this reason, snakes enable to feed on broad ranges of prey (Cundall and Greene, 2000). Because of snake cannot reduce size of prey and have to swallow them the whole body. Therefore, the prey size is often limited by corner of the mouth and slowdown the swallow process (Kardong, 1977). Many studies indicated that larger prey often requires longer feeding time and more mandibular movements than smaller prey in gape-limited predator (Arnold, 1993; Cundall and Greene, 2000; Hampton, 2011; Vincent et al., 2006a). However, functional meaning of prey size is involved in prey transportation not only prey mass, but the possible effects of prey shape (relative height, width or length) on predation efficiency or on prey selection have rarely been investigated.

The prey size and shape affect the ingestion time and number of jaw retraction. For example in the piscivorus snake, *Nerodia fasiata*, spends a longer time to swallow a short and wide body of prey (Vincent et al., 2006b). Vincent et al. (2009) compared feeding performance among piscivorus natric snakes. The results showed that the swallowing time varies among snake species and the quadrate length plays a positive role for predation on prey with irregular shape by reducing the swallowing time. However, narrow head shape indicated to relatively small gape size in piscivore.

In *Natrix tessalana*, exclusively piscivorus, in this case consumed mass gained and capturing time do not differ between small and large prey, but minimal absolute size are the most important for capturing efficiency (Bilcke et al., 2007). In *Thamnophis proximus*, its ontogeny affects the dependence of feeding performance on the prey size. Juvenile of the snake has the larger head (relative to the body size) can consume larger prey than adults. The prey size relative to the snake body size and prey type influence snake's feeding performance and difficulty of prey ingestion as well (Hampton, 2011).

The most snake predator consumed prey by swallow whole body without tare to small pieces. Chiefly for this reason, feeding performance in specialist predators showing that prey morphology is influence prey transportation. However, functional morphology study suggested that prey size in gape-limited snakes is typically determined by the relative sizes of prey in various dimensions.

Many of the Southeast Asian snake, Pareidae, are regarded as snail eating specialist, which feeding technique are evolved for snail extraction by using lower jaw retraction to pull only snail soft body instead of swallowing whole shelled prey (Cundall and Greene, 2000; Götz, 2002; Hoso et al., 2007). Previous study on Japanese species *Pareas iwasakii* with flat snail indicated that the size and coiling direction of snail prey affect snakes' feeding performance. According to feeding technique, prey size in term of shell width and coiling direction are affected their feeding performance (Hoso et al., 2010). Leading to this study, the influence of prey attributes on feeding performance (transport time, number of jaw protractions and consumed weight) have been examine as well as on the asymmetry of mandibular teeth of this species.

Chapter III

Material and methods

Experimental design

The aim of this study is to investigate the functional response of *P. carinatus* to different prey types and the functional morphology of their lower jaws in respect to their feeding efficiency. The experiment was set up in the laboratory from October 2012 to June 2014 at the Chulalongkorn University (Thailand). The experimental protocol was approved by the Animal Care and Use Committee of the Faculty of Science, Chulalongkorn University (Protocol Review No. 1223003). Six adult females of *P. carinatus* (snout-vent length about 510-720 mm; head width 6.8-11.5 mm) were collected from Chantaburi province, eastern Thailand. Each of the snakes was housed in a separate terrarium (30 x 45 x 25 cm). The wooden bar ca. 30 cm in length and 4 cm in diameter was fixed horizontally 15 cm above the ground of the shelter. The snakes were acclimated by keeping them individually for 3 days with no food prior to the predation experiment. For each experiment, a snail was placed 100 mm ahead of a snake while sitting on a horizontal wooden bar. The individual combination between snake and snail was randomized in each bout. Each feeding bout was started at 2100, the approximate earliest time at which active individuals of snakes have been observed in the field (P. Danaisawadi personal observation). All the experiments were conducted at 25–28 °C under the illuminance of 100 lux. The observation was set up twice a week for 50 weeks. Behavioral response of the snakes was recorded by a video camera (Nikon Coolpix P100, VDO mode HD) until the snakes finished their all feeding process.

Feeding bout started when the active snail was placed in front of the observed snake until the snake finished the feeding process or disregarded the prey. Predation was defined as successful when the snake fed the prey's soft body. Predation failure was defined as cases in which the predator struck on the prey but missed to capture the prey or did not feed on the soft body of the snail.

Experiment I: Predatory behavior of Pareas carinatus

To evaluate the feeding behavior of captive snail-eating snake, *P. carinatus* on various prey types, five adult females of *P. carinatus* (51-72 cm in snout-vent length), all collected from Chanthaburi, eastern Thailand. As prey candidates, 16 adult snails of *Cryptozona siamensis*, ten adult semi-slugs of *Durgella* sp. and five adult slugs of *Semperula siamensis* were used. Hereafter a fully shelled pulmonate called a snail, a pulmonate with the largely-reduced shell called a semi-slug, and a pulmonate with no shell called a slug. Those three types of pulmonate co-occur with *P. carinatus*. As prey candidates, 16 adult snails of *Cryptozona siamensis*, ten adult semi-slugs of *Durgella* sp. and five adult slugs of *Semperula siamensis* were used. Each snake was conditioned with no food for 3 days before each predation trial (hereafter called experiment) began at 21:00. The experiments start when a snail was placed and let it crawl 100 mm ahead of a snake perching on the horizontal bar. The combination of individuals between the snake and prey candidate was randomized (Table 1). All experiments were conducted in the laboratory at 25 to 28°C under the illuminance of 100 lux. Behavioral responses of each snake were recorded with a video camera.

Statistical analyses for experiment I

The video records of predation experiments were compared and behavioral displayed of snake among experiment with the same type of prey candidates were extracted. The ethogram was constructed to describe the standard predatory behavior according to the results with the putative standard prey *Cryptozona siamensis*. A major function of each distinguishable behavior was inferred. These behavioral displays were grouped into functional categories, which were below indicated in capital letters.

Differences in time lengths of the three predatory phases between the cases with the snail and the semi-slug were examined by using the general linear mixed models (GLMMs). The numbers of tongue flicks before strike, mandibular retractions, gapes after feeding, and differences in the frequency of those behaviors were examined by GLMMs.

Experiment II: Decision making to predation

This part was extended from pre-capture phase (Experiment I) to understand prey selection by *P. carinatus*. This experiment was divided into 2 parts. (1) The response of snake to different coiling direction and size of snail in the pre-capture phase was used to investigate snake's decision making. (2) Experiments on the snake's responses to visual or chemical stimuli were conducted to detect the role of visual and chemical stimuli in prey recognition. The number and size of prey candidates are show in Table 2. The results of these were included in the analysis of predation efficiency in Experiment III.

Part I. Decision making for predation

Decisions of snakes in experiments with 76 dextral and 38 sinistral snails which vary in size were examined in the pre-capture phase. Visual recognition was investigated by examining eye-fixing behavior and the role of chemical cues by examining tongue flicking activities. Video-records of trials were evaluated in order to obtain and measure the following variables: the number of approaching and the number of strike on prey, the number of tongue flicking, time intervals from start to approach and time interval from approach to strike.

Statistical analyses for experiment II part I:

The effects of coiling direction and shell size and of interaction between those on the occurrence of approach or strike at a snail with different were tested by constructing generalized linear mixed models (GLMMs) with the random effects of snake individual and snail species.

Eye-fixing and tongue flicking behaviors were recorded to investigate prey recognition by visual and chemical cues, respectively. The effects of coiling direction and prey size and of their interaction on the tongue flicking behavior were analyzed by GLMMs analysis with the random effects of snake individual and snail species.

Part II. The role of visual and olfactory cues in prey recognition

In order to investigate the role of visual and chemical stimuli in the snakes' decision making, experiments with only on visual or olfactory stimuli were conducted. Different types of stimuli were presented to the snakes as (A) visual stimuli, (B) chemical stimuli, and (C) a combination of visual and chemical stimuli. To understand how the snake recognizes and makes decision for predation, the dextral prey species, *Cryptozona siamensis* (mean of shell width 28.35 ± S.E. 0.25 mm), and sinistral prey species, *Dyakia salangana* (mean of shell width 29.82 ± 0.30 mm) were used as representative dextral and sinistral prey species. Experiments were set up every two days. Each stimulus condition was randomly used for each snake. Responding behaviors of the snake (tongue flick, and eye–fix to the target), time interval from start to display these responses (hereafter called responding time), the frequency of approaching and the total number of tongue flicking response were recorded.

Visual-chemical stimuli tests were set up by using a cubic plastic box (150 x 150 x 150 mm) as shown in Figure 1. The presence of this plastic container did not affect to staring behavior (GLMMs, $F_{1,60}$=3.69, p=0.06) or the decision to approach (GLMMs, $F_{1,60}$=0.71, p=0.40), which implies that the snakes responded to the prey target only because of the stimulation of the prey but not the container. For the **visual treatment**, a crawling snail was placed inside a box, which was then sealed with Parafilm around the edge of the container and a lid to protect the leakage of odor. The boxes were cleaned every time after use. For the **olfactory treatment**, a non-transparent box with 2 mm pinpricks at 20 holes at each side was used. The outside of the box was coated with snail mucus and a snail was allowed to crawl inside the box to produce more odors during the experiment. For the **combined treatment**, a snail was placed in front of the snake in a distance of 10-15 cm without barriers, so that the snake could response to the odor and image. For **the control treatment**, a new and clean cubic plastic box of the same size as used in those stimulus treatments was used as the control.

Statistical analyses for experiment II part II

Generalized linear mixed models (GLMMs) were used to investigate the ability of prey recognition. The effects of different types of stimuli on behaviors, responding time, approaching frequency and the total number of tongue flicks were examined. The stimulus, coiling direction and their interaction were set as fixed factors and effects of snake individual were set as random factors.

Experiment III: Feeding efficiency to difference prey morphology

The data of all successful feeding bouts (49 dextral and 19 sinistral snails) with the varying prey size were used to investigate the feeding efficiency. To examine the effects of the snails' body size, the relative shell size (square root of the product of shell height by width, √HxW) was used. The mean snail sizes used in predation experiment are showed in Table 2. Snakes' feeding efficiency was evaluated by time duration and the number of mandibular movements in the feeding phase. The time from snakes' strike to dropping the shell was recorded as the feeding time. The total number of left and right jaw movements required for snail extraction in the swallowing phase was recorded as the number of jaw movements. The total weights of the prey and of the empty shell were used to calculate the weight of the prey mass gained by the snake. This value was used to evaluate the snakes' feeding efficiency regardless of the shell morphology.

Statistical analyses for experiment III

The effects of coiling direction, prey size and of their interaction on the snake's feeding efficiency were tested by generalized linear mixed model (GLMMs) with random effects regarding individual snakes and snail species.

Experiment IV: Role of snake's feeding apparatus for predation success

To investigate the effect of the asymmetry of the feeding apparatus on snake's predation success, dextral and sinistral snails with similar shell sizes (t-test, d.f. = 30, p = 0.49) were used in the experiment. The sample included 18 dextral snails *Cryptozona siamensis* (12 snails) and *Sarika resplendens* (6 snails); mean shell width 14.29 ± 0.77 mm S.E., and 14 sinistrals *Dyakia salangana* (5 snails) and *Ganesella rhombostomus* (9 snails); mean shell width 12.85 ± 0.67 mm) snails.

In experiment I, the snake performed head tilting behavior which might be a factor related to predation success. This experiment was to determine the role of mandibular asymmetry and the behavioral response of snakes for their predation success. The head-tilting direction of strikes, feeding time (from striking to dropping the shell) and total number of jaw retractions were recorded. Four of the six snakes, which died after finished the experiment were dissected, and the numbers of teeth on left and right mandibles were counted under a stereomicroscope.

Statistical analyses for experiment IV

The asymmetry index was calculated as 100x(R-L)/(R+L) following Hoso et al. (2007) where R referred to the number of teeth on right mandible and L referred to the number of teeth on left mandible.

The effects of coiling direction and prey size and of their interaction on the direction of snake's head tilting were tested by a generalized linear mixed model (GLMMs) with random effects of snake individual and snail species. The fixed effects of prey coiling direction, prey size and their interaction on feeding time and on the number of retractions were examined by GLMMs with random effects of snake individual and snail species.

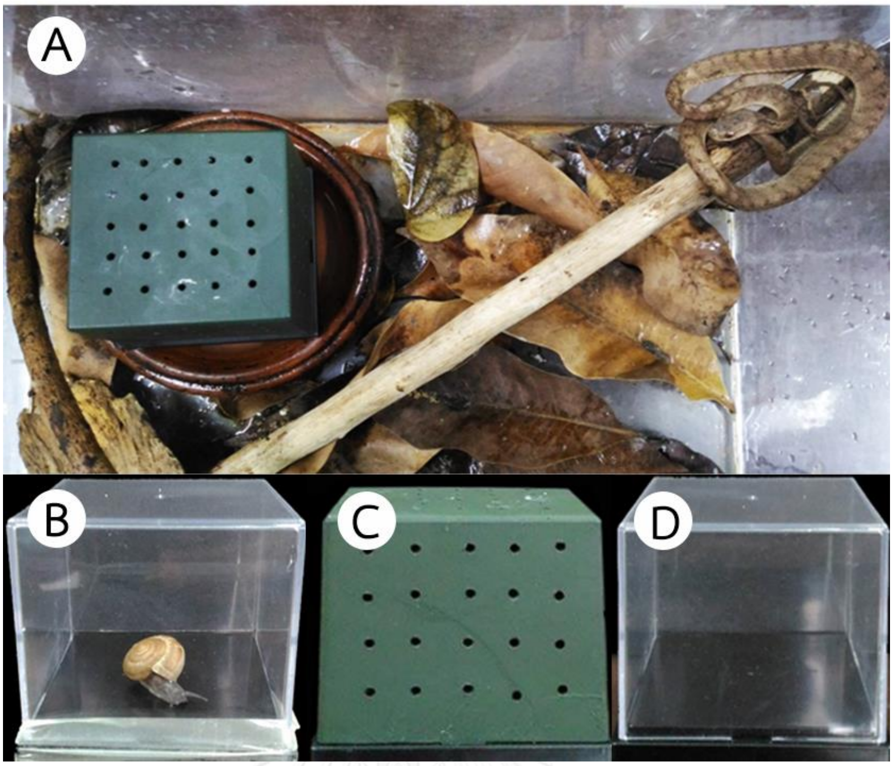


Figure 1 (A) Experimental setting to examine the role of visual and chemical stimuli in prey recognition (B) Visual stimuli (C) Chemical stimuli and (D) Control clear box

Table 1 The number of prey candidates presented to each snake

Snake no.	No. individuals presented to the snake		
	Snail	Semi-slug	Slug
1	1	2	0
2	3	1	1
3	7	1	0
4	4	1	2
5	1	4	2

Table 2 Mean size of snail used in predation experiment

Coiling	Prey species	n	Height (H)	Width (W)	Shell size (Square root of W*H)		
					(Mean ±S.E.)	Min	Max
Dextral	*Cryptozona siamensis*	56	13.3±0.5	21.0±1.0	16.7±0.7	7.01	27.08
	Ganesella capitium	2	12.2±0.1	14.5±0.1	13.3±0.2	13.27	13.30
	Sarika resplendens	16	10.3±0.4	19.6±0.9	14.2±0.6	9.16	17.17
	Satsuma sp.	2	18.6±0.1	26.8±0.2	22.3±0.1	22.28	22.35
Sinistral	*Dyakia salangana*	29	22.4±1. 7	15.1±1.1	18.0±1.3	4.65	29.96
	G. rhombostomus	9	11.1±0.2	12.5±0.5	12.0±0.4	10.29	13.53

Chapter IV

Results and discussion

Experimental I: Predatory behavior of the snail-eating snake

The snake began to stare at a prey candidate immediately when the latter was placed in front of the snake. The snake successfully preyed on a snail or a semi-slug provided in each experiment. In these cases with the snail or semi-slug, the snake performed closely similar behaviors for predation in sequence, which we described into the ethogram below in text, a table and figures.

On the other hand, the snake struck at none of the 5 slugs, although it fixed the eyes onto the slug in each case. In two of the five experiments with the slugs, the snake approached but moved away from each slug as soon as the snake touched the slug with the tongue. In the other three experiments, the snake even did not approach the slug.

The snake flicked the tongue more times toward the slug than toward the snail or semi-slug (p = 0.026), while the number of tongue flicks did not differ between the cases with the snail and semi-slug (p= 0.39) (Table 3). The snake, however, did not exhibit a behavior of strong breath to none of the five slugs, although the snake performed this behavior to every snail.

Three sequential phases can be recognized in predatory behaviors that result in successful extraction of the prey’s soft-body from the shell (Table 4, Figure 2). The first is a pre-capture phase from the moment of fixing the eyes at the prey candidate to the stage of pointing the head closely to the shell aperture. The second is a feeding phase from the moment of strike to the end of feeding, which was defined as the moment of dropping the shell. The third is a post-feeding phase from the stage of retracting the mandibles alternately to the end of characteristic behavioral displays. After this, the snake becomes inactive sitting on the substrate with no particular motions.

The fifteen behavioral displays which were visually distinguishable during the three phases and classified into nine categories of function inferred (Table 4). The snake performs some of these displays not in a determined sequence but alternately in many cases. The diagramed a typical sequence of these behaviors showed in a flow chart (Figure 2).

1. Pre-capture phase

The snake displays seven different behaviors in this initial phase. Major functions of these behaviors are hypothetically DETECTION, APPROACH and INVESTIGATE.

DETECTION: The snake begins two behavioral displays, eye-fix and tongue-flick,” immediately after the prey candidate is placed in front of them (Figure 3A). This suggests that these displays result from noticing the presence of potential prey. Subsequently the snake breathes by inflating and deflating its trunk strongly and frequently. The snake uses its eyes for vision and flicks its tongue for vomeronasal olfaction. Thus, the three displays, eye-fix, tongue-flick and strong-breath probably function to detect prey for the snake.

APPROACH: The snake begins to approach to the prey candidate only after the latter fully protrudes the soft body. After the three behavioral displays of the category DETECTION, the snake does not necessarily approach the prey candidate. This suggests that the snake decides not to approach when the snake does not obtain a positive sign by performing the preceding displays.

INVESTIGATE: Behavioral displays of this functional category occur after the snake approach the prey candidate. The snake displays neck-arch by moving the head closer down to the prey candidate and raising the anterior body part behind the head, which shapes an arch (Figure 3B). Then, toward the snail, the snake tilts the head leftward or rightward and pursues the head-on display by directing the head to face and point the shell aperture further closely (Figure 3B). These suggest that the snake investigates the exact where and how to strike at the prey. However, the snake tilted the head rightward toward five of the 10 semi-slugs, but struck the other semi-slugs without tilting the head.

2. Feeding phase

Four behavioral displays, which occur to feed on the preys' soft body, can be classified into the following three categories.

CAPTURE: The snake strikes and captures the prey. The snake captures the snail and the semi-slug by different manners. When preying on the snail, the snake locates the shell aperture by facing closely and then strikes. At the moment of strike, the snake handles the prey to insert the mandibles into the aperture and to lean the upper jaws against the ventral outer surface of the aperture (Figure 3C). One the other hand, the snake captures the prey by holding the mid body near the reduced shell with jaws and mandibles.

EXTRACTION: While feeding on the prey’s soft body, the snake alternately retracts the mandibles. These retractions of mandibles probably function to extract the soft body from the shell.

SWALLOW: While retracting the mandibles, the snake moves the anterior trunk zigzag in the air without creeping. During this action, a swollen part of the trunk moves rearward from the throat. This behavior may indicate that the snake transports the prey’s soft body from the mouth to the digestive tract.

3. Post-feeding phase

SHELL-DROP: The snake drops the shell without holding with the jaws, while continuing mandibular retractions.

MUSCULAR RECOVERY and/or MOUTH CLEANING: The snake continues to retract the left and right mandibles alternately, in a closely similar manner to mandibular retractions during feeding. There should be no need of extracting the soft body or feeding in this phase unless some part remains in the mouth. However, the snake consistently repeats retracting the mandibles after preying on a snail or semi-slug. Mandibular retractions therefore must be necessary, may be to recover the conditions of mouthparts. One possibility is to recover muscular conditions for mandible operation. The other is to remove mucus and/or soft body remains inside the mouth.

After feeding on the semi-slug, the snake pursued 3.4 times as many mandibular retractions as after feeding on the snail (p = 0.001) (Table 3). Mandibular retraction after feeding on the semi-slug was also 8 times as frequent as that after feeding on the snail (p = 0.002).

The snake also consistently displays two other behaviors that are characteristic to the post-feeding phase. One is gaping for several seconds (Figure 3D). The other is rubbing the mouth (Figure 3E-G). The snake opens the mouth widely at least once or multiple times between or at the end of mandibular retractions. This behavior may function to remove mucus remains inside the mouth and/or for muscular recovery. The snake tilts the head and rubs their mouth and chin with the available substrate several times (Figure 3E-G). After this behavior, an excessive remain of mucus outside the mouthpart disappears (Figure 4). This supports the present hypothesis that the mouth-rubbing behavior functions for removing mucus remains.

In average, gapes after feeding on the semi-slug were 3.2 times as many as those after feeding on the snail (p = 0.001) (Table 3). Gape frequency in the case of the semi-slug was also 4.8 times as high as that in the case of the snail (p = 0.003).

Prey-dependence of temporal pattern

The pre-capture phase in predation on the semi-slug was 3.3 times as long as that on the snail ($p < 0.001$) (Table 5). There was no difference between time lengths from fixing the eyes to striking at the snail and to averting the eyes from the slug, although the latter was not necessarily approached ($p = 0.33$). On the other hand, the snake finished feeding on the semi-slug's body after strike 13 times as fast as feeding on the snail's body ($p < 0.001$). During the feeding phase, the snake performed a smaller number of mandibular retractions ($p < 0.001$) when preying on the semi-slug than on the snail. The time lengths of the post-feeding phase in predations of the snail and semi-slug did not significantly differ from each other ($p = 0.14$).

The total time length over the three phases for predation was longer with the snail than that with the semi-slug ($p < 0.04$) (Table 5). The proportions of time consumption for the three phases depended on the prey type as follows. The proportion of time consumption for the pre-capture phase was larger with the semi-slug (59.7%) than that with the snail (14.5%) ($p < 0.002$) (Figure 5). The length of the feeding phase was, however, smaller in proportion with the semi-slug (4.4%) than that with the snail (45.5%) ($p < 0.01$). The proportions of the post-feeding phase in time length were not significantly different between these prey types ($p = 0.22$).

Discussion on Predatory behavior of the snail-eating snake

This study disclosed that *Pareas carinatus* achieves diverse behaviors in sequence for specialized predation on terrestrial pulmonates, exclusive of the present slug species. This study described 15 discrete displays of behavior in the three predatory phases. The snake performs behaviors of mandibular retraction, gape and mouth-rub with no exception, while no longer feeding after dropping the shell.

This result suggested the snake changes its predatory behavior by recognizing the present three types of pulmonates: snail, semi-slug and slug. The snake captured the semi-slug by striking down from the above of the prey in five of the total of 10 experiments. In these cases, the snake did not tilt the head before striking. The snake never showed this type of capturing manner to the snail prey. Thus, the snake changes behavioral manners to capture depending on the prey type.

Once the snake struck after the extended pre-capture phase, the snake finished feeding on the semi-slug one order of magnitude faster than feeding on the snail. The reduced shell of the present semi-slug only covers a small area of the dorsal surface and should not require specialized soft-body extraction unlike the shell of the present snail. These suggest that it is physically simpler or easier to eat the semi-slug’s body than the snail’s body. After feeding, however, the semi-slug required mandibular retractions and gapes more times and more frequently than the snail. Thus, the present semi-slug is probably more costly for *P. carinatus* than the snail in terms of energy expenditure for these post-feeding actions, while less costly in terms of feeding time.

The snake necessarily pursues mandibular retractions and gapes after dropping the shell. For these actions in the post-feeding phase, the snake spends around 40% of the entire time for predation. This indicates the importance and necessity of mandibular retractions and gapes after feeding. Various functions of similar gaping behaviors have been inferred to be for stretching the mandibles (Sazima 1989), facilitating vomerolfaction (Graves and Duvall, 1983) and examining mucus remains in the mouth (Cunningham and Burghardt, 1999). If the post-feeding behaviors (mandibular retraction and gape) are for stretching or reconditioning the mandibles, easier prey would require these actions fewer times. In the present study, however, the snake retracted the mandibles and gaped after feeding on the semi-slug far more times and frequently than after feeding on the snail, despite the remarkably prompt completion of semi-slug feeding. Thus, post-feeding mandibular retractions and gapes may play a major role for removing mucus remains in the mouthpart. However, it is crucially important to consider possible confusion of gaping with yawning (Cunningham and Burghardt, 1999). The results in this study indicate the importance of further investigation on the function of the post-feeding behaviors.

The South American snail-eating snake *Dipsas indica* preys on a snail *Drymaerus interpunctus* and a slug *Sarasinula linguaeformis* (Sazima, 1989). In contrast, the present snake *P. carinatus* stuck none of the five slugs presented. The snake approached two of these slugs and tilted the head, but did not proceed for the further steps of predation. Slugs and semi-slugs in general expose their soft bodies with no shell or only the reduced shell. Instead of forming the shell, slugs secrete sticky mucus (Smith, 2007) for physical protection, with defensive chemical compounds in some species, against predators (e.g. Pakarinen (1994); and see Luchtel and Deyrup-olsen (2001) for review). The snake does not prey on the present species of slug by distinguishing from the present semi-slug and snail species. There may be an ecological reason for this snake not to strike or prey on slugs. The results in this study present an empirical basis to investigate why and how the snake avoids the present shell-less slug.

This study compared behavioral responses of the snake to three types of pulmonate gastropods to obtain a basis that is necessary to design further experiments to answer questions of ecology and evolution on interactions between specialized snail-eating snakes and their prey. The present study provided a crucial ground to test confounding effects of species, phylogeny, structure, odor, behavior, and size of prey candidates to identify the causes of predator’s responses by conducting experiments in necessary designs.

Arboreal and ground snakes may differ in feeding techniques from each other. Ground dipsadid in the genera *Sibon* and *Tropidodipsas* drag the prey against a rock and twist their heads to pull the soft body out of the shell (Sheehy III, 2012). *Dipsas indica* usually coils around the snail and holds the shell against the snake body to extract the snail body (Sazima, 1989). On the other hand, snakes of the arboreal genus *Sibynomorphus* extract the snail body chiefly by mandibular actions (Peters, 1960; Sheehy III, 2012). This results show that the present arboreal species *P. carinatus* also captures the snail and extracts the soft body primarily by means of mandibular retractions as well as arboreal *P. iwasakii* (Hoso et al., 2007). This pattern suggests that similarities in predation behavior between South American dipsadid and Southeast Asian pareid may have resulted from convergent evolution.

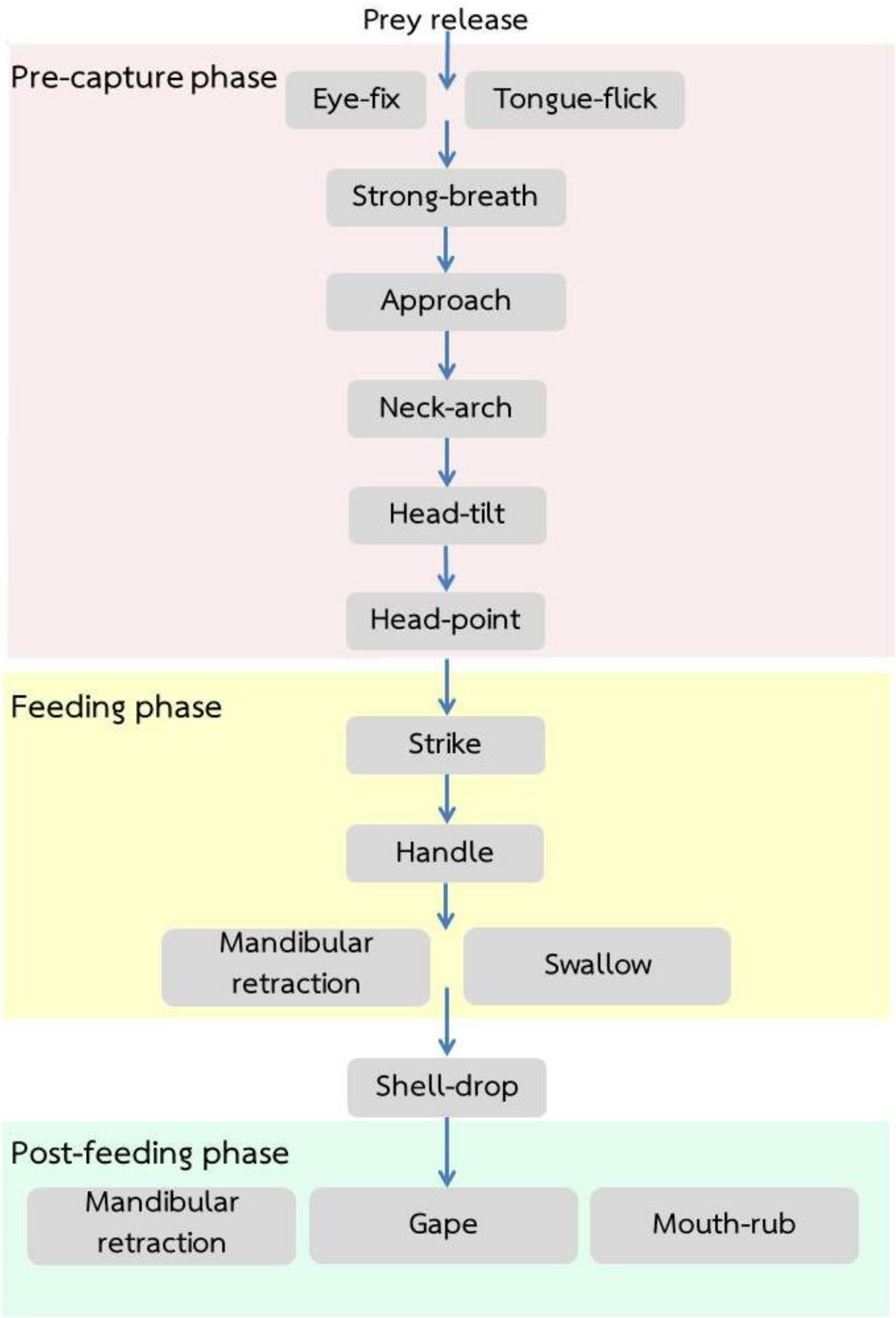


Figure 2 Flow chart of predatory behavior of the keeled-scaled snail-eating snake *Pareas carinatus*

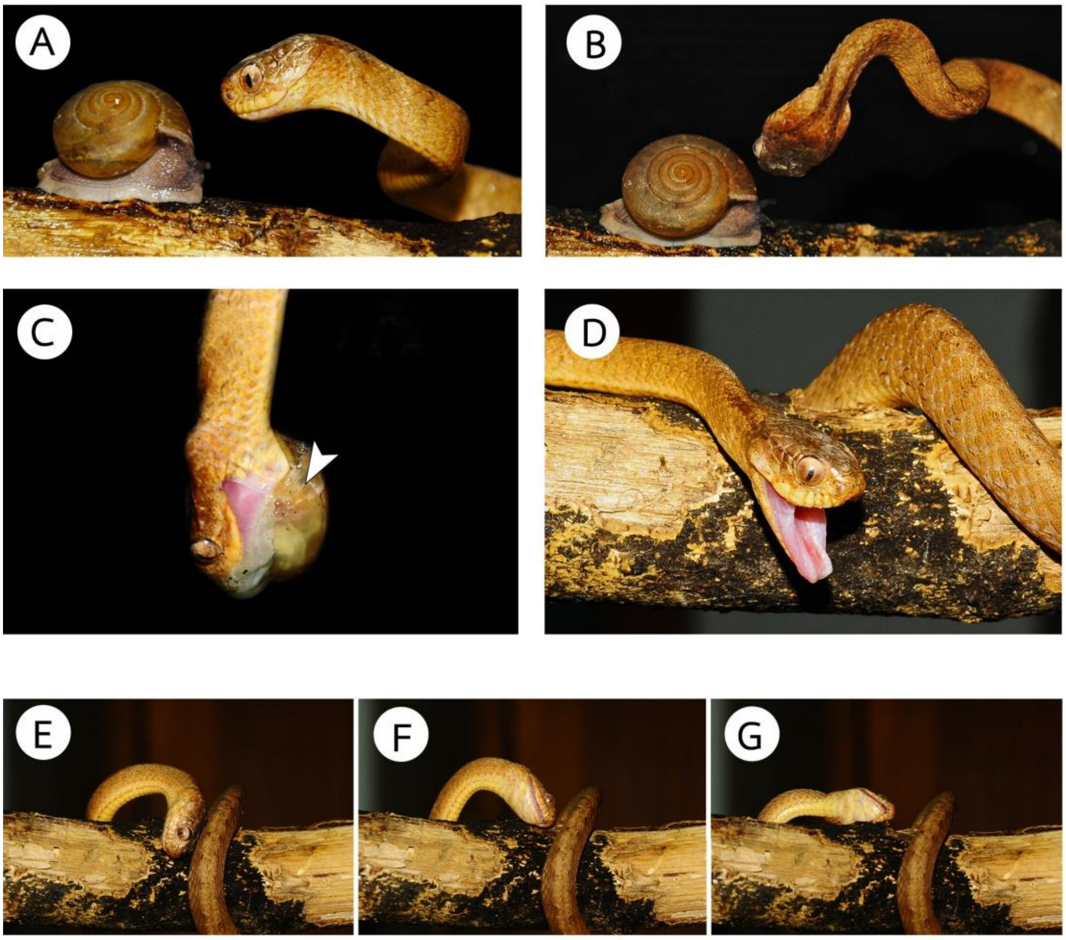
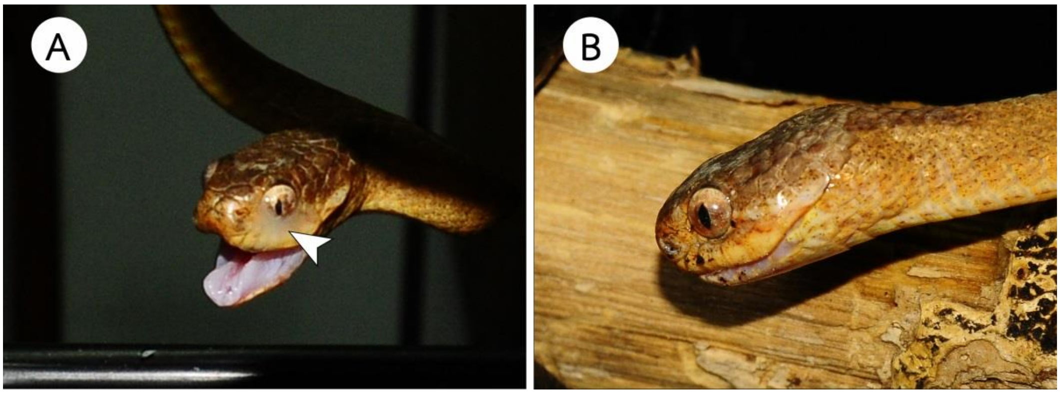


Figure 3 Typical behavioral displays of *Paras carinatus* in predation on a snail. (A) Eye fix. (B) Neck-arch and head-tilt. (C) Feeding by inserting the mandibles into the shell aperture. The arrow indicates the inserted left mandible. (D) Gape. (E)-(G) Sequential steps of mouth-rub.



.**Figure 4** Removal of mucus remains by mouth-rub behavior. (A) Before mouth- rub. A mass of mucus remains on the left upper jaw. (B) After mouth-rub. No mucus remains visible on the same snake.

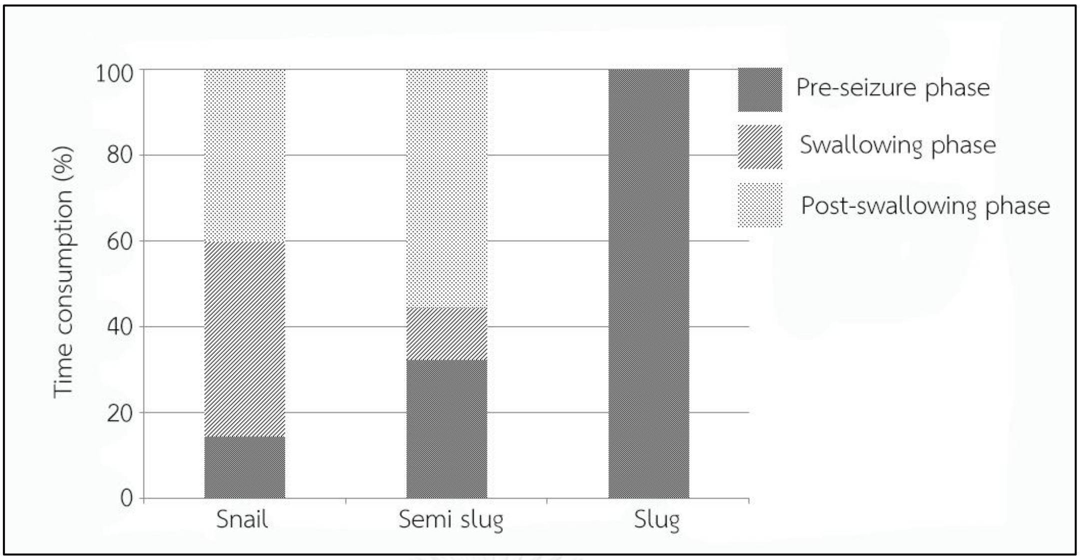


Figure 5 Prey-type dependence of temporal pattern of predatory phases

Table 3 Mean ± S.E. of numbers and frequencies of tongue-flicks before strike and of mandibular retractions and gapes after feeding

	Tongue-flick		**Mandibular retraction**		**Gape**	
	No.	**Freq.**	**No.**	**Freq.**	**No.**	**Freq.**
Snail **(n = 16)**	1.1 ± 0.6	0.02 ± 0.01	10.9 ± 2.5	0.05 ± 0.01	7.7 ± 0.8	0.06 ± 0.01
Semi-slug **(n = 10)**	1.6 ± 0.7	0.01 ± 0.01	36.9 ± 2.9	0.40 ± 0.9	24.6 ± 2.5	0.29 ± 0.09
Slug **(n = 5)**	9.4 ± 4.2	1.7 ± 0.8	-	-	-	-

Table 4 Predatory ethogram of the keeled snail-eating snake *Pareas carinatus*

Predatory phase	**Functional category**	**Behavioral display**	**Description**
Pre-capture	DETECTION	Eye fix	Staring at the prey candidate
		Tongue flick	Protruding and withdrawing the tongue
		Strong breath	Inflating and deflating the trunk strongly and frequently
	APPROACH	Approach	Creeping to the prey candidate
	INVESTIGATE	Neck arch	Raising the anterior body part and pulling the head down to the prey
		Head tilt	Turning the head leftward or rightward
		Head-point	Directing the head down to the aperture
Feeding	CAPTURE	Strike	Striking at the prey
		Handle	Seizing and lifting the prey up from substrate by inserting the lower jaws into the shell aperture and placing the upper jaws onto the ventral outer surface of the shell
	EXTRACTION	Mandibular retraction	Retracting left and right lower jaws alternately
	SWALLOW	Swallow	Transporting the prey's soft body to the esophagus
Post-feeding	SHELL-DROP	Shell-drop	Dropping the shell
	MUSCULAR RECOVERY	Mandibular retraction	Retracting left and right lower jaws alternately
	MOUTH CLEANING	Gape	Opening the mouth widely
		Mouth-rub	Rubbing the mouthparts onto a hard substrate

Table 5 Mean ± S.E. of time length (sec.) of each predatory phase

Prey types	Pre-capture	Feeding	Post-feeding	Total
Snail	67.1 ± 10.0	210.1 ± 48.0	184.3 ± 31.4	462.31 ± 104.40
Semi-slug	220.8 ± 31.8	16.1 ± 1.5	132.9 ± 24.7	400.00 ± 51.62
Slug	67.0 ± 43.7	-	-	-

Experiment II: Decision making of P. carinatus in predation

Part I: Decision making in predation

This part was extended from the pre-capture phase of the behavioral study (Experiment I) to understand prey selection in *P. carinatus*. The results of the feeding experiments indicate that *P. carinatus* completes feeding on both dextral and sinistral snails without cases of failing, however, not all prey specimens were struck by the snakes. During the pre-capture phase, the snake had twice decision making before striking, which is shown in Figure 6. The snake first decides either to approach or not to approach to the prey (decision I). After approaching, the second decision is either to strike or not to strike at the prey (decision II).

Feeding bouts started after placing the prey into the terrarium. The snakes began to fix their eye to the crawling snails after placing them there. However, in 43 of 144 cases the snails were not struck by the snakes. During period 1, the snakes approached to 64 of 76 (84.2 %) of the presented dextral and 26 of 38 (68.4 %) sinistral specimens. In the remaining cases, the snakes averted their heads from the snails and did not approach. The snakes kept staring at the snails during approaching and often repeated reorienting their heads towards the snails by shifting the head-tilting direction in a distance of 10 to 20 mm from the snails. This behavior during continuous staring suggests the importance of vision for critical operation of the mandibles and upper jaws at a moment of strike. The snakes struck at 52 of 64

(81.2%) dextrals and 19 of 26 (73.1%) sinistrals. In the other approaching cases, the snakes moved away from the snails without striking.

There was no difference in shell size between approached and not-approached dextral snails. In contrast, approached sinistrals were smaller than not-approached ones. This was significant in terms of the interaction effect between shell size and coiling direction on positive or negative approach decisions ($F_{1,110} = 5.4$, $p = 0.013$, Figure 7A). Similarly, struck and not-struck dextrals did not differ in shell size, whereas struck sinistrals were significantly smaller than not-struck sinistrals ($F_{1,86} = 6.0$, $p = 0.016$, Figure 7B). However, the mean shell size of the snails presented to the snakes did not differ between dextrals and sinistrals ($t = -0.56$, d.f. = 112, $p = 0.58$). Therefore, the snakes can distinguish the coiling direction of the prey before approaching and striking.

Squamates reptiles use tongue-flicking for vomeronasal chemoreception. However, in most cases of the present experiment, the snakes did not flick their tongues in 85 of 111 (76.6 %) cases before deciding to approach, and in 54 of 88 (61.4 %) cases before striking. In the other tongue-flicking cases, the number of tongue-flicks did not depend on the shell size ($F_{1,11} = 0.03$, $p = 0.86$ before deciding to approach, $F_{1,20} = 0.001$, $p = 0.99$ before the deciding to strike) or on the snails' handedness ($F_{1,11} = 0.08$, $p = 0.78$ before deciding to approach, $F_{1,20} = 3.5$, $p = 0.076$ before deciding to strike).

Without flicking the tongue, the snakes cannot obtain odors for vomeronasal chemoreception. Nevertheless, the snakes kept staring at, but did not approach to relatively large sinistrals ($F_{1,81}$ = 7.1 , p = 0.009, Figure 7A). After approaching, the snakes also made decisions for striking at small sinistral without tongue-flicking (Figure 7B). Thus, the snakes are assumed to recognize the prey handedness without relying on vomeronasal chemoreception by tongue-flicking.

Neither the time duration of staring nor approaching depended on the subsequent decisions ($F_{1,64}$ = 1.1 , p = 0.29; $F_{1,79}$ = 1.3, p = 0.26, respectively) or on the snails' handedness ($F_{1,64}$ = 0.03, p = 0.87; $F_{1,79}$ = 0.15, p = 0.70, respectively). In average, the snakes decided to approach in 10.3 sec ± 2.45 S.E. and to strike in 63.9 sec ± 7.93 S.E.

The frequency of tongue flicking did neither depend on the decision to approach nor on the coiling direction (Figure 8A), but it depended on the decision to strike, because the snakes exhibited lower flicking frequencies for positive decisions to strike regardless of the shells' coiling (GLMM, $F_{1,20}$=8.223, p=0.009, Figure 8B). Thus, the recognition of prey handedness did not rely on olfactory stimulus. However, olfactory reception was correlated with making the decision to strike.

Discussion on the prey selection of P. carinatus

It would be a considerable selective advantage for predators to avoid striking at low profitable prey specimens (Ferry-Graham et al., 2002). The present study evidences that the snail-eating snake *P. carinatus* shows a trend of prey-size selection especially for sinistral snails. In particular larger sinistrals were avoided by the snakes before striking. The size of dextrals did not influence the decision to prey. Once the snake decided to strike, predation was always successful regardless of prey size or coiling direction.

However, prey recognition does not occur in the congeneric species *P. iwasakii* (Hoso et al., 2007). *P. iwasakii* strikes by tilting its head leftwards consistently and fails in predation on a sinistral more frequently than on a dextral. It is likely that prey selection and recognition of the prey's coiling direction by snake predators facilitate to successfully capture the prey.

As soon as prey was placed in front of the snake, *P. carinatus* fixed their eyes onto the prey. This means that visual stimuli tempted the first response of the snake. Visual signals would provide physical information such as prey size, shape and also coiling direction. However, visual cues may add to or interact with chemical stimuli when both cues are simultaneously available (Chiszar et al., 1981). Interestingly, in most feeding bouts tongue flicking behavior occurred. It seems that *P. carinatus* does not rely on chemical stimuli of the prey. However from the period 2, critical for decision making, the frequency of tongue flicking was correlated with the decision to strike (Figure 8). This result implies that *P. carinatus* uses visual cues as a primary response and that these are crucial for making the decision to strike. Thus, in cases of positive decision, the snakes struck with relatively low frequency of tongue flicking behavior and flicked the tongue more frequently in negative decisions.

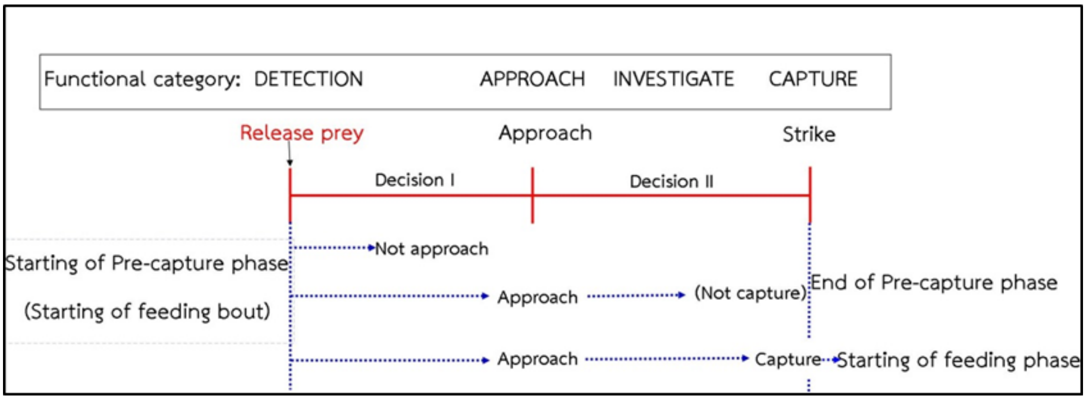


Figure 6 Schematic diagram presenting the two periods of decision making of *P. carinatus* related to their functional categories. Decision making of the snake occurred twice, before APPROACH and before CAPTURE.

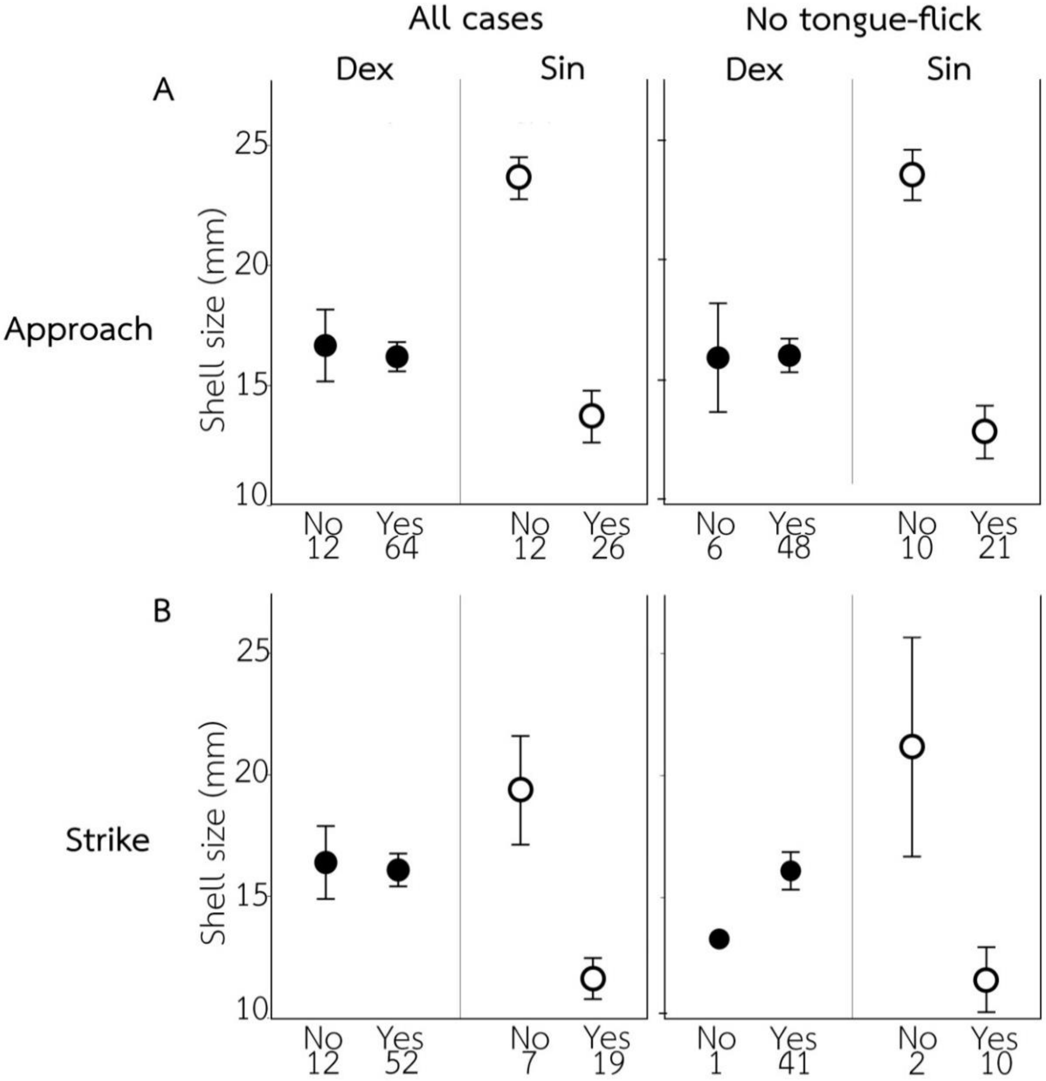


Figure 7 Handedness-dependent size effects on decision making reagarding approach and strike. (A) For the decision to approach (B) For the decision to strike. No and Yes are the negative and positive decisions, respectively. The snakes struck on snails only after approaching. Each number under the decision category indicates the number of replicates. The error bars indicate the mean and the standard error.

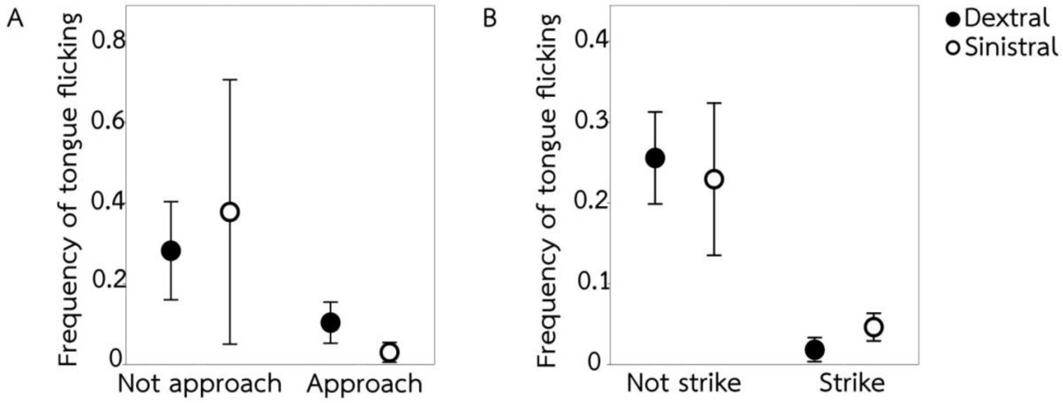


Figure 8 Frequency of tongue flick. (A) Mean ± S.E. until the snake averted the eyes from a snail without approach (no approach) and those until the snake approached a snail (approach). (B) Mean ± S.E. from approach to the end of approach without strike (no strike) and those from approach to strike (strike).

Part II. The role of visual and chemical cues in prey recognition

This part deals with the response of the snakes by means of visual and chemical cues to different prey species, which differ in coiling direction and transmission of chemical signals. Once the target (visual treatment, chemical treatment, combination treatment and control treatment) was placed into the terrarium, the snakes responded to the target by fixing their eyes or exhibited tongue flicking behavior. The initial response to the target was different depending on the type of stimuli ($F_{9,57}$= 2.435, p=0.02). The results indicate that the snakes exhibit eye fixing behavior stronger than other responding behaviors, and that they do not exhibit tongue flicking behavior as initial response to combination treatment. While visual or chemical signals were present, the snakes usually exhibited tongue flicking as the first response and in most cases of the control treatments but the snakes did not approach to the target (Figure 9).

The time interval from placing the target to the first responding behavior is related to the types of stimuli ($F_{2,14}$=11.554, p=0.006), regardless of the shell coiling ($F_{1,14}$=0.001, p=0.986). The snakes spent most time (16.25 ± 2.60 sec) to detect the control boxes without showing signs of prey stimulation while the snakes detect the target immediately (0.62 ± 0.17) during combination treatment. When the stimulation by prey is limited and only visual or chemical stimuli are provided, the snakes respond to the snail image more rapidly than to the snail odor (3.70 ± 1.95 and 10.49

± 4.01 sec respectively). The responding time of each type of stimuli showed in Figure 10.

The snakes did not approach to the control treatment at all, however among stimuli treatments, the approaching frequency was significantly different between visual, chemical and combined treatments ($F_{1,51}$ = 5.944, p = 0.005), with no effect regarding the coiling direction. The frequency of approaching to dextral prey between visual and combination treatment was similar ($F_{1,38}$ = 3.869, p = 0.06). However, the frequency of approaching to chemical stimuli was lower than to other treatments ($F_{1,44}$ = 7.653, p = 0.008) and did not different between snails of different coiling directions (Figure 11).

The role of chemical cues obtained by the total number of tongue flick demonstrate that the number of tongue flick is influenced by the type of stimuli ($F_{2,37}$ = 14.479, p = 0.001), which are not affected by the snail's coiling direction ($F_{1,37}$ = 0.398, p = 0.53). The snakes showed signs of strong chemical response by exhibiting a higher number of tongue flick for visual (19.83 ± 0.77 times) or chemical treatments (14.45 ± 0.01 times) and had lower tongue flicking responses (1.77 ± 0.04) during combination treatment (Figure 12).

Discussion on the role of visual and chemical cues in prey recognition

The relative importance of visual and chemical cues in predatory behavior of *P. carinatus* to stimulation by snail prey was examined in this experiment. The responding time of the snake is shortest when a combination of visual and chemical stimuli was presented, while the visual or chemical treatment and the control treatment are not significantly different in responding time. This means that the combination of visual and chemical stimuli facilitates the prey detection by for the snake.

Nevertheless, the snakes primarily use visual cues to recognize their prey. Nonetheless, they take advantage of chemical cues when visual or chemical cues are limited. Interestingly, the frequency of approaching was different between different types of stimuli and was influenced by the coiling direction of the snails. The snakes showed the lowest frequency of approaching to chemical treatments when visual and combined treatments were oriented towards the same patterns. For visual and combined stimuli, the snakes tended to approach to the stimulus by dextral prey, but did not respond to the stimulus by sinistral prey. The snakes' approaching towards chemical stimuli was not significantly different between prey specimens of different coiling direction, which means that the snails' images might affect the snakes' decision to approach or not to approach the prey specimens. In addition, the snakes are able to distinguish the coiling direction of the prey before approaching.

Different snail species produce varying kinds of chemical substances (odors), but *P. carinatus* does not seem to rely on odors to distinguish its prey. However, tongue flicking behavior was observed during the decision period before approaching towards the prey, so it is possible that chemical stimuli facilitate the prey detection while visual stimuli play the most important role for the snake to discriminate between different coiling directions.

Most snakes use visual and chemical cues in prey detection. However, the relative importance of sensory cues depends on the foraging mode and activity patterns of the prey (Cooper Jr, 1995). When snake loss of particular cue (visual or chemical), chemical response obtained by tongue flicking behavior was distinctively occur for initial response. While snake exhibited eye fixing response rather than flicking tongue when image and odor of prey were presented. Moreover, tongue flicking behavior was distinctively occurring for visual and chemical stimuli while insignificant when combination of cue was present.

These results suggest that the snakes use a combination of visual and chemical cues to make the decision to approach and support that visual cues might play the major role in distinguishing between dextral and sinistral prey specimens before the approaching decision is made.

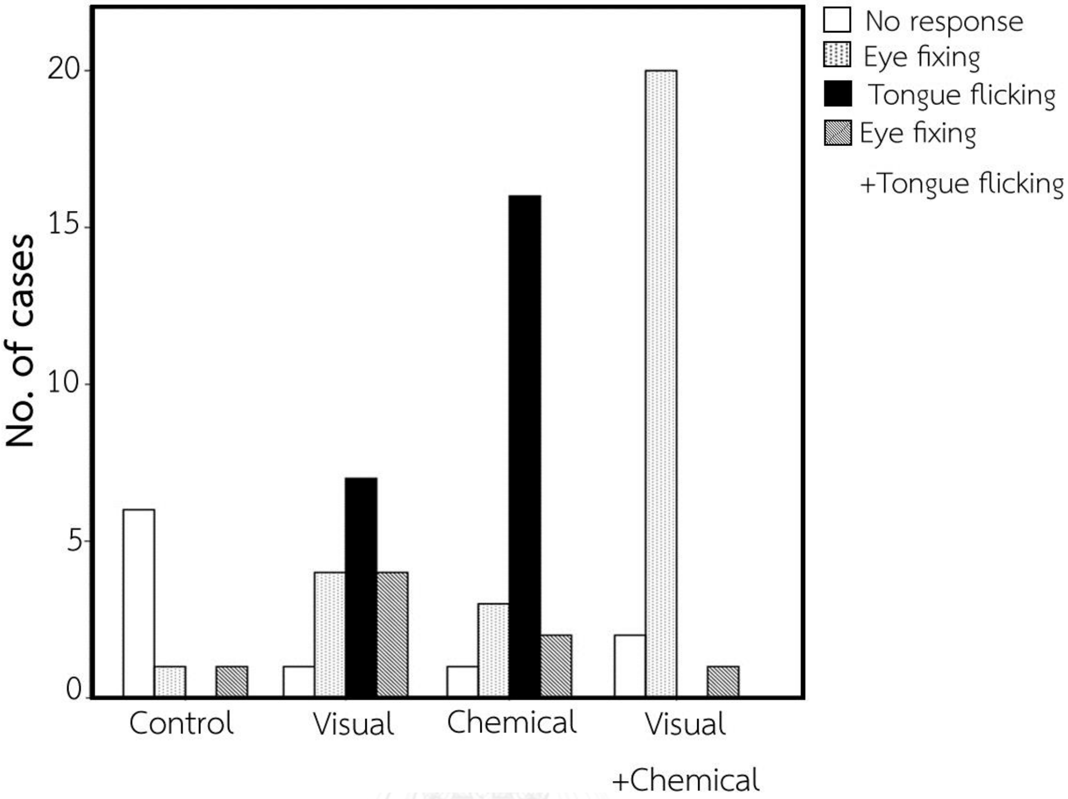


Figure 9 Proportion of initial responses of the snakes to each type of stimulus

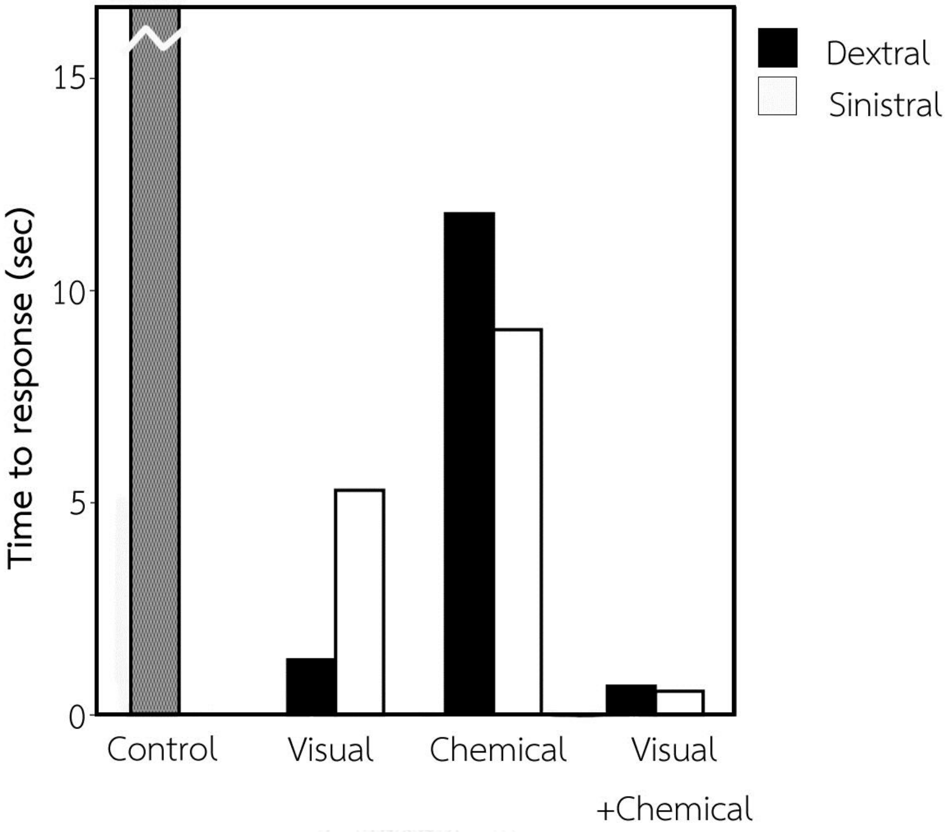


Figure 10 Responding time of the snakes to various types of stimuli from snail prey

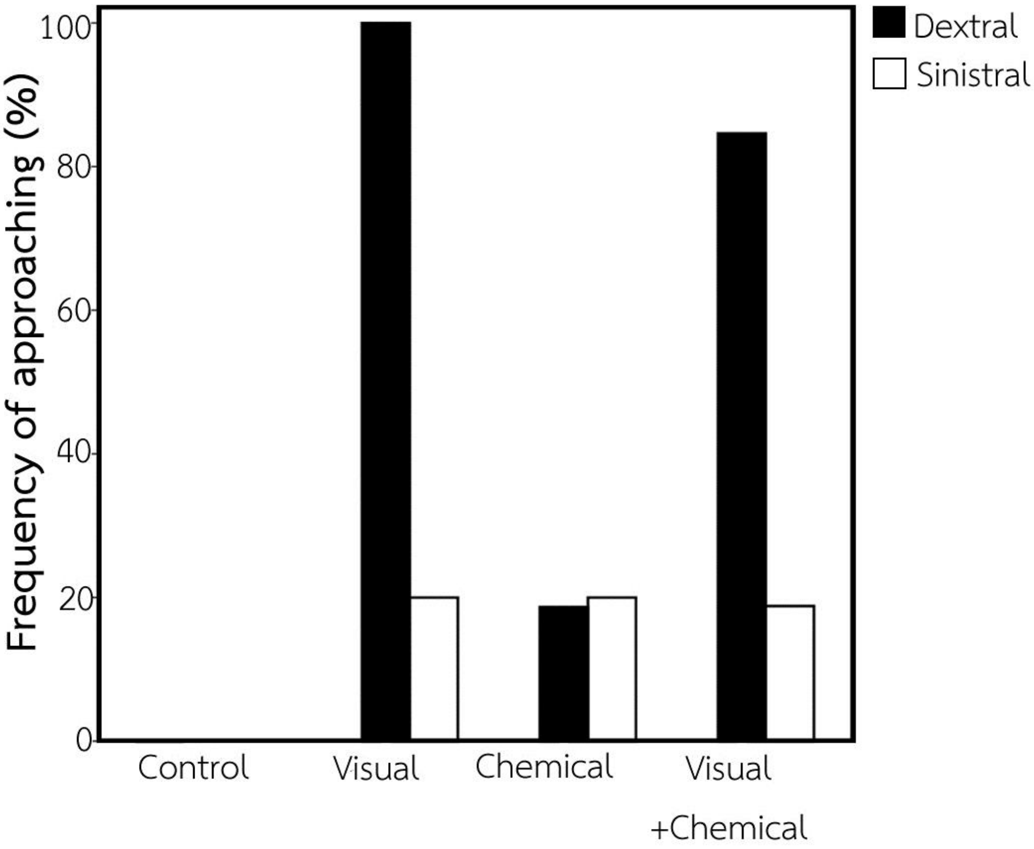


Figure 11 Approaching frequency of the snakes to different types of stimuli

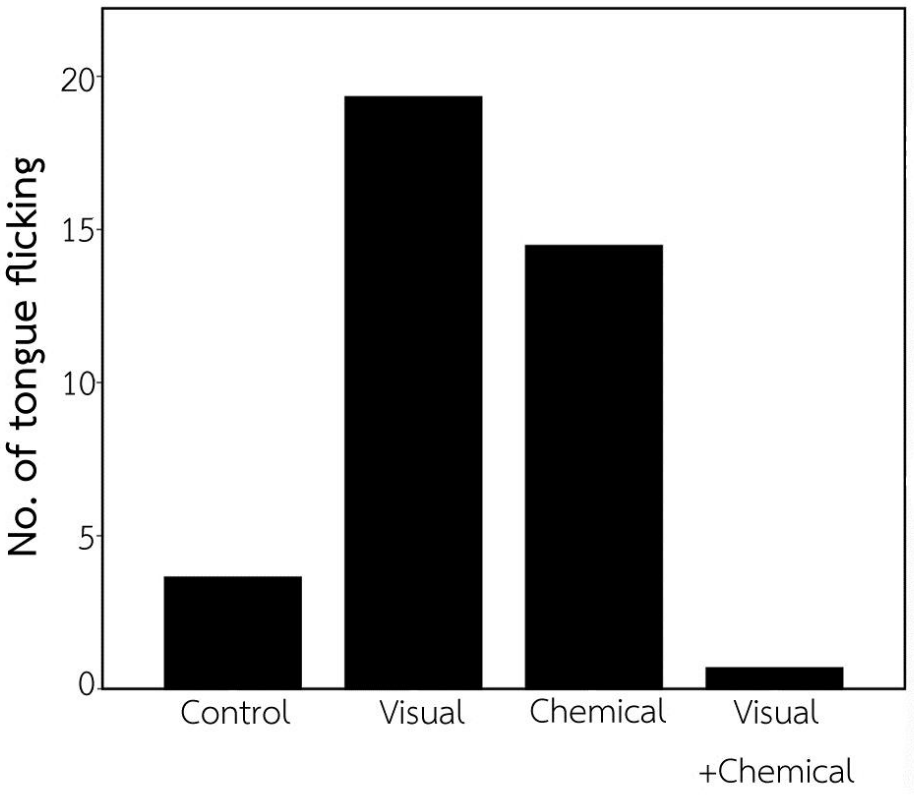


Figure 12 Number of tongue flick of the snakes towards different types of stimuli

Experiment III: Effect of prey morphology on feeding efficiency

The snake took a longer time to finish feeding on a larger snail, regardless of prey handedness ($F_{1,64}$ = 4.6, p = 0.036, Figure 13A) and retracted the mandibles more times while feeding longer ($F_{1,64}$ = 057, p < 0.001, Figure 13B). However, the number of retractions increased only with the size of dextral prey ($F_{1,47}$ = 31, p < 0.001) but did not with the sinistral's size ($F_{1,17}$ = 0.65, p = 0.43, Figure 13C). Thus, difference in the number of retractions between enantiomorphs depended on the prey size ($F_{1,64}$ = 9.7, p = 0.003).

The snake rectracted the mandibles more frequently while preying on the dextral than the sinistral ($F_{1,64}$ = 5.3, p = 0.024, Figure 13D). The prey mass gained per retraction increased with the dextral prey size ($F_{1,47}$ = 66, p = 0.024) but did not with the sinistral prey of difference size ($F_{1,17}$ = 0.008, p = 0.93, Figure 13E). The interaction between the size and handedness was accordingly significant ($F_{1,30}$ = 8.1, p = 0.008). Thus, when preying on the dextral, mandibular retractions are not only more frequent but also increasingly more efficient with the prey size in terms of gain per retraction. This suggests that physical difficulties of extracting the soft body from the sinistral shell may be responsible for reductions in the total number and frequency of retraction.

Superior performances in dextral-feeding in terms of retraction frequency and efficiency synagetically resulted in a significantly larger gain per time than a gain by sinistral-feeding ($F_{1,30}$ = 8.5, p = 0.007) (Figure 13F). This benefit of preying on the dextral instead of the sinistral increased with the shell size ($F_{1,30}$ = 8.0, p = 0.008), as the gain per time positively depended on the dextral's size ($F_{1,47}$ = 57, p = 0.001) but not on the sinistral's size ($F_{1,17}$ = 0.15, p = 0.70).

In Figure 13A, 14C and 14D, regression lines for the dextral and sinistral cases cross at the shell sizes of 11.4, 12.1 and 12.7 mm, respectively. This predicts that the relative value of sinistral prey declines with the increase of the size. In practice, the snake preyed on all of the sinistrals smaller than 12.4 mm. However, the snake did not strike at 18 of the 26 (69.2%) sinistrals snails larger than this size. These cases of avoidance do not appear in Figure 13, but nevertheless correspod to the range beyond the predicted threshold of around 12 mm. These results support that the size-dependent increase of cost for preying on a sinistral instead of a dextral has driven the evolution of prey-handedness recognition and size-dependent avoidance of sinistral-predation.

Discussion for Experiment III

The results of this experiment demonstrate that the efficiency of predation on dextral and sinistral prey is related to the prey size. Predation efficiency of the snake with dextral prey was relatively high when the prey was large. The efficiency of predation was low when the snake preyed on large sinistral prey. Consistent with the prey size selection before striking (shown in experiment II), the snakes did not strike at 18 of the 26 (69.2%) sinistrals in cases where the prey size was larger than 12.4 mm. This means that the size-dependent increase of cost for preying on a sinistral instead of a dextralis a reason for prey-handedness dependent prey-size selection in *P.carinatus*.

In terms of the optimum foraging theory, feeding efficiency may involve maximizing the net energy or nutrient gain or minimizing the time and energy spent to gain the same amount of resources (Pedro and Castellanos, 2005; Pyke, 1984; Stephens and Krebs, 1986). Predator preference depends on prey abundance as well as prey size and predation cost in many predators. For example, savannah monitor *Varanus albigularis* eats large and small snails indiscriminately when the prey is available in low density. However, at high density, *V. albigularis* prefers eating large snails rather than smaller ones (Kaufman et al., 1994). The tiger snake *Notechis scutatus* shows behavioral plasticity in response to different proportions of prey types (Aubret et al., 2006). Prey preference and behavioral adaptations of predators depend on feeding habit and availability of prey. Especially in widespread predators, local adaptation in response to the varying proportion of prey was observed (Aubret et al., 2006; Burghardt and Krause, 1999; Cooper et al., 2000).

In the results of this study, avoidance of preying on a large sinistral in *P. carinatus* corresponds with reduction in feeding efficiency. The size-dependent increase of cost for preying on sinistral rather than dextral preys might be affected by the proportions of dextral and sinistral in their habitat.

The field records evidenced that *P. carinatus* is an arboreal snake and frequently active on trees, co-occuring with pulmonate tree snails. Within the distribution range of *P. carinatus*, dextal and sinistral snails could be a potential prey for the snakes. These coexisting tree snail species are almost invariably sinistral (subgenus *Syndromus*) or chirally dimorphic within populations (subgenus *Amphidromus*). Their high abundances are well established (Craze et al., 2006; Nakadera et al., 2010; Schilthuizen et al., 2005; Sutcharit et al., 2007; Sutcharit and Panha, 2006). Within the distribution range of *P. carinatus*, dextal and sinistral preys represent potential prey for the snakes, however, sinistral taxa make up only 17.0% in 900 potential prey species (17.3% in 75 genera) (Table A1). In this case, the predator does not seem to have evolved to better exploit sinistral prey by arms race. Instead, snake has shifted to avoids the cost of unsuccessful or inefficient sinistral-predation attempts because the "easier" prey type (dextrals) is more abundant. This behavioral response by visual recognition reduces the risk for the snake to expend foraging time and energy by handling unsuitable prey on the other hand, also reduced the risk for sinistral snails to undergo physical attacks by the snakes. Sinistrality therefore functions as a warning sign to the predator. Predator's recognition of prey handedness, which benefits both the snake predator and sinistral prey, could further accelarate ecological prey speciation by a reversal gene.

Results from this study demonstrates different patterns of size-dependent predation by previous study in *P. iwasakii*. Previous study showed that *P. iwasakii* fed on the dextral wild-type of *Bradybaena similaris* more efficiently than on its sinistral mutants (Hoso et al., 2007). However, the snake struck on both dextral and sinstral prey without distinction and lead to less percentage of predation success on the sinistral compared with the dextral. Interestingly, no sinistral tree snails are found within the distribution range of *P. iwsakii*, this snake lives only on two islands with a ground-dwelling sinistral species (4.3%) and 22 dextral species. Thus, it would rarely encounter a sinistral compared to a dextral. Possible that advantageous to predation on dextral prey are relatively high when prey was larger and the proportion of sinistral snails in the snake habitat may have driven the ability to recognize prey-handedness for size-dependent avoidance of sinistral-predation.

A single gene is responsbile for the reversal of primary and secondary asymmetries in pulmonate snails (Asami et al., 2008; Okumura et al., 2008). The snail-eating snake *P. carinatus* notices the coiling direction by staring at the snail and exhibits signs of prey recognition before striking (see also experiment I and II). The visual recognition of snail handendess is accordingly assumed to be an evolutionary response of the snake to sinistral snails, which have increased under specialized dextral-predation by *Pareas* snakes (Hoso et al., 2007; Hoso et al., 2010). Thus, a chirality specialized predators can evolve the ability to recognize prey asymmetry where dimorphic prey was presented in their habitat especially in *P. carinatu*s.

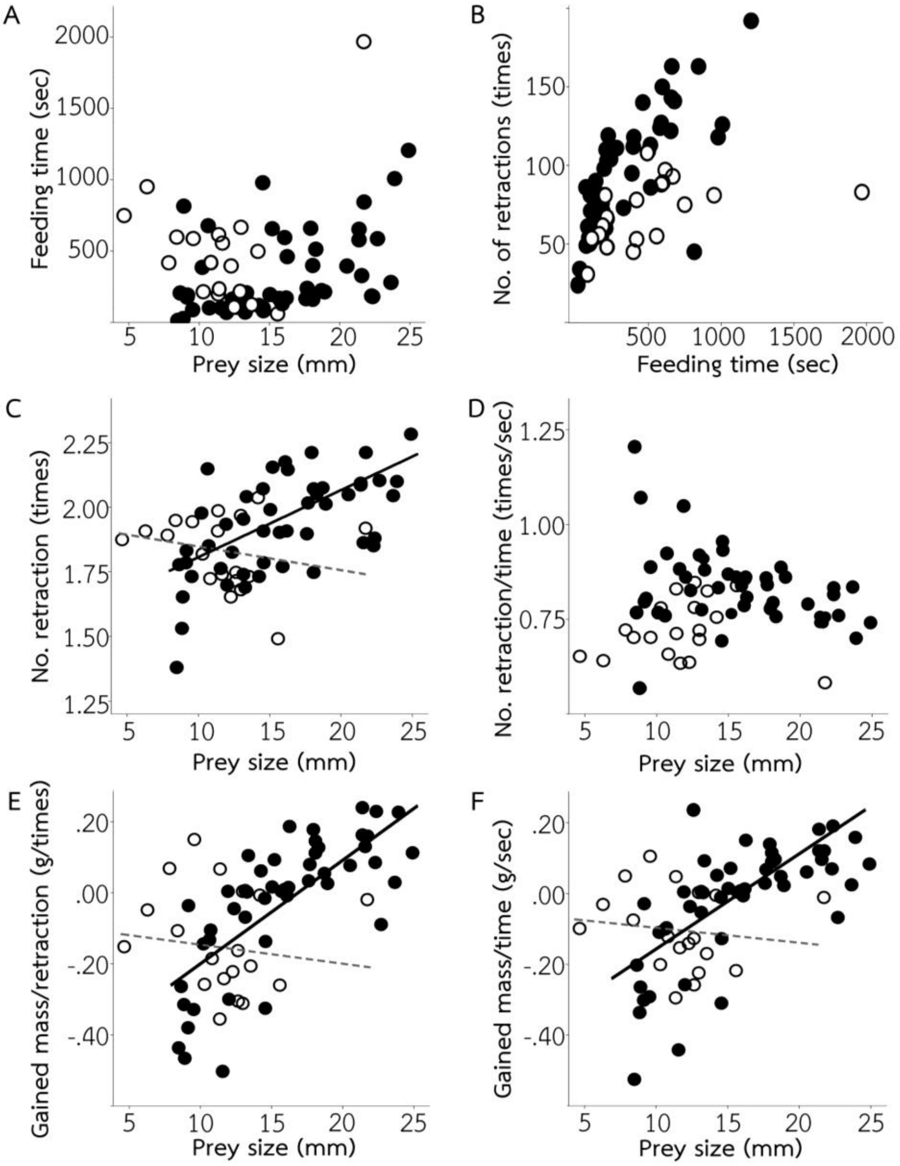


Figure 13 Size-dependent efficiencies and benefits of preying on dextral snails. (A) Feeding time of the snakes depending on the prey size regardless of the prey's handedness (B) The Number of retractions increased with feeding time (C) Size dependent increase of the number of mandibular retractions only in dextral-predation. (D) Higher retraction frequency in dextral-predation than in sinistral-predation. (E) Size-dependent increase of soft-body mass gained per retraction only in dextral-predation. (F) Size-dependent increase of relative benefit only in dextral-predation. Solid and open circles indicate predations on dextrals and sinistrals, respectively. Solid and dash line indicate regression line of predation efficiency on dextrals and sinistrals respectively.

Experiment IV: The role of the snake's feeding apparatus for predation success

The numbers of left-right mandibular teeth of the four snakes are shown in Table 6. The results demonstrate that the morphological asymmetry of the present specimens of *P. carinatus* was quantitatively weak. Prey size affected to snake's decisions to prey and feeding efficiency.

The mean feeding time (± S.E.) was 257 ± 65 seconds for dextral prey and 345 ± 56 seconds for sinistral prey. The mean number of retractions was 70 ± 6 times for dextral prey and 66 ± 6 for sinistral prey. Between dextral and sinistral prey, there were no significant differences in feeding time (GLMM, $F_{1, 28} = 0.95$, $p = 0.34$) or in the number of retractions ($F_{1, 28} = 2.46$, $p = 0.13$) on these measurements of predation performance.

Moreover, for this experiment also the behavioral responses of the snakes to the different coiling of prey by head tilting behavior were recorded. The results indicated that the snakes tilted their heads either leftwards or rightwards towards the prey before striking. Among the 32 cases, however, there was no statistically significant between the directions of head-tilt and prey coiling (Fisher's exact test, $p = 0.15$, Table 7). Likewise, the tilting direction did not depend on the prey size (GLMM, $F_{1, 28} = 2.83$, $p = 0.10$) or its interaction with coiling direction ($F_{1, 28} = 2.55$, $p = 0.12$). Each snake struck at prey in the same direction as tilting the head. Thus, the left-right direction of strike, as well as the head tilting direction, was neither fixed nor dependent on the direction of prey coil. *P. carinaus* does not fail in dextral or sinistral-predation either by leftward or rightward striking.

Discussion for Experiment IV

Many studies of animal behavior have shown the association of ecological performance and asymmetry in morphology (Asami et al., 1998; Hori, 1993; Hoso et al., 2007; Inoda et al., 2003; Lucky et al., 2012; Takeuchi and Hori, 2008; Yasugi and Hori, 2012).

The response to left-right reversed snail prey might vary between species in the genus *Pareas*. *P. iwasakii* failed in about 25% of predation attempts on sinistral *Bradybaena similaris* by leftward-fixed strike (Hoso et al., 2007). In contrast, the results of the present study suggest that the direction of either head-tilting or striking is not functionally crucial for predation in *P. carinatus*. The snakes do not fail in predation on dextral or sinistral regardless of whether they strike leftwards or rightwards. This means that specialized handling of asymmetric prey does not necessarily rely on the striking direction opposing to the deduction from the previous studies.

These two species do not only differ in their behavioral responses, but also in dentition asymmetry. The individuals of *P. carinatus* used in the present study showed a weaker dentition asymmetry than previously known. These two species do not only differ in their behavioral responses, but also in dentition asymmetry. The individuals of *P. carinatus* used in the present study showed a weaker dentition asymmetry than previously known. In contrast, the previously examined specimens of *P. iwasakii* were highly asymmetric with an index of 17 (Hoso et al., 2007). Consequently the results regarding feeding efficiency of *P. iwasakii* were interpreted as higher efficiency of dextral-predation compared to sinistral-predation in terms of feeding time and number of mandibular movements.

The efficiency of feeding on dextral prey relative to sinistral prey may depend on the strength of dentition asymmetry. If so, weaker dentition asymmetry may represent weaker specialization in dextral-predation.

Within the distribution ranges of *P. carinatus* and *P. iwasakii*, dextal and sinistral snails could be potential prey for the snakes. However, the proportion of co-existing sinistral prey within the range of *P. carinatus* is relatively high (Table A1) compared to the number of sinistral snails within the range of *P. iwasakii*.

This study highlights the importance of quantitative examinations on the role of the predator’s handedness regarding predation on asymmetric prey with clear attention to the variability within the genus *Pareas*. However, this study does not aim at quantifying the geographic variation of handedness within the genus *Pareas*. *Pareas carinatus* is widely distributed in both continental and insular regions of Southeast Asia (Wallach et al., 2014). In contrast, *P. iwasakii* is confined to two small islands (Ota et al., 1997). Further studies on the geographic variability of the degree of asymmetry within predator species and on the functional role of asymmetry are needed to understand the evolutionary history of asymmetries in morphology and behavior.

Table 6 Asymmetry index of four snakes which died after finished the experiment.

Snake no.	No. of mandibular teeth		Asymmetry
	Left	Right	index
1	21	23	4.55
2	16	19	8.60
3	19	20	2.56
4	20	21	2.44

Table 7 The numbers of leftward and rightward head-tilts and strikes at dextral and sinistral snails

Coiling direction	**Head-tilt/striking direction**	
	Leftward	**Rightward**
Dextral	13	5
Sinistral	6	8

Chapter V

Conclusion

Specialist predators exhibit more specialized feeding apparatuses or feeding techniques than predators with broader diets (Abrams, 2000; Dawkins and Krebs, 1979). However, so far there has been limited number of studies on prey specialization and feeding efficiency in specialized predators.

This study is of crucial importance for the understanding of morphological adaptations and behavioral responses of the keeled-scaled snail-eating snake *Pareas carinatus* Wagler, 1830 to its prey. This study examined predatory behavior of *P. carinatus* in three predatory phases. The snake displays fifteen serial behaviors. The snake changes its predatory behavior by recognizing differences between pulmonate prey: semi-slug (*Durgella* sp.) and slug (*Semplerula siamensis*).

This study emphasize the response of snake to dextral and sinistral snail, which provide different odors (Lloyd, 1970). However, striking behavior does not depend on species or coiling of the prey. Before striking, the snakes show a trend of prey-size selection, especially for sinistral snails. Although the mean shell sizes presented to the snakes in this study did not differ between dextrals and sinistrals which no choice of prey was given. The size of struck and not-struck dextrals was similar, while sinistrals, which were not struck, were generally larger than those which were struck. Therefore, the snakes distinguish the prey enantiomorphs during the pre-capture phase.

In the present experiment, however, the snakes did not flick their tongues in 85 of 111 (76.6%) cases before deciding to approach and in 54 of 88 (61.4%) cases before deciding to strike. In the rest of the cases (tongue-flicking cases), the number of tongue-flicks did not depend on the shell size or on snail handedness, respectively. These results rule out olfactory recognition of sinistral specimens by the vomeronasal system, which is typically important for the reptiles' chemical recognition (Weaver and Kardong, 2010). This suggests that visual structure perception is necessary for the chiral-specific predation and overrides chemical odor distinction when the prey is visible. Dextral and sinistral shells are physically discrete in coiling direction and lateral location of the aperture, through which the soft body is extracted. These major differences in shell structure may serve as a visual cue for the snake to distinguish between prey enantiomorphs. However, the snake exhibits tongue flicking behavior more frequently when visual or chemical stimuli are limited. It is possible that *P. carinatus* may rely on odors to investigate the surrounding environment.

Once the snake has chosen the convenient prey, predation on prey of both chirality types is always successful by using lower jaw retraction to extract the snails' soft body from the shell. It is possible that sinistral prey-size selection during the pre-capture phase influences the predation success in *P. carinatus*. However, sinistrals are more costly than dextrals. The results from experiment III support that there is a size-dependent increase of cost for preying on a sinistral relative to preying on a dextral in terms of prey mass gained per retraction and per feeding time. Moreover, specialized handling of asymmetric prey by the present snake species does not rely on the direction of striking behavior or the strong asymmetry of mandibular morphology.

Many studies have shown that the ecological performance of species can be correlated with the direction of asymmetry in morphology and/or behavior (Asami et al., 1998; Hori, 1993; Hoso et al., 2007; Inoda et al., 2003; Lucky et al., 2012; Takeuchi and Hori, 2008; Yasugi and Hori, 2012). However, asymmetry of feeding apparatus is may be advantageous for predators for chirality specific predation (Dietl and Vega, 2008; Hoso et al., 2007; Quensen Iii and S Woodruff, 1997; Shigemiya, 2003). Previous studies suggest that the low efficiency of sinistral predation in *P. iwasakii* is due to its leftward-fixed striking behavior without prey-handedness recognition and to its most extreme dentition asymmetry within the genus *Pareas* (Hoso et al., 2007). Accordingly, in *P. iwasakii*, the efficiency of dextral predation is clearly stronger than that of sinistral predation. This limitation of this snake predator might lower the predation potential regarding sinistral prey within their distribution range. Frequent failure in predation on a sinistral and the survival of the latter suggests that sinistral variants better survive snake predation and thus are positively selected within the range of *P. iwasakii*, which may lead to the fixation of sinistral populations (Hoso et al., 2010).

Through predator-prey interactions, predation may drive the evolution of morphological traits in prey species. The shell morphology of snail prey might show anti-predator characteristics, which correspond to their survival rate and are under selection pressure by predation (Covich, 2010). Sample cases on predation of *P. iwasakii* on snails of the genus *Satsuma* indicate that sinistral linages could further accelerate adaptive speciation by evolving from dextral ancestors, especially when populations are co-existing with snake predators (Hoso et al., 2010). Not only predation pressure, but also reproductive limitations regarding the copulation of dimorphic prey might result in the fixation of sinistral populations. Once sinistrals exceed 50% in phenotype, positive frequency-dependent selection eliminates the dextral minority even with no further predation on dextrals, because of physical difficulty in mating between dextrals and sinistrals.

In contrast, *P. carinatus* does not fail in dextral or sinistral predation neither by leftward nor rightward striking as long as it strikes. The mean dentition asymmetry among four of the six snakes used in this study was low (4.5%) (Danaisawadi et al., 2015). It is possible that the adaptation to dimorphic prey among snail-eating species occurs at different levels. In this case, prey-handedness recognition and prey-handedness dependent selection of prey size, the snake feed on small sinistral prey. The snake avoids preying on large sinistrals, while preying on dextrals regardless of the shell size in the range of prey size used in this study. The snake only prey on a sinistral that is small enough to feed with an equivalent efficiency of feeding on a dextral of the same size.

On the other hand, the proportion of dimorphic prey might affect the predator's recognition of the prey handedness.

These different responses of P. carinatus to dextral and sinistral snails can be understood by the relative abundance of sinistrals in its habitat.

Within the distribution range of *P. carinatus*, dimorphic tree snails are highly abundant (Craze et al., 2006; Nakadera et al., 2010; Schilthuizen et al., 2005; Sutcharit et al., 2007; Sutcharit and Panha, 2006). Sinistral taxa that could be potential prey constitute around 17.0% in 900 species (17.3% in 75 genera) (Table A1). My field records show that specimens of *P. carinatus* are frequently active on trees where pulmonate tree snails co-occur. These tree snail species are almost invariable sinistral (subgenus *Syndromus*) or chirally dimorphic within populations (subgenus *Amphidromus*), in contrast to the snail species in the habitat of the congeneric snake *P. iwasakii*. The latter snake lives on two islands with only one sinistral (4.3%) and 22 dextral species (Hoso et al., 2010). Thus, it rarely encounters a sinistral compared to a dextral.

Since sinistral snails are rare in the habitat of *P. iwasakii*, prey-handedness recognition is not necessary. The probability of encountering dextral prey is extremely high, which may explain that the snake does not recognize prey handedness and frequently fails in preying on a sinistral. Since sinistral snails are relatively more abundant in the habitat of *P. carinatus*, prey recognition should be advantageous to avoid striking on costly sinistral prey. The snakes' morphology and behavior are believed to have shifted to avoid the costs of inefficient sinistral predation because easier dextral prey still remains predominant. It is likely that the recognition of snail handedness is an evolutionary response of the snake to sinistral snails, which have increased under specialized dextral predation by *Pareas* snakes (Hoso et al., 2007; Hoso et al., 2010).

The currently available molecular phylogeny including *P. iwasakii* suggests that *P. carinatus* may represent a relatively basal lineage within the genus (You et al. 2015; but see Pyron et al, 2013 for a different view). However, this study does not aim at quantifying the geographic variation of handedness within and between snake species, although response to prey handedness of pareid snakes might be occur in different levels. This study may not entirely explain the arms-race between snake predators and snail prey however the results extend our knowledge on the responsiveness of specialist predators to different prey coiling and also point out the advantages of reversal of prey coiling as a result of predation by snail-eating snakes. The present study provide crucial information for understanding the co-evolution of these taxa and represent a solid basis for further investigations on this subject.

REFERENCES

Abrams, P.A. 1986. Adaptive responses of predators to prey and prey to predators: the failure of the arms-race analogy. Evolution 40: 1229-1247.

Abrams, P.A. 2000. The evolution of predator-prey interactions: Theory and evidence. Annual Review of Ecology and Systematics 31: 79 - 105.

Allen, W.L., Baddeley, R., Scott-Samuel, N.E., and Cuthill, I.C. 2013. The evolution and function of pattern diversity in snakes. Behavioral Ecology 24: 1237-1250.

Amo, L., López, P., and Martín, J. 2004. Chemosensory recognition of its lizard prey by the ambush smooth snake, *Coronella austriaca.* Journal of Herpetology 38: 451-454.

Apesteguía, S., and Zaher, H. 2006. A Cretaceous terrestrial snake with robust hindlimbs and a sacrum. Nature 440: 1037-1040.

Arnold, S.J. 1977. Polymorphism and Geographic Variation in the Feeding Behavior of the Garter Snake *Thamnophis elegans.* Science 197: 676-678.

Arnold, S.J. 1981. The microevolution of feeding behavior. In Kamil, A. and Sargent, T. (eds.), Foraging Behavior: Ecological, Ethological and Psychological Approaches, pp. 409-453. New York: Garland Press.

Arnold, S.J. 1993. Foraging theory and preysize-predatorsize relations in snakes. In Seigel, R.A. and Collins, J.T. (eds.), Snakes: Ecology and Behavior, pp. 87-115. New York: McGraw-Hill, Inc.

Asami, T., Cowie R. H. , and Ohbayashi K 1998. Evolution of mirror images by sexually asymmetric mating behavior in hermaphroditic snails. The American Naturalist 152: 225-236.

Asami, T., Gittenberger, E., and Falkner, G. 2008. Whole-body enantiomorphy and maternal inheritance of chiral reversal in the pond snail *Lymnaea stagnalis.* Journal of Heredity 99: 552-557.

Aubret, F., Burghardt, G.M., Maumelat, S., Bonnet, X., and Bradshaw, D. 2006. Feeding preferences in 2 disjunct populations of tiger snakes, *Notechis scutatus* (Elapidae). Behavioral Ecology 17: 716-725.

Bay, E.C. 1974. Predator-prey relationships among aquatic insects. Annual Review of Entomology 19: 441-453.

Benkman, C. 1996. Are the ratios of bill crossing morphs in crossbills the result of frequency-dependent selection? Evolutionary Ecology 10: 119-126.

Bilcke, J., Herrel, A., and Aerts, P. 2007. Effect of prey-and predator size on the capture success of an aquatic snake. Belgian Journal of Zoology 137: 191.

Bizerra, A., Marques, O.A.V., and Sazima, I. 2005. Reproduction and feeding of the colubrid snake *Tomodon dorsatus* from south-eastern Brazil. Amphibia-Reptilia 26: 33-38.

Branch, W.R. 1975. *Duberria variegata* life history. Herpetological Review 6: 20.

Burghardt, G.M. 1967. Chemical-cue preferences of inexperienced snakes: comparative aspects. Science 157: 718-721.

Burghardt, G.M. 1969. Comparative prey-attack studies in newborn snakes of the genus *Thamnophis*. Behaviour 33: 77-114.

Burghardt, G.M., and Krause, M.A. 1999. Plasticity of foraging behavior in garter snakes (Thamnophis sirtalis) reared on different diets. Journal of Comparative Psychology 113: 277.

Burghardt, G.M., and Pruitt, C.H. 1975. Role of the tongue and senses in feeding of naive and experienced garter snakes. Physiology & Behavior 14: 185-194.

Caldwell, M.W., Nydam, R.L., Palci, A., and Apesteguía, S. 2015. The oldest known snakes from the Middle Jurassic-Lower Cretaceous provide insights on snake evolution. Nature Communications 6.

Chen, Q., Deng, H., Brauth, S.E., Ding, L., and Tang, Y. 2012. Reduced performance of prey targeting in pit Vipers with contralaterally occluded infrared and visual senses. PLOS ONE 7: e34989.

Chiszar, D., Melcer, T., Lee, R., Radcliffe, C., and Duvall, D. 1990. Chemical cues used by prairie rattlesnakes (*Crotalus viridis*) to follow trails of rodent prey. Journal of Chemical Ecology 16: 79-86.

Chiszar, D., Shannon, V.T., Radcliffe, C.W., Smith, H.M., and O'Connell, B. 1981. Effects of chemical and visual stimuli upon chemosensory searching by garter snakes and rattlesnakes. Journal of Herpetology 15: 415-423.

Cooper Jr, W.E. 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. Animal Behaviour 50: 973-985.

Cooper, W.E., Burghardt, G., and Brown, W.S. 2000. Chemical stimuli from potential prey and predators: behavioural responses by hatchling racers (*Coluber constrictor*) from two geographically distinct populations. Amphibia-Reptilia 21: 103–115.

Covich, A. 2010. Winning the biodiversity arms race among freshwater gastropods: competition and coexistence through shell variability and predator avoidance. Hydrobiologia 653: 191-215.

Cowles, R.B., and Phelan, R.L. 1958. Olfaction in Rattlesnakes. Copeia 1958: 77-83.

Craze, P.G., Bin Elahan, B., and Schilthuizen, M. 2006. Opposite shell-coiling morphs of the tropical land snail *Amphidromus martensi* show no spatial-scale effects. Ecography 29: 477-486.

Cundall, D., and Greene, H.W. 2000. Feeding in Snakes. In Schwenk, K. (ed.), Feeding, Form, Function, and Evolution in Tetrapod Vertebrates, pp. 293–333. San Diego: Academic Press.

Cunningham, D.S., and Burghardt, G.M. 1999. A Comparative study of facial grooming after prey ingestion in colubrid snakes. Ethology 105: 913-936.

Daghfous, G., Smargiassi, M., Libourel, P.-A., Wattiez, R., and Bels, V. 2012. The function of oscillatory tongue-flicks in snakes: Insights from kinematics of tongue-flicking in the banded water snake (*Nerodia fasciata*). Chemical Senses 37: 883-896.

Danaisawadi, P., Asami, T., Ota, H., Sutcharit, C., and Panha, S. 2015. Subtle asymmetries in the snail-eating snake *Pareas carinatus* (Reptilia: Pareatidae). Journal of Ethology 33: 243-246.

Dawkins, R., and Krebs, J.R. 1979. Arms Races between and within Species. Proceedings of the Royal Society of London B: Biological Sciences 205: 489-511.

Dietl, G.P., and Hendricks, J.R. 2006. Crab scars reveal survival advantage of left-handed snails. Biology Letters 2: 439-442.

Dietl, G.P., and Vega, F.J. 2008. Specialized shell-breaking crab claws in Cretaceous seas. Biology Letters 4: 290-293.

Domenici, P., Claireaux, G., and McKenzie, D.J. 2007. Environmental constraints upon locomotion and predator–prey interactions in aquatic organisms: an introduction. Philosophical Transactions of the Royal Society of London B: Biological Sciences 362: 1929-1936.

Ferry-Graham, L.A., Bolnick, D.I., and Wainwright, P.C. 2002. Using functional morphology to examine the ecology and evolution of specialization. Integrative and Comparative Biology 42: 265-277.

Gans, C. 1961. The feeding mechanism of snakes and its possible evolution. American Zoologist 1: 217-227.

Gans, C. 1983. Snake Feeding Strategies and Adaptations: Conclusion and Prognosis. American Zoologist 23: 455-460.

Gittenberger, E., Hamann, T.D., and Asami, T. 2012. Chiral speciation in terrestrial pulmonate snails. PLOS ONE 7: e34005.

Gordon, M.B. 1968. Chemical preference studies on newborn snakes of three sympatric species of *Natrix.* Copeia 1968: 732-737.

Götz, M. 2002. The feeding behavior of the snail-eating snake *Pareas carinatus* Wagler 1830 (Squamata: Colubridae) Amphibia-Reptilia 23: 487-493.

Govind, C.K. 1989. Asymmetry in Lobster Claws. American Scientist 77: 468-474.

Graves, B.M., and Duvall, D. 1983. Occurrence and function of prairie rattlesnake mouth gaping in a non-feeding context. Journal of Experimental Zoology 227: 471-474.

Greene, H.W. 1997. Snakes: The Evolution of Mystery in Nature. Berkeley: University of California Press.

Gvoždík, L., Černická, E., and Van Damme, R. 2013. Predator-Prey interactions shape thermal patch use in a newt larvae-dragonfly nymph model. PLOS ONE 8: e65079.

Halpern, M., and Kubie, J.L. 1980. Chemical access to the vomeronasal organs of garter snakes. Physiology & Behavior 24: 367-371.

Hampton, P.M. 2011. Feeding performance in the Western Ribbon Snake (*Thamnophis proximus*): ontogeny and the effects of prey type and size. Canadian Journal of Zoology 89: 945-950.

Hori, M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. Science 260: 216-219.

Hoso, M., Asami, T., and Hori, M. 2007. Right-handed snakes: convergent evolution of asymmetry for functional specialization. Biology Letters 3: 169-173.

Hoso, M., and Hori, M. 2008. Divergent shell shape as an antipredator adaptation in tropical land snails. The American Naturalist 172: 726-732.

Hoso, M., Kameda, Y., Wu, S.P., Asami, T., Kato, M., and Hori, M. 2010. A speciation gene for left–right reversal in snails results in anti-predator adaptation. Nature Communications 1: 133.

Hsiang, A., et al. 2015. The origin of snakes: revealing the ecology, behavior, and evolutionary history of early snakes using genomics, phenomics, and the fossil record. BMC Evolutionary Biology 15: 1-22.

Inoda, T., Hirata, Y., and Kamimura, S. 2003. Asymmetric mandibles of water-scavenger larvae improve feeding effectiveness on right-handed snails. American Naturalist 162: 811-814.

Kardon, K.V., and Smith, P.R. 1991. The role of sensory receptors in the predatory behavior of the brown tree snake, *Boiga irregularis* (Squamata: Colubridae). Journal of Herpetology 25: 229–231.

Kardong, K.V. 1977. Kinesis of the jaw apparatus during swallowing in the cottonmouth snake, *Agkistrodon piscivorus.* Copeia 338-348.

Kaufman, J.D., Burghardt, G., and Phillips, J.A. 1994. Density-dependent foraging strategy of a large carnivorous lizard, the Savanna monitor (*Varanus albigularis*). Journal of Comparative Psychology 108: 381-384.

Krebs, C.J. 1985. Ecology: The Experimental Analysis of Distribution and Abundance. 3. New York: Harper & Row.

Laporta-Ferreira, I.L., and Salomão, M.G. 2004. Reptilian predators of terrestrial gastropods. In Barker, G.M. (ed.), Natural Enemies of Terrestrial Molluscs, pp. 427-481. CABI.

Lee, M.S.Y., Bell, G.L., and Caldwell, M.W. 1999. The origin of snake feeding. Nature 400: 655-659.

Lewis, T.R., et al. 2013. Morphology and ecology of *Sibon* snakes (Squamata: Dipsadidae) from two forests in Central America. Hyllomedusa 12: 47-55.

Lloyd, D.G. 1970. The origin of the odour of the garlic snail *Oxychilus alliarius* (Müller) (Pulmonata, Zonitidae). Journal of Molluscan Studies 39: 169-174.

Luchtel, D.L., and Deyrup-olsen, I. 2001. Body Wall: Form and Function. In Barker, G.M. (ed.), The Biology of Terrestrial Molluscs, pp. 147–178. Wallingford, UK: CABI Publishing.

Lucky, N.S., Ihara, R., Yamaoka, K., and Hori, M. 2012. Behavioral laterality and morphological asymmetry in the cuttlefish, *Sepia lycidas.* Zoological Science 29: 286-292.

Mehta, R.S. 2003. Prey-handling behavior of hatchling *Elaphe helena* (Colibridae). Herpetologica 59: 469-474.

Mertens, R. 1952. On snail-eating snakes. Copeia 4: 279.

Minton, S.A. 1963. Feeding habits of the kukri snake, *Oligodon taeniolatus.* Herpetologica 19: 147.

Mori, A. 1991. Effects of prey size and type on prey-handling behavior in *Elaphe quadrivirgata.* Journal of Herpetology 25: 160–166.

Nakadera, Y., et al. 2010. Enantiomorphs differ in shape in opposite directions between populations. Journal of Evolutionary Biology 23: 2377-2384.

Ng, P.K.L., and Tan, L.W.H. 1985. 'Right Handedness' in heterochelous calappoid and xanthoid crabs: suggestion for a functional advantage. Crustaceana 49: 98-100.

Okumura, T., Utsuno, H., Kuroda, J., Gittenberger, E., Asami, T., and Matsuno, K. 2008. The development and evolution of left-right asymmetry in invertebrates: Lessons from *Drosophila* and snails. Developmental Dynamics 237: 3497-515.

Ota, H., Lin, J.T., Hirata, T., and Chen, S.L. 1997. Systematic review of colubrid snakes of the genus *Pareas* in the East Asian islands. Journal of Herpetology 31: 79-87.

Pakarinen, E. 1994. The importance of mucus as a defence against carabid beetles by the slugs *Arion fasciatus* and *Deroceras reticulatum.* Journal of Molluscan Studies 60: 149-155.

Pedro, B., and Castellanos, I. 2005. Ecology of predator-prey interactions. Oxford: Oxford University Press.

Peters, J.A. 1960. The snakes of the subfamily Dipsadinae. Miscellaneous Publications Museum of Zoology, University of Michigan 114: 1-224.

Pianka, E.R. 1976. Natural selection of optimal reproductive tactics. American Zoologist 16: 775-784.

Pough, F.H. 1983. Snake feeding strategies and adaptations: Conclusion and prognosis. The American Naturalist 23: 339-342.

Pyke, G.H. 1984. Optimal Foraging Theory: A Critical Review. Annual Review of Ecology and Systematics 15: 523-575.

Pyron, R.A., Burbrink, F.T., and Wiens, J.J. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology 13: 93.

Quensen Iii, J.F., and S Woodruff, D. 1997. Associations between shell morphology and land crab predation in the land snail *Cerion.* Functional Ecology 11: 464-471.

Ray, J.M., Montgomery, C.E., Mahon, H.K., Savitzky, A.H., and Lips, K.R. 2012. Goo-Eaters: Diets of the Neotropical Snakes *Dipsas* and *Sibon* in Central Panama. Copeia 2012: 197-202.

Rossman, D.A., and Myer, P.A. 1990. Behavioral and morphological adaptations for snail extraction in the North American brown snakes (genus *Storeria*). Journal of Herpetology 24: 434-438.

Saviola, A.J., McKenzie, V.J., and Chiszar, D. 2012. Chemosensory responses to chemical and visual stimuli in five species of colubrid snakes. Acta Herpetologica 7: 91-103.

Sazima, I. 1989. Feeding behavior of the snail-eating snake, *Dipsas indica.* Journal of Herpetology 23: 464–468.

Schilthuizen, M. 2011. Community ecology of tropical forest snails: 30 years after Solem. Contributions to Zoology 80: 1-15.

Schilthuizen, M., Scott, B.J., Cabanban, A.S., and Craze, P.G. 2005. Population structure and coil dimorphism in a tropical land snail. Heredity 95: 216-220.

Sheehy III, C.M. 2012. Phylogenetic relationships and feeding behavior of neotropical snail-eating snakes (Dipsadinae, Dipsadini). Doctoral dissertation, The University of Texas at Arlington.

Shigemiya, Y. 2003. Does the handedness of the pebble crab *Eriphia smithii* influence its attack success on two dextral snail species? Journal of Zoology 260: 259-265.

Shine, R., and Sun, L.X. 2003. Attack strategy of an ambush predator: which attributes of the prey trigger a pit-viper's strike? Functional Ecology 17: 340-348.

Smith, A.M. 2007. The Biochemistry and Mechanics of Gastropod Adhesive Gels. In Smith, A.M. and Callow, J.A. (eds.), Biological Adhesives, pp. 167-182. Berlin: Springer.

Stephens, D.W., and Krebs, J.R. 1986. Foraging Theory. New Jersey: Princeton University Press.

Stewart, T.A., and Albertson, R.C. 2010. Evolution of a unique predatory feeding apparatus: functional anatomy, development and a genetic locus for jaw laterality in Lake Tanganyika scale-eating cichlids. BMC Biology 8: 8.

Sutcharit, C., Asami, T., and Panha, S. 2007. Evolution of whole-body enantiomorphy in the tree snail genus Amphidromus. Journal of Evolutionary Biology 20: 661-672.

Sutcharit, C., and Panha, S. 2006. Taxonomic review of the tree snail Amphidromus Albers, 1850 (Pulmonata : Camaenidae) in Thailand and adjacent areas: Subgenus *Amphidromus*. Journal of Molluscan Studies 72: 1-30.

Takeuchi, Y., and Hori, M. 2008. Behavioural laterality in the shrimp-eating cichlid fish *Neolamprologus fasciatus* in Lake Tanganyika. Animal Behaviour 75: 1359-1366.

Thompson, J.N. 1999. Specific hypotheses on the geographic mosaic of coevolution. The American Naturalist 153: S1-S14.

Ueshima, R., and Asami, T. 2003. Evolution: Single-gene speciation by left-right reversal. Nature 425: 679.

Utsuno, H., and Asami, T. 2010. Maternal Inheritance of racemism in the terrestrial snail *Bradybaena similaris.* Journal of Heredity 101: 11-19.

Vermeij, G.J. 1994. The Evolutionary Interaction Among Species: Selection, Escalation, and Coevolution. Annual Review of Ecology and Systematics 25: 219-236.

Vincent, S., Dang, P., Herrel, A., and Kley, N. 2006a. Morphological integration and adaptation in the snake feeding system: a comparative phylogenetic study. Journal of Evolutionary Biology 19: 1545-1554.

Vincent, S., Moon, B., Shine, R., and Herrel, A. 2006b. The functional meaning of “prey size” in water snakes (Nerodia fasciata, Colubridae). Oecologia 147: 204-211.

Vincent, S.E., Brandley, M.C., Herrel, A., and Alfaro, M.E. 2009. Convergence in trophic morphology and feeding performance among piscivorous natricine snakes. Joural of Evolutionary Biology 22: 1203-1211.

Vincent, S.E., Shine, R., and Brown, G.P. 2005. Does foraging mode influence sensory modalities for prey detection in male and female filesnakes, *Acrochordus arafurae*? Animal Behaviour 70: 715-721.

Vitt, L.J., and Caldwell, J.P. 2009. Herpetology: An Introductory Biology of Amphibians and Reptiles. 3. California: Academic Press.

Vogel, G. 2015. A new montane species of the genus *Pareas* Wagler, 1830 (Squamata: Pareatidae) from northern Myanmar. TAPROBANICA: The Journal of Asian Biodiversity 7: 1-7.

Wallach, V., Williams, K.L., and Boundy, J. 2014. Snakes of the World: A Catalogue of Living and Extinct Species. Florida: CRC Press (Taylor & Francis Group).

Weaver, R.E., and Kardong, K.V. 2010. Behavioral responses to potential prey through chemoreception by the sharp-tailed snake (*Contia tenuis*). Northwestern Naturalist 91: 58-62.

Yasugi, M., and Hori, M. 2012. Lateralized behavior in the attacks of largemouth bass on Rhinogobius gobies corresponding to their morphological antisymmetry. Journal of Experimental Biology 215: 2390-2398.

You, C.W., Poyarkov, N.A., and Lin, S.M. 2015. Diversity of the snail-eating snakes Pareas (Serpentes, Pareatidae) from Taiwan. Zoologica Scripta 44: 349-361.

Zug, G.R. 1993. Herpetology: An Introductory Biology of Amphibians and Reptiles. San Diego: Academic Press.

APPENDIX

Table A1. Approximate numbers of potential-prey taxa for *Pareas carinatus*

Family	Genera	Number of species			References
		Dextral	Sinistral	Dimorphic	
Ariophantidae	*Ariophanta*	17	0	0	15,16
	Baiaplecta	1	0	0	
	Cryptaustenia	20	0	0	
	Euplecta	30	0	0	
	Hemiplecta	20	0	0	
	Koratia	1	0	0	
	Macrochlamys	120	0	0	
	Naninia	10	0	0	
	Oxytesta	8	0	0	
	Porratella	9	0	0	
	Sakiella	3	0	0	
	Sarika	10	0	0	
	Sitala	30	0	0	
	Sitalinopsis	3	0	0	
	Sivella	10	0	0	
	Sophina	6	0	0	
	Taphrospira	4	0	0	
Bradybaenidae	*Aegista*	40	0	0	18
	Bradybaena	25	0	0	
	Chalepotaxis	2	0	0	
	Landouria	15	0	0	
	Nesiohelix	9	0	0	
	Thaitropis	2	0	0	
	Torobaena	3	0	0	
	Trichocathaica	1	0	0	
	Vitrinula	20	0	0	

Table A2. Approximate numbers of potential-prey taxa for *Pareas carinatus* (cont.)

Family	Genera	Number of species			References
		Dextral	Sinistral	Dimorphic	
Camaenidae	*Amphidromus*	2	0	48	1,11,17,19,20,21
	Burmochloritis	3	0	0	
	Camaena	35	5	0	
	Camaenella	1	0	0	
	Eustomopsis	20	0	0	
	Ganesella	49	1	0	
	Giardia	0	3	0	
	Globotrochus	1	0	0	
	Minacispira	3	0	0	
	Moellendorffia	4	0	0	
	Moellendorffiella	1	0	0	
	Neocepolis	8	0	0	
	Oreobba	2	0	0	
	Pseudoportula	0	3	0	
	Ptychochloritis	6	0	0	
	Stegodera	0	1	0	
	Syndromus	1	44	1	
	Trachia	18	0	0	
	Traumatophora	1	0	0	
	Trichelix	6	0	0	
	Trichochloritis	12	0	0	
Dyakiidae	*Asperitas*	16	0	0	16
	Bertia	0	1	0	
	Dyakia	0	20	0	
	Elaphroconcha	10	0	0	
	Everettia	16	0	0	
	Inozonites	10	0	0	
	Kalamantania	1	0	0	

Table A3. Approximate numbers of potential-prey taxa for *Pareas carinatus* (cont.)

Family	Genera	Number of species			References
		Dextral	Sinistral	Dimorphic	
Dyakiidae	*Pseudoplecta*	1	0	0	16
	Quantula	1	0	0	
	Rhinocochlis	0	1	0	
	Rhinocochlis	0	1	0	
	Sasakina	4	0	0	
Enidae	*Coccoderma*	5	0	0	12
Helicarionidae	*Geotrochus*	3	0	0	15
	Platymma	1	0	0	
Plectopylidae	*Chersaecia*	2	18	0	2,3,4,5,6,7,8,9,10,13
	Endoplon	2	0	0	
	Endothyrella	2	0	0	
	Plectopylis	0	6	0	
Ryssotidae	*Exrhysota*	0	1	0	16
	Lamarckiella	14	0	0	
Trochomorphidae	*Benthemia*	2	0	0	14
	Eurybasis	15	0	0	
	Trochositala	1	0	0	

REFERENCES

1. Geret, P. 1912. Description d'un nouvel Amphidromus. Journal de Conchyliologie 55-56.
2. Gude, G.K. 1899a. Armature of Helicoid landshells. Science Gossip 6: 174–177.
3. Gude, G.K. 1899b. Armature of Helicoid landshells and new sections of *Plectopylis.* Science Gossip 6: 147–149.
4. Lehmann, H., and Maassen, W.J. 2004. A new species of Amphidromus from Laos (Gastropoda, Pulmonata, Camaenidae). Basteria 68: 17-20.

5. Lok, A., and Tan, S. 2008. A review of the Singapore status of the green tree snail, Amphidromus atricallosus perakensis Fulton, 1901 and its biology. Nature in Singapore 1: 225-230.

6. Páll-Gergely, B., and Asami, T. 2014. Additional information on the distribution, anatomy and systematics of living and fossil Chinese Plectopylidae (Gastropoda: Pulmonata). Genus 25: 527-564.

7. Páll-Gergely, B., Budha, P.B., Naggs, F., Backeljau, T., and Asami, T. 2015. Review of the genus *Endothyrella* Zilch, 1960 with description of five new species (Gastropoda, Pulmonata, Plectopylidae). ZooKeys 1-70.

8. Páll-Gergely, B., and Hunyadi, A. 2013. The family Plectopylidae Möllendorff 1898 in China. Archiv für Molluskenkunde: International Journal of Malacology 142: 1-66.

9. Páll-Gergely, B., Hunyadi, A., Ablett, J., Lương, H.V., Naggs, F., and Asami, T. 2014. Systematics of the family Plectopylidae in Vietnam with additional information on Chinese taxa (Gastropoda, Pulmonata, Stylommatophora). ZooKeys 1-118.

10. Páll-Gergely, B., Hunyadi, A., and Asami, T. 2013. A peculiar new species in the genus Landouria Godwin-Austen, 1918 from China (Gastropoda: Heterobranchia: Stylommatophora: Camaenidae). Molluscan Research 33: 130-134.

11. Richardson, L. 1985. Camaenidae : catalog of species. Tryonia 12: 1-479.

12. Schileyko, A.A. 1988. Treatise on recent terrestrial pulmonate molluscs. Part 2: Gastrocoptidae, Hypselostomatidae, Vertiginidae, Truncatellinidae, addition to Vertiginoidea, Pachnodidae, Enidae, Sagdidae. Ruthenica, Supplement 2: 129-261..

13. Schileyko, A.A. 1999. Treatise on Recent Terrestrial Pulmonate Molluscs. Part 4 Draparnaudiidae, Caryodidae, Macrocyclidae, Acavidae, Clavatoridae, Dorcasiidae, Sculptariidae, Corillidae, Plectopylidae, Megalobulimidae, Strophocheilidae, Cerionidae, Achatinidae, Subulinidae, Glessulidae, Micractaeonidae, Ferrussaciidae. Ruthenica., Supplement 2 435-564.

14. Schileyko, A.A. 2002a. Treatise on Recent Terrestrial Pulmonate Molluscs. Part 8. Punctidae, Helicodiscidae, Discidae, Cystopeltidae, Euconulidae, Trochomorphidae. Ruthenica, Supplement 2 1035–1166.

15. Schileyko, A.A. 2002b. Treatise on recent terrestrial pulmonate mollusks. Part 9. Helicarionidae, Gymnarionidae, Rhysotinidae, Ariophantidae. Ruthenica, Supplement 2 1167-1307.

16. Schileyko, A.A. 2003a. Treatise on recent terrestrial pulmonate mollusks. Part 10. Ariophantidae, Ostracolethaidae, Ryssotidae, Milacidae, Dyakiidae, Staffordiidae, Gastrodontidae, Zonitidae, Daudebardiidae, Parmacellidae. Ruthenica, Supplement 2 1711-1895.

17. Schileyko, A.A. 2003b. Treatise on recent terrestrial pulmonate mollusks. Part 11.Trigonochlamydidae, Papillodermidae, Vitrinidae, Limacidae, Bielziidae, Agriolimacidae, Boettgerillidae, Camaeidae. Ruthenica, Supplement 2 1467-1626.

18. Schileyko, A.A. 2004. Treatise on Recent terrestrial pulmonate molluscs. Part. 12. Bradybaenidae, Monadeniidae, Xanthonychidae, Epiphragmophoridae, Helminthoglyptidae, Elonidae, Humboldtianidae, Sphincterochilidae, Cochlicellidae. . Ruthenica, Supplement 2 1627-1763.

19. Schileyko, A.A. 2011. Check-list of land pulmonate molluscs of Vietnam (Gastropoda: Stylommatophora). Ruthenica 21: 1-68.

20. Sutcharit, C., Asami, T., and Panha, S. 2007. Evolution of whole-body enantiomorphy in the tree snail genus Amphidromus. Journal of Evolutionary Biology 20: 661-672.

21. Sutcharit, C., and Panha, S. 2006. Taxonomic review of the tree snail Amphidromus Albers, 1850 (Pulmonata : Camaenidae) in Thailand and adjacent areas: Subgenus Amphidromus. Journal of Molluscan Studies 72: 1-30.

VITA

Ms. Patchara Danaisawat was born on October 2nd, 1984 in Bangkok, Thailand. Her interest in amphibians and reptiles occurred during Herpetology class at Department of Zoology, Faculty of Science, Kasetsart University. She also received her bachelor’s degree in Zoology with Second-class honors from same institute in 2006.

Then, she decided to start Master degree in field of Zoology at Department of Biology, Faculty of Science, Chulalongkorn University and finish her Master degree with thesis entitled “Species diversity of amphibian in Khao Sip Ha Chan Proposed National Park, Chanthaburi Province” in 2010. During the course of her graduate studies, she had the opportunity to be the teaching assistant for few undergraduate courses, including Herpetology and received mainly responsible for the arrangements of field trips and partial teaching.

Subsequently, she continuously worked with snakes with inspired by Prof. Dr. Takahiro Asami and Prof. Dr. Somsak Panha. She was granted from Thailand Research Fund through The Royal Golden Jubilee Ph.D. Program (RGJ) and 90th Year Chulalongkorn Scholarship for doctoral degree and started in Biological Sciences program at the same university since 2010.