5-2011

Demography of the monocled cobra (Naja kaouthia) in the central region of Thailand.

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Recommended Citation

Chaitae, Apinya 1977-, "Demography of the monocled cobra (Naja kaouthia) in the central region of Thailand." (2011). *Electronic Theses and Dissertations.* Paper 228.
https://doi.org/10.18297/etd/228

DEMOGRAPHY OF THE MONOCLED COBRA (*NAJA KAOUTHIA*) IN THE CENTRAL REGION OF THAILAND

By

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A Thesis
Submitted to the Faculty of the University of Louisville
in Partial Fulfillment of the Requirements
for the Degree of

Master of Science

Department of Biology
University of Louisville
Louisville, Kentucky

May 2011

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A Thesis Approved on

April 6, 2011

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ACKNOWLEDGMENTS

I would like to express my sincere appreciation to my major professor, Dr. David H. Reed, for his patient guidance, advice and support throughout the course of the study. I also express my gratitude to my other committee members, Dr. Brian D. Greene and Dr. Tommy S. Parker, for providing guidance and sharing their expertise. I thank staff and faculty from the Department of Biology, University of Louisville, for their generous assistance.

I am thankful to my chief, Mr. Adisorn Noochdumrong, and other CITES colleagues at the Department of National Parks, Wildlife and Plant Conservation, Thailand, in particular Nilubol Khaha and Daraporn Chairat for their continuous assistance and support. I am greatly indebted to my field colleagues, Nattakarn Suttanont and Somchai Poungmalee, for their tireless perseverance and for taking the risk of being bitten by a cobra throughout period of collecting field data. Additionally, I would like to express my gratitude to Dr. Prateep Duengkae for his advice and guidance. I thank Dr. Chatchai Ngernsaengsaruay, Manop Poophat, and Sasithorn Hasin for their support and help in species identification of cobra diet. I thank those who gave me encouragement, in particular Surangkana Rawangyot and Athikom Boonsue, for their support and friendship during my study at University of Louisville. Finally, I take this opportunity to express my profound gratitude to my beloved family for their moral support and patience, which contributed greatly to my success.

ABSTRACT

DEMOGRAPHY OF THE MONOCLED COBRA (*NAJA KAOUTHIA*) IN THE CENTRAL REGION OF THAILAND

Apinya Chaitae

April 6, 2011

Naja kaouthia is a significant species because it feeds primarily on agricultural pests, causes human mortality, and is commercially exploited. Understanding the life history and demography of harvested populations is essential to providing guidelines for proper management. This study was conducted within two rice fields in central Thailand. I found that all age classes of *N. kaouthia* primarily prey on rats. Prey size increases ontogenetically with snake size. Besides rats and mice, first year snakes feed on frogs. Adults add snakes, lizards, fish, birds, and bird's eggs. Young cobras grow significantly faster than older cobras and the growth rate did not differ between sexes. Mean clutch size was 23.5±10 eggs. Using capture-mark-recapture techniques, I estimated survival rate of first year snakes to be 0.48±0.06, while adults had survival rates of 0.93±0.02. Estimated population densities were 768±168 individuals of first year snakes and 96±48 adults per km^2. Females were encountered more frequently during the egg-laying season. Temporal overlap between the reproductive period and harvesting season may increase the threat to harvested populations.

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CHAPTER I

DIET OF THE MONOCLED COBRA (*NAJA KAOUTHIA*)

Introduction

Adult cobras in Southeast Asia have been recorded as preying on other snake species, frogs, lizards, birds, and small mammals (Cox 1991; Cox *et al.* 1998). However, the only detailed study of diet on a cobra species from Southeast Asia is a study on the diet of *Naja sputatrix* on the island of Java. *N. sputatrix* consumes mostly mammals (Boeadi *et al.* 1998), whereas the diets of African congeners contain a wide variety of prey items including amphibians, reptiles, mammals and birds (Shine *et al.* 2007). There is a record of a large cobra (*N. annulifera*) feeding on two tortoises (Mackie 1994).

Cobras are primarily terrestrial; however, they also enter water and climb trees in search of food (Cox 1991; Jintakune 2000), explaining the occasional appearance of fish in the diet (Das 2002). Though cobra species typically consume live prey, scavenging of road-killed snakes had been observed in *N. nivea* and *N. nigricollis woodi* in Africa (Loehr 2005; Phelps 2007), as well as opportunistic predation on a snake injured by a motor vehicle in Botswana (Clauss and Clauss 2002).

Prey size is related to body size of the snake and temporal changes in body size during growth often cause an ontogenetic shift in the diet of reptiles (Zug *et al.* 2001). Greene *et al.* (1994) observed a significant positive relationship between prey size and snout-to-vent length (SVL) in *Nerodia harteri.* Neonates mainly fed on minnows, whereas juveniles and adults fed on variety of larger fish. A study on *Thamnophis radix* by Tuttle and Gregory (2009) found that neonates ate only smaller frog species, while juveniles and adults added larger-sized prey species to their diet, including small mammals.

Ontogenetic changes in dietary composition of cobra species has been recorded in several African congeners. Juveniles of *N. nigricollis* were found to prey primarily upon lizards, whereas adults fed on small mammals, birds, and lizards (Luiselli *et al.* 2002). The prey of *N. annulifera* and *N. nigricincta* changed from ectotherm species to endothermic species as the snakes grew larger (Shine *et al.* 2007).

Here, I investigate the diet of the monocled cobra (*Naja kaouthia*). I examine the diet with respect to first year, juvenile, and adult cobras in order to look for ontogenetic shifts in the diet with increasing size. Diet may also be important to the conservation of this species in Thailand, as a diet of mostly rodents that are destructive to rice crops may provide considerable ecosystem services to farmers.

Methods

STUDY SPECIES

The Monocled Cobra (*Naja kaouthia*) is a member of the Elapidae which includes 11 Asiatic and 17 African and Arabian congeners (Wallach *et al.* 2009). This species is widely distributed across inland countries of Southeast Asia and nearby areas in China and India (Cox *et al.* 1998). It can be found throughout Thailand, and appears to be abundant in the central and southern parts of the country (Wüster *et al.* 1995; Chanhome *et al.* 1998). *N. kaouthia* is primarily found in burrows and other hiding places around agricultural areas or near human habitation (Cox 1991; Cox *et al.* 1998; CITES TH 2007).

N. kaouthia is a large Elapid snake, with an average adult size of approximately 1.5 meters in total length (CITES TH, 2007) and a maximum size of 2.3 meters in length (Vogel 2006). There is considerable variation in body color of the species. It is usually a shade of brown, but ranges from light to blackish brown (Jintakune 2000; Cox 1991). Almost 70% of *N. kaouthia* have a monocellate hood marking, but there is considerable variation in the hood pattern among the remaining 30% of individuals (Jintakune, 2000; Figure 1).

Figure 1. Two morphs of *N. kaouthia* found in my study sites; a specimen having light brown body color without monocellate hood mark (above) and individual with black/dark brown color body with monocellate hood marking.

STUDY AREAS

The study was conducted in paddy fields located in Thachang District of Singburi Province in the central-plains region of Thailand (Figure 2). The two study sites are approximately two kilometers apart within primarily alluvial lowland in the Chao Phraya watershed. Rivers and irrigation canals are common throughout the region.

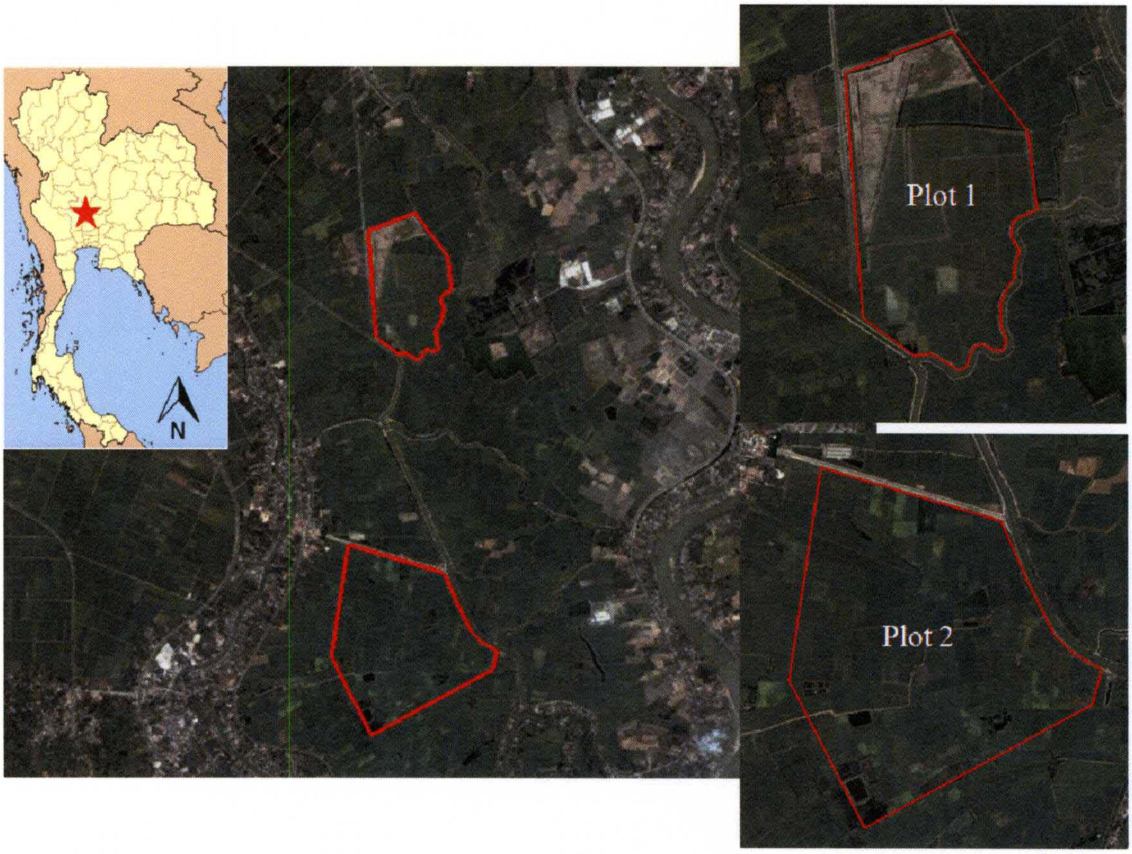

Figure 2. Location and aerial photography of the study sites locating Singburi province in the central region of Thailand (Google Earth 2011).

The study sites are part of a flood plain and the area floods each year, though the degree of flooding is variable. The timing and extent of flooding at the study sites depends not only on rainfall in the area, but also on the amount of water released from dams located north of the rice farms. Flooding mostly occurs during September-October. The study area receives 672 mm of rain annually, on average, during the rainy season; and has 62 rain days per year on average (Royal Irrigation Department 2011). See Figure 3 for temperature and rainfall data.

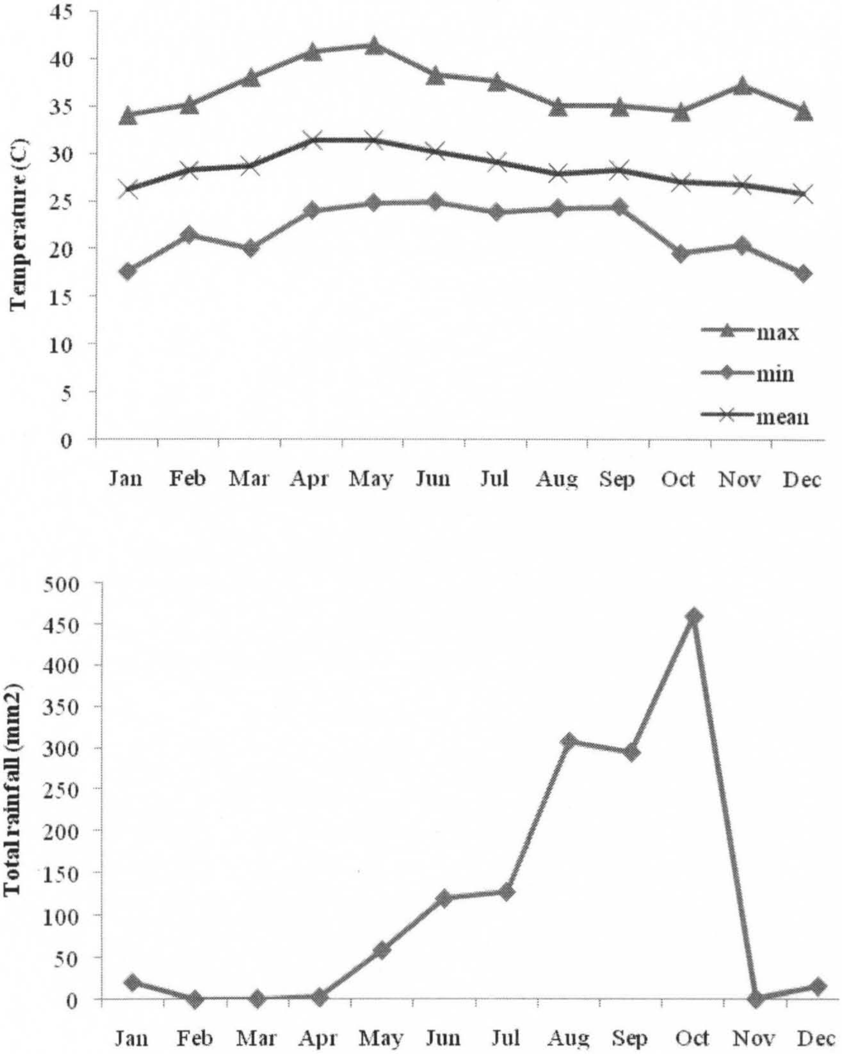

Figure 3. Maximum, minimum, and mean air temperatures (above), and total rainfall (below) on monthly basis for 2010 (Thai Meteorological Department 2011).

PLOTS

Plot 1 is located at 14°48'17.66"N, 100°24'45.61"E, and is approximately one km^2 in area. Approximately 85% of the area is intensive paddy fields, whereas the remaining areas are mostly covered with shrubs. Raised earthen embankments >1 meter in height are located at the edges of the site (Figure 4). The embankments are high enough that they are not submerged during flooding. Vegetation cover is thick, especially in the wet season. The plot is surrounded by an earthen local road, embankments, and a river. Streams, ponds, and irrigated canals are scattered across the plot.

Plot 2 is located at 14°46'21.74"N, 100°24'37.85"E, and covers a two km^2 area. Most of the site consists of intensively-cultivated paddy fields, with a number of small, isolated patches of trees and shrubs (Figure 5). Irrigated canals, streams, and ponds are dispersed across the plot. Large parts of the plot are submerged or very wet during flooding. Few high embankments are found in this plot compared with Plot 1. Almost half of this plot's edge is surrounded by asphalt roads.

Each site was surveyed on alternating weeks from December 29, 2009 to December 21, 2010. Twenty-six field surveys were conducted at each site. On five additional occasions, surveys of the area around the plots were conducted in order to check for potential migration of snakes.

Figure 4. Photographs of Plot 1 during the dry season and the wet season.

Figure 5. Photographs of Plot 2 during the dry season and the wet season

The research was conducted on private lands which are potentially accessible by people and domestic animals; however, no permanent household exists on either of the study areas. Tall grasses, shrubs, and climbers grow at edges and embankments of both plots. The most common tree species found in the paddy fields are rain tree saman (*Samanea saman*), manila tamarind (*Pithecellobium dulce*) and jam tree (*Muntingla calabura*). Rice is harvested at the sites 2-3 times during the year. Paddy fields were tilled after each crop harvesting.

The harvesting of cobras, for skins and live animal trade, mostly takes place in agricultural areas, especially paddy fields. The two sites assayed for this study are regularly harvested for tradable snakes, including monocled cobras, by both professional snake harvesters and local farmers. Agricultural workers collect or kill snakes opportunistically, and this hunting may occur throughout the year. Professional harvesters visit the sites primarily in the dry season during periods of extreme heat (when paddy fields are mostly clear after crop harvesting) and snakes can be collected at night; and in the wet season, especially during flooding, when snakes may gather in high densities in trees or other elevated areas (*e.g.* road and pond embankments).

ANIMALS IN THE STUDY SITES

Paddy fields are inhabited by a diverse group of animals. Rodents, especially rats, have high abundances in agricultural areas. Seven species of rodents from three genera, including *Bandicota*, *Rattus*, and *Mus* are important pests, causing extensive damage to rice crops in Thailand (Bureau of Rice Research and Development 2011; Department of Agricultural Extension 2011; Khorprasert *et al.* 2001; Khorprasert 2011). Squirrels

(Sciuridae), tree shrews (Tupaiidae), siamense hare (*Lepus peguensis*), and Javan mongoose (*Herpestes javanicus*) also inhabit cultivated areas of this region (Lekagul and McNeely 1977). A variety of bird species can be also found in paddy fields. Some common species in the central plains region are ducks and other waterfowl (Anseriformes), grebes (Podicipedidae), doves and pigeons (Columbidae), egrets (Ardeidae), storks (Ciconiidae), swifts (Apodiformes), kingfishers (Alcidinidae), plovers (Charadriiformes), as well as a number of passerines (Passeriformes) (Lekagul and Round 1991). Groups of reptiles dwelling in paddy fields include lizards: geckos (Gekkonidae), agamas (Agamidae), skinks (Scincidae), and monitor lizards (Varanidae); snakes: pipe snake (Aniliidae), vipers (Viperidae), pythons (Pythonidae), sunbeam snake (Xenopeltidae), cobras (Elapidae), rat snakes and water snakes (Colubridae), blind snakes (Typhlopidae); as well as freshwater turtles (Testudines) (Cox *et al.* 1998; Nabhitabhata *et al.* 2000). Amphibian species commonly found in the rice fields are frogs (Ranidae and Microhidae) and toads (Bufonidea) (Nabhitabhata *et al*, 2000). Other animal species that can be found in the paddy field are freshwater fish, insects, arthropods, and numerous invertebrates.

SNAKE COLLECTING

The study areas were generally searched for snakes during daylight hours, however, night searching was also occasionally conducted during the dry season and when paddy fields were clear. Cobras mainly hide in a burrow or in thick, woody vegetation during daylight hours (Cox *et al.* 1998; CITES TH 2007). Digging out burrows is the traditional method used for capturing snakes during daylight searches. Harvesters carefully search for cobra sign (Figure 6), such as a smooth area of surface soil indicating a burrow entrance, shed skins, or feces. The burrow is then dug out until the snake was located and captured. Snakes can be found outside of their burrow, particularly during night hours and after rain at the beginning of the rainy season.

Figure 6. Track and sign of snakes: track on recently burned grass (a), shed skin (b), smooth and slippery soil surface at burrow openings (c-d)

DATA COLLECTING

Food items were obtained by palpating the abdomen until regurgitating ingested items or defecating (Shine 1986; Greene *et al.* 1994; Luiselli *et al.* 2002). Prey items were counted and identified. Bird eggs and rat nestlings found in a single stomach were considered as one item (Rodríguez-Robles and Greene 1999). Prey items were identified to the lowest possible taxon. Identification was conducted by comparing morphological characteristics of non-digested or partially digested prey, especially teeth, hair and scale characteristics. For mammals, I primarily used characteristics of the teeth and skull parts to identify prey to genus level (Lekagul and McNeely 1977; Khorprasert 2011). I also used hair cuticle imprints on polyvinyl acetate for mammal identification (Brunner and Coman 1974), which was effective for distinguishing mice in genus *Mus*. Identification of bird feathers was attempted, but even the foremost experts on Thai birds were unable to identify species or genus with any certainty (Order Charadriiformes). For reptiles, scales from fecal contents were compared to those of species living in the study area and from collections owned by the Department of National Parks, Wildlife and Plant Conservation. Most of regurgitated items could be identified to at least genus level using morphological characteristics

Figure 7. Prey items obtained by a) palpation, from b) fecal content, c) regurgitated prey, and, d) and killed prey not yet consumed.

ANALYSES

Dietary data from all snakes were pooled and grouped into prey types. The following data are analyzed for evaluating importance of each prey type:

(i) Number of each prey type.

(ii) Frequency (number of snakes that contained each prey type to total feeding snake).

(iii) Relative biomass contributions for each prey type. This was calculated by multiplying the number of each prey item by the average adult mass of that prey type and dividing by the total biomass of all prey consumed. Masses of prey were typically compiled from the literature, however, I estimated the mean mass of prey species for which no data were available by comparing with other known-weight species

To determine the relationship between snake size and prey size, linear regression was employed by using snake mass as the independent variable and mass of identifiable prey items as the dependent variable. I used Fisher's exact test of independence to explore if proportions of consumed prey size categories differ among age classes. Snakes were grouped into three age classes, first year snake, juvenile, and adult. First year snake is defined as an individual in its first year of life, with mass not exceeding 0.3 kg., individuals with a body mass between 0.3 kg and 0.7 kg were classified as juveniles , and individuals with snout-to-vent length (SVL) ≥100 cm and body mass ≥0.7 kg of weight were classified as adults. Prey items were grouped into prey size by cobra age class. Identified preys were grouped into 4 size classes based on their average adult mass: ≤5 g, 10-20 g, 50-150 g, and ≥300g.

Results

DIET OF N. KAOUTHIA

Of the 200 independent capture events, 37.5% of cobras had food items in their stomach. A total of 93 prey items was obtained from 75 specimens of *N. kaouthia*. For snakes containing prey the number of prey items ranged from one to five ($\bar{x}$ =1.25± 0.68, *n* =75). Most individuals (84%) contained only one item.

Prey of *N. kaouthia* includes mammals, birds, reptiles, amphibians, fish, and arthropods (Figure 8). Some prey items were so completely digested that I could not identify them. *N. kaouthia* in the habitat studied, principally preys on small mammals (Table 1). At least three genera of rodents are eaten: mouse (*Mus* spp.), rice field rat (*Rattus* spp.) and bandicoot (*Bandicota* spp.). Rodents account for 75.8% (n = 66) of the total number of individual prey species identified, and were found in the stomach of 59 snakes (79.7% of individuals). Some cobra stomachs contained several mouse nestlings or even multiple adult mice (Figure 9).

Figure 8. Prey of *N. kaouthia*: a) mice (Muridae), b) bird eggs, c) sunbeam snake (*Xenopeltis unicolor*),*limnocharis*), d) red-tailed pipe snake (*Cylindrophis rufus*), e) skink (*Eutropis* spp.), f) grass frog (*Fejervarya*

Birds represented 3.4% (n=3) of prey items, and were consumed by two snakes. Seven eggs of *Dendrocygna javanica* (lesser whistling duck) and five eggs of *Anas platyrhuclus* (domestic duck) had been regurgitated by a 162.3 cm SVL female. Seven prey items were either lizards or other snakes (8.0% of prey items), these were consumed one each by seven individual snakes. *Cylindrophis rufus* (red-tailed pipe snake), *Xenopeltis unicolor* (sunbeam snake), and other undetermined snakes were found in the stomachs of *N. kaouthia*. One individual was found to have preyed upon a skink (*Eutropis* spp.). A Grass frog (*Fejervarya limnocharis*) had been eaten by a first year snake. Arthropods represented 9.2% (n=8) of total prey items, and were consumed by three individuals (4.1% of frequency). Arthropod prey consisted of members of a variety taxa (*e.g.*, Dermaptera (Earwigs), Blattodae (Cockroaches), Elarteridae (Click beetles), Aranidae (Spiders) and Gryllidae (Crickets). Presence of arthropods in the cobra diet probably resulted from secondary consumption, when the snake consumed arthropod predators, particularly frogs and toads which are abundant at both study sites. Two fish (2.3% of total prey items), species unknown, had been preyed upon by two snakes. Six prey items could not be identified.

Venom fangs of cobra were also found along with prey items from the feces of four individuals. Fangs are probably broken and replaced in this species. Since fecal samples containing fangs also contained body parts and hair of mice, and no part of any other prey type found, this would suggest those fangs were broken off in prey items and swallowed.

Figure 9. Multiple prey items consumed by individual *N. kaouthia*; a) One mature and two immature specimens of *Rattus* spp.; b) One adult *Mus* sp. and six mouse nestlings.

Table 1. Prey of *N. kaouthia* based on 87 identifiable prey items obtained from 74 individuals.

	Prey type	**n_x (% total number of prey items**	**Frequency (% of frequency)**
Mammals	*Mus* spp.	66 (75.8%)	59 (79.7%)
	Rattus spp.		
	Bandicota spp.		
Birds	*Dendrocygna javanica*	3 (3.4%)	2 (2.7%)
	(Lesser whistling duck)		
	Anas platyrhuclus		
	(Domestic duck)		
	Undetermined non-passerine		
Reptile	*Eutropis* spp. (Skinks)	7 (8.0%)	7 (9.5%)
	Cylindrophis rufus (Pipe snake)		
	Xenopeltis unicolor (Sunbeam snake)		
	Undetermined snakes		
Amphibian	*Fejervarya limnocharis*	1 (1.1%)	1 (1.4%)
	(Grass frog)		
Arthropod	Dermaptera spp. (Earwigs)	8 (9.2%)	3 (4.1%)
	Blattodae spp. (Cockroaches)		
	Elarteridae spp. (Click beetles)		
	Aranidae spp. (Spiders)		
	Gryllus bimaculatus		
	(Two-spotted cricket)		
Fish	Undetermined fish	2 (2.3%)	2 (2.7%)

Of the 56 identified prey items, most of the biomass consumed by the cobras was contributed by rodents (65.7%), with about half of the total biomass (49.3%) contributed by the genus *Rattus*. Reptiles, especially other snakes, made up 23.1% of the prey biomass consumed by *N. kaouthia* in this study. Somewhat surprisingly, 11.3% of the biomass consumed by cobras in this study was bird's eggs (Table 2).

Table 2. Proportional biomass of identified prey species consumed (n=56)

Prey type	**Number Consumed**	**Mean Mass (g)**	**Proportion of Diet**	**Percent of Biomass**
Mus spp.	15	13.5	0.27	3.5%
Rattus spp.	19	150	0.34	49.3%
Bandicota spp.	2	372	0.04	12.9%
Eggs of *Dendrocygna javanica*	7	50	0.13	6.1%
Eggs of *Anas platyrhuclus*	5	60	0.09	5.2%
Eutropis spp.	1	80	0.02	1.4%
Cylindrophis rufus	3	300	0.05	15.6%
Xenopeltis unicolor	1	350	0.02	6.1%
Fejervarya limnocharis	1	5	0.02	0.0%

Remark Mass reference: *Mus*, *Rattus*, and *Bandicota* (Lekagul and McNeely, 1977); *Anas platyrhuclus* egg (CP-Veterinary Medicine, 2011); *Cylindrophis rufus* (Bergman, 1953).

Regurgitated prey items may provide information on feeding behavior. Twelve duck eggs showed varied levels of digestion, four eggs were recently eaten (Figure 10a-1), whereas some of the other eight eggs show different stages of digestion from softened shells to deformed eggs (Figure 10a-2). Large regurgitated items, *e.g.* ricefield rats (*Rattus* spp.) and red-tailed pipe snake (*Cylindrophis rufus*), indicate something about the feeding methods, as the level of digestion corresponds to the swallowing direction, with the prey's head being more digested than the posterior end. This suggests that large prey are swallowed head first (Fig 10 b-c). In addition to hunting live prey, *N. kaouthia* also scavenges carrion. A number of fly larvae were found on rats regurgitated by two snakes (Figure 11).

Figure 10. Prey items showing direction of ingestion: a) eggs of *Dendrocygna javanica* (a-1and a-2) and *Anas platyrhuclus* (a-2); b) a partially digested *Cylindrophis rufus* ; c) partially digested *Rattus* sp. and *Mus* sp.

Figure 11. Two regurgitated mice with fly larvae confirming scavenging behavior of *N. kaouthia*.

DIET AND SNAKE AGE CLASS

Captured snakes were placed into one of three age classes: first year snake, juvenile and adult. All three age classes of *N. kaouthia* mainly feed upon rats (Table 3). Bandicoots (*Bandicota* spp.) are the largest rats dwelling in the study site, the largest species, *Bandicota indica* (Great bandicoot) can weigh up to 800 grams. *Bandicota* rats are only found as prey of adult *N. kaouthia*, and had low frequency in the cobra diet (n=2, 4.9% of total identified prey). Birds and fish were also only found to be preyed upon by adults, though juveniles should be able to eat many birds and fish and even juveniles could consume bird nestlings and small fish (e.g., minnows). Species in the genus *Rattus* were consumed more often than the other rodent genera by both juveniles and adults. From casual observation it seems that these intermediate-sized rats (100-200 gram in weight) were much more frequently encountered during surveys than were mice (*Mus* sp.) and bandicoots (*Bandicota* sp.). *Rattus* rats are highly abundant and commonly found in paddy fields of central region of Thailand (Khorprasert *et al.* 2001; Bureau of Rice Research and Development 2011). The contents of first year snake stomachs consisted of mice (Muridae), an amphibian (*Fejervarya limnocharis*), insects and spider. Rodents mainly eaten by first year snakes are *Mus* species (33% of total preys ate by first year snakes, n= 11). *Mus* is smaller than *Rattus* and *Bandicota*, approximately 80 mm. of head and body length and 13.5 gram of mass (Lekagul and McNeely. 1977) (Figure 12). Both first year snakes (n=3) and juveniles (n=2) also consumed mouse litters. No nestling predation was found in adult snakes, but two egg clutches of different birds were consumed by adults. Amphibians (n=1) and arthropods (n=8) were found only in the stomach of first year snakes during this study.

Figure 12. Size comparison of mature *Mus* sp. (above) and immature *Rattus* sp. (below).

Table 3. Number and percentage of prey type by cobra age class.

Prey type	Prey items eaten by given cobra age class					
	1st year snake		Juvenile		Adult	
	N	%	N	%	N	%
Mammal						
Nestlings of mice	3	9.1	2	15.4	-	-
Mus sp.	11	33.0	1	7.7	3	7.3
Rattus sp.	2	6.1	6	46.2	11	26.8
Bandicota sp.	-	-	-	-	2	4.9
Undetermined rodent	8	24.2	1	7.7	16	39.0
Bird						
Eggs of *Dendrocygna javanica*	-	-	-	-	1	2.4
Eggs of *Anas platyrhuclus*	-	-	-	-	1	2.4
Undetermined non-passerine	-	-	-	-	1	2.4
Reptile						
Eutropis sp.	-	-	1	7.7	-	-
Cylindrophis rufus	-	-	1	7.7	2	4.9
Xenopeltis unicolor	-	-	-	-	1	2.4
Undetermined snakes	-	-	1	7.7	1	2.4
Amphibian						
Fejervarya limnocharis	1	3.0	-	-	-	-
Arthropod						
Dermaptera sp.	1	3.0	-	-	-	-
Blattodae sp.	1	3.0	-	-	-	-
Elarteridae sp.	1	3.0	-	-	-	-
Aranidae sp.	1	3.0	-	-	-	-
Gryllus bimaculatus	2	6.1	-	-	-	-
Undetermined cricket	2	6.1	-	-	-	-
Fish						
Undetermined fish	-	-	-	-	2	4.9

Linear regression shows a positive relationship between snake size (mass) and prey size ($r^2=0.235$, $p=0.0004$, df=47). Arthropods were excluded from the analysis due to possibility of secondary digestion. Thus, larger *N. kaouthia* eat larger prey. Individuals of different age classes also consume prey of different size classes in different proportions (Fisher's Exact Test $p<0.0001$). The largest prey items (≥300g.) were consumed only by the large snakes (juveniles and adults). Adults also consume the widest range of prey sizes, continuing to include smaller prey items (≥10 g.) in their diet, but eliminating the very smallest prey species (small frogs).

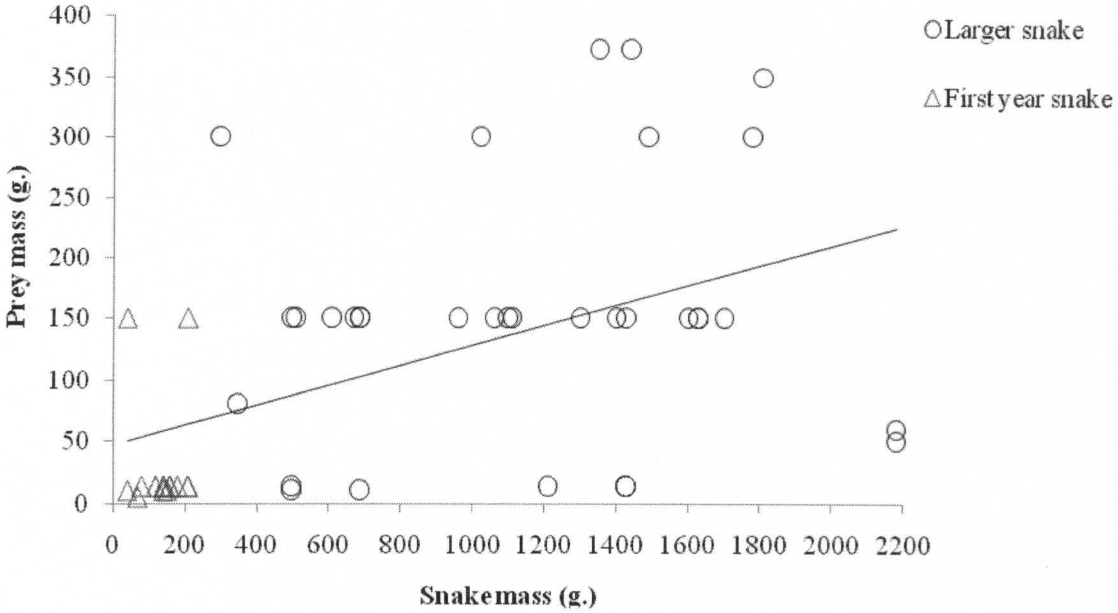

Figure 13. Ontogenetic shift in prey size of *N. kaouthia*.

Discussion

DIET OF N. KAOUTHIA

N. kaouthia is a dietary generalist consuming a variety of prey species including small mammals, snakes, skinks, frogs, birds (and eggs), and fish. However, the primary food item in all age classes is rodents. This is the first study of cobra diet on the mainland of Southeast Asia. Prey of *N. kaouthia* in this study is broadly similar to other congeners both in Africa and Asia (e.g. Boeadi *et al.* 1998; Luiselli *et al.* 2002; Shine *et al.* 2007

Rodents were the primary prey (71% of total prey items) consumed by *N. kaouthia*, which is consistent with the one other study on an Asian congener, *N. sputatrix* (Boeadi *et al.* 1998). This similar dietary habit of *N. kaouthia* and *N. sputatrix* is likely due to the high abundance of rats and mice in agricultural areas where both species commonly dwell. Availability of prey species is an important factor affecting the dietary habits of animals. *N. nigricollis* preys almost exclusively upon lizards, because of the high abundance of lizards in their habitats (Luiselli *et al.* 2002). Mice can breed up to once a month in the paddy fields, due to the availability of food, water, and habitat (Khorprasert 2011). This results in a high abundance of rats and mice in these habitats all year round. This suggests that *N. kaouthia* provides an important ecological service in controlling rice-field rats that are serious pests in rice paddy fields in Thailand and other areas across Southeast Asia. Particularly, *Rattus*, which is abundant and a most serious pest in paddy field of the central region (Department of Agricultural Extension 2011), about half of the estimated total biomass consumed by *N. kaouthia* was contributed by the genus *Rattus*, probably due to their high abundance and intermediate size.

Reptiles were also important prey of *N. kaouthia*. Red-tailed pipe snake (*Cylindrophis rufus*), a semi-aquatic species, was the most frequent snake species consumed by *N. kaouthia*. Two tentacled water snakes (*Erpeton tentacula*) were found to be eaten in my previous study. These aquatic snakes along with fish in the diet, suggests that *N. kaouthia* may search for food more often in the water than generally assumed.

Adult birds accounted for a very small proportion of prey consumed by *N. kaouthia*. Shine *et al.* (2007) indicated that birds were also rarely preyed upon by African cobras.

Egg and nest predation appears to be a very important feeding strategy for *N. kaouthia*. In the present study, I found that 8% of prey items were bird eggs and mice nestlings. Clutches of eggs and broods of mouse/rat nestlings were easily taken, resulting in shorter handling times and less risk of injury compared to hunting live, fully mobile prey (Rodriguez-Robles 2002). The total mass of the eggs or nestlings consumed together often equals that of one adult (Pleguezuelos *et al.* 2007).

N. kaouthia appears to be an opportunistic predator. Scavenging behavior was confirmed by this study. I observed fly larvae on two regurgitated mice which suggests that they had been dead for some time before being swallowed by the cobra. Scavenging has also recorded in African congeners, including consuming injured prey (Clauss and Clauss 2002; Loehr 2005; Phelps 2007) and fish stuck in fish traps (Kyi and Zug 2003). The latter probably also occurs in paddy fields. A number of opportunistic harvesters of *N. kaouthia* mentioned catching cobras in fish traps.

Differences in prey morphology may lead to detection bias in diet studies. Hair, teeth, claws and bones of mammals remain undigested in feces, which were beneficial for prey species identification. Similarly, feathers of birds, scales of reptiles and fish were undigested parts of those prey items. For anurans, only one frog was discovered to be eaten, this was regurgitated by a first year snake. No frog body parts were found in cobra feces, though frogs were abundant in both study sites. Anurans may typically be completely digested and leave little evidence of their having been consumed in the fecal contents of the predator. Anurans are probably another important prey group for cobras, especially for juvenile stage. Boeadi *et al.* (1998) assumed undetermined prey in stomach contents of *N. sputatrix* were mainly frogs. Additionally, underrepresentation of small prey items may occur in studying diets by forced-regurgitation because small prey items were digested more rapidly (Dorcas and Willson 2009). For arthropods, there is a high probability that the arthropods found in cobra feces were secondarily ingested when the snake consumed arthropod predators, in particular frogs. Even though arthropods are small, their exoskeleton often leaves some body parts undigested in feces, while the frog leaves no evidence of having been consumed due to its soft body structure. Presence of arthropods may indirectly represent consumption of amphibians by the cobra.

DIET AND SNAKE AGE CLASS

Snakes have a particularly strong morphological constraint on the size of prey they can consume, gape-size, because they swallow prey whole. Maximum size of prey thus varies among snakes of different sizes, since gape increases as snakes grow larger. Another constraint of small snakes is an increase in handling time as they try to manipulate larger prey (Shine 1991).

The results of my study confirm a positive relationship between prey size and snake size in this species. I detected an ontogenetic shift in dietary habits of *N. kaouthia*, with larger individuals eating larger prey on average. However, adults appear to add larger species of mammals and other prey groups into their diet, while continuing to consume many of the smaller mammals and reptiles eaten as first year snakes and juveniles. Small frogs seem to be so energetically poor that they are dropped from the diet of individuals after the first year.

First year snakes preyed mainly upon small frogs, small mice, and mice/rat nestlings. It appears that once snakes pass the first year of age, their diet stabilizes. Snakes in their second year of life have similar SVL to older snakes and seem to be capable of ingesting similar sized prey. Hatchling size differs substantially from snakes in other years of life. Thus prey size was restricted for small snakes, and diet shifted when snakes grow larger *i.e.* reach their second year of life, by dropping very small prey items such as small frogs and increasing the maximum size of prey consumed.

A dietary shift from ectothermic to endothermic prey has been observed in the African cobras, *N. annulifera, N. nigricincta*, *N. nigricollis* and *N. melanoleuca* (Luiselli *et al.* 2002; Shine *et al.* 2007). Studies on ratsnake (*Elaphe* sp.) and viper (*Vipera* sp.)

also recorded a similar dietary shift (Kjaergaard 1981; Fitch 1999). However, *N. kaouthia* of all age classes mainly consumed rodents in this study. Of those rodents, the smallest in body size were mice (*Mus* sp.) and were mostly taken by first year snakes, while the largest rats (*Bandicota* sp.) was solely preyed upon by adults. Intermediate-sized rats (*Rattus* sp.) were the greatest proportion of rodent prey for both juveniles and adults. Larger snakes did not drop ectothermic animals from their diet. Reptiles, in particular snakes, were the second most important prey group for adults after mammals.

CHAPTER II

GROWTH AND REPRODUCTION OF THE MONOCLED COBRA (*NAJA KAOUTHIA*)

Introduction

Snakes continue to grow throughout their lives, and differences in growth rate among individuals can influence individual life history and fitness traits, such as age and size of maturation, reproductive output, and lifespan (Andrews 1982). Initial growth in snakes is quite rapid and then continues at a decreasing rate, with a pronounced reduction in growth after reaching sexual maturity (Bellairs 1969; Andrews 1982). Variation in growth rate is common in the wild, and can vary greatly among populations within species (Bronikowski and Arnold 1999; Bronikowski 2000). Naturally occurring variation in growth rates among individuals of the same cohort is due to intrinsic factors such as genotype and maternal effects; as well as extrinsic factors such as micro- and macrohabitat differences, especially food availability and temperature (Heatwole and Taylor 1987; Andrews 1982; Mattison 2007; Bronikowski 2000).

A study of growth rate in known-age captive-raised specimens of *N. kaouthia* found that snout-vent length (SVL) of individuals typically doubles during their first year of life, and growth continues at a decreasing rate in the following years, with sexual maturity being reached at three years of age (Cox 1991). However, captive snakes grow more rapidly than wild snakes because of more optimal conditions (*e.g.*, abundant food and absence of natural dormancy). Thus, captive snakes likely attain sexual maturity at younger ages than wild individuals (Groombridge and Luxmoore 1991; Himes *et al.* 2002). There is no information available on growth rates and time to sexual maturity in the wild for this species. Thus, in this study I examine growth rates of different aged individuals in the wild and estimate time until sexual maturity.

Adult *N. kaouthia* usually exceed one meter in SVL (Jintakune 2000; Cox 1991). Average snout-vent length of captive-raised *N. kaouthia* at three years of age was 98.6±7.0 cm (CITES TH 2007). The smallest of thirty five reproductively active females caught from the wild had a 93 cm snout-vent length (CITES TH 2007). Sexual maturity in snakes is related more directly to size than to age (Bellairs 1969). Males may mature earlier and at smaller sizes than females of the same species, because of the lower amount of energy allocated to reproduction compared with females (Shine 1994; Mattison 2007). Shine et al. (2007) noted that males and females of African cobras attain maturity at similar body size, with males having a larger head and longer tail than females of the same SVL.

Difference in size between males and females is prevalent among animals (Darwin 1871; Andersson 1994), often as the result of sexual selection. Male-male combat is a competition form that is widespread among snakes and provides a selective advantage for larger body size among male snakes (*e.g.* Shine 1994; Shine *et al.* 2007) and snake species in which males grow larger than conspecific females tend to exhibit male-male combat behavior (Shine 1994). Male-male combat was recorded in many elapid snakes, including seven cobra species, *e.g.* *N. naja*, *N. oxiana*, *N. sputatrix*, *N. annulifera*, *N. haje* (Shine 1978,1994; Shine *et al.* 2007). Male body size is known to be larger than female body size in *N. naja* and *N. haje* (Shine 1994; Fitch 1981).

N. kaouthia is oviparous and a seasonal breeder (*e.g.* Cox 1991; Chanhome *et al.* 2001), breeding in October-January (Chatchavalvanich *et al.* 1994; Chanhome *et al.* 2001; CITES TH 2007) and laying eggs from December-March (Jintakune 2000). Mean clutch size of wild *N. kaouthia* is 21.9 eggs (SD = 7.6) (CITES TH 2007). Fecundity in snakes commonly depends on maternal body size (Fitch 1970). Shine et al. (2007) found fecundity increases as females grow larger in African cobras, which agrees with a study on *N. atra* by Ji and Wang (2005). Variation in clutch size and egg size were also observed within and among populations, with clutch size more varied than egg size (Ji and Wang 2005).

Hatchlings appear during February-May, and the incubation period ranges from 50-73 days (Cox 1991; Chanhome *et al.* 2001). Size of lab-hatched neonates from wild-caught females averaged 33.4 cm (SD = 1.3 cm) in total length and16.4 g (SD = 1.3 g) in weight. Hatching success of lab-hatched neonates, both from wild-caught and captive-raised females, averaged 73.5% (n = 343 over five years, SD among years = 16.6%) (Chanhome *et al.* 2001).

Nest attendance has been reported in cobras (Fitch 1970), *e.g.* *N. naja* (Campbell and Quinn 1975) and *N. kaouthia* (Kopczynski 1993). Female *N. kaouthia* remained with every egg clutch of eighteen clutches reproduced in captivity (Kopczynski 1993).

The finding is consistent with data from wild populations, for example all nine clutches of *N. kaouthia* eggs discovered by CITES TH (2007) found a female in the burrow with the eggs. Presumably the presence of the female deters potential egg predators and probably helps maintain more optimal incubation temperatures.

Frequency of reproduction can also vary with female size or age (Greene *et al.* 1999). Interbirth intervals for snakes depends on individual foraging success and temporal variation in resource availability (Aldridge 1979; Heatwole and Taylor 1987; Seigel and Ford 1987; Pough *et al.* 2004). Breeding frequency of *N. kaouthia* in the wild is not known, however, captive specimens are capable of producing offspring annually (L. Chanhome, pers. comm.). Kopczynski (1993) recorded that one captive female was capable of reproducing annually for seven consecutive years, but the breeding frequency of captive females varied among individuals.

In this chapter I explore natural growth rates in two wild population of *N. kaouthia*. I examine growth rates in an age- and sex-specific way, as well as estimating time until sexual maturity for females from the age-specific growth rates. I also compare male and female size to look for evidence of sexual dimorphism.

Methods

DATA COLLECTING

The study species, the study area and snake collection methods were described in Chapter I. Captured snakes were additionally processed and then released at the capture site. The newly captured snakes were given an individual mark by implanting PIT tags into the body cavity on lateral position of left ventral posterior body (e.g. Whiting *et al.* 2008). Appropriate sized PIT tags do not affect the growth rate and locomotor performance of snakes (Keck 1994; Jemison *et al.* 1995). I used 12.5-mm. RFID PIT Tags (BioMark) with frequency of 134.2 kHz. The PIT tag was injected using a BioMark implant gun, and identified by using "Multi Tag Pocket Tracker" reader. Ventral scale-clipping was also performed to create an external identification mark (Brown and Parker, 1976). The recaptured snakes were processed identically to captured individuals except there is no need to inject a PIT tag. The following measurements were taken on captured cobras: 1) Head length (HL), snout-vent length (SVL) and tail length (TL) were measured using a flexible tape. Body mass was measured using a spring balance. 2) Sex was determined by tail shape (males have a thicker and longer tail) or probing the hemipenial sac at the base of the tail. Sex of captive-born neonates was not determined. 3) Age class was determined using SVL, weight and reproductive condition. Individuals with SVL $\geq$ 100 cm and mass > 0.7 kg are classified as adult. However, if smaller-sized individuals show signs of sexual maturity (see below) during abdominal palpation, they were classed as adults. 4) Reproductive condition was assessed by abdominal palpation (*e.g.* Fitch 1987; Greene *et al.* 1999). Abdominal palpation in females will assess the presence of enlarged follicles or eggs, a definitive characteristic of sexual maturity in females (*e.g.* Fitch 1987; Greene *et al.* 1999). All laid eggs were counted and collected from the field for incubation. Eggs were placed in a covered basket which was suspended over a water bucket, and maintained at room temperature (approximately 25° C). Neonates were measured, marked by injecting a PIT tag, and released at the site (Figure 14). 5) Date, time, and GPS location of captured individuals were recorded.

Figure 14. Egg incubation and neonate processing.

ANALYSIS

Growth rate

Estimates of daily growth rate were performed by using recapture data. Snakes were aged into three groups: first year snake, juvenile and adult. I included all data for each interval between recapture occasions for snakes with more than one recapture. Daily growth rates are calculated as increments in SVL and mass between two capture occasions divided by number of days elapsed between captures. Mass of gravid females was excluded from the analysis. Linear regression was used to develop best-fit growth rates for each sex separately. Means and standard errors for length and weight of each age class are reported separately. ANCOVA was used to test for a difference in growth rate among sizes of snake and between sexes.

Total records of snake body sizes observed were used to infer age of snake. To avoid violation of assumption of independence, one record of each recaptured snakes was used for the recaptures when a snake was recaptured multiple times. The mean weight and snout-vent length for recaptured adults, and for first year snakes, I used snout-vent length and mass for the last capture. I used ANOVA to compare growth rates (mass and length) among age classes.

Sexual size dimorphism

Total pooled data, including off-plot snakes, were used to test intersexual differences in mass and length relationships. Gravid females were excluded from the analysis, whereas non-gravid measurement of recaptured female was used for those recaptures. To avoid violation of assumption of independence, one record of each recaptured snakes was used as mentioned previously. Differences in snout-vent length (SVL) between sexes are examined by using t-test, whereas analysis of covariance (ANCOVA) was used to test for sex differences in mass, head length (HL) and tail length (TL), using snout-vent length (SVL) as a covariate (Shine *et al.* 2007).

Reproduction

Mean clutch size and its standard deviation for adult females were estimated from the number of eggs found in nest burrows. The data from 2009-2010 will be combined with data from my previous work on this species in 2007. The relationship between maternal body mass and clutch sizes was examined using least-squares linear regression. Besides direct monitoring of the marked females during two consecutive breeding seasons for obtaining information on individual reproductive frequency, breeding frequency was also estimated by calculating the proportion of reproductive females.

Results

GROWTH RATE

To investigate the growth rate of *N. kaouthia*, I used data from 24 snakes recaptured at least once during the study period. Thirty-two growth rate estimates were used in total (Appendix 1). I used snout-vent length (SVL) as the independent variable and daily growth rate as the dependent variable. Linear regression fit the data best and revealed a significant negative relationship between SVL and growth rate in both sexes (Male: $F_{1,16}=140.7$, $p < 0.0001$, $r^2=0.898$, Female: $F_{1,12}=105.1$, $p < 0.0001$, $r^2=0.897$) (Figure 15). Thus, as expected, individuals grow at a slower rate as they increase in size. The decrease is so consistent and linear. ANCOVA comparing growth rates among snake sizes, indicates that growth was significantly faster in smaller or younger snakes than larger or older cobras ($F_{1,28}=208.5634$, $p< 0.0001$). However, growth rates do not significantly differ between sexes ($F_{1,28}=2.3566$, $p= 0.136$) and there is no significant interaction between sex and size for growth rate ($F_{1,28}=2.2185$, $p =1.475$). Growth increment data are shown in Table 4.

Table 4. Summary of growth increment estimates in snout-vent length (mm) of *N. kaouthia*.

Age class		Sex		All sexes
		Male	**Female**	
1st year snake	Mean±SE	2.617±0.266	2.547	2.603±0.207
	n	4	1	5
Juvenile	Mean±SE	1.607±0.562	1.159±0.122	1.383±0.268
	n	2	2	4
Adult	Mean±SE	0.281±0.08	0.423±0.145	0.349±0.08
	n	12	11	23
All sizes	Mean±SE	0.947±0.254	0.68±0.196	
	n	18	14	

The smallest snake with zero growth is a 123.4 cm.- SVL male. However, from looking at individuals longer than 125 cm, it appears that many individuals continue to grow, even if very slowly, up to around 150 cm or more (Figure 15). Because of the relatively short periods of time between capture occasions, it is unlikely that the very small growth increments of large individuals can be detected.

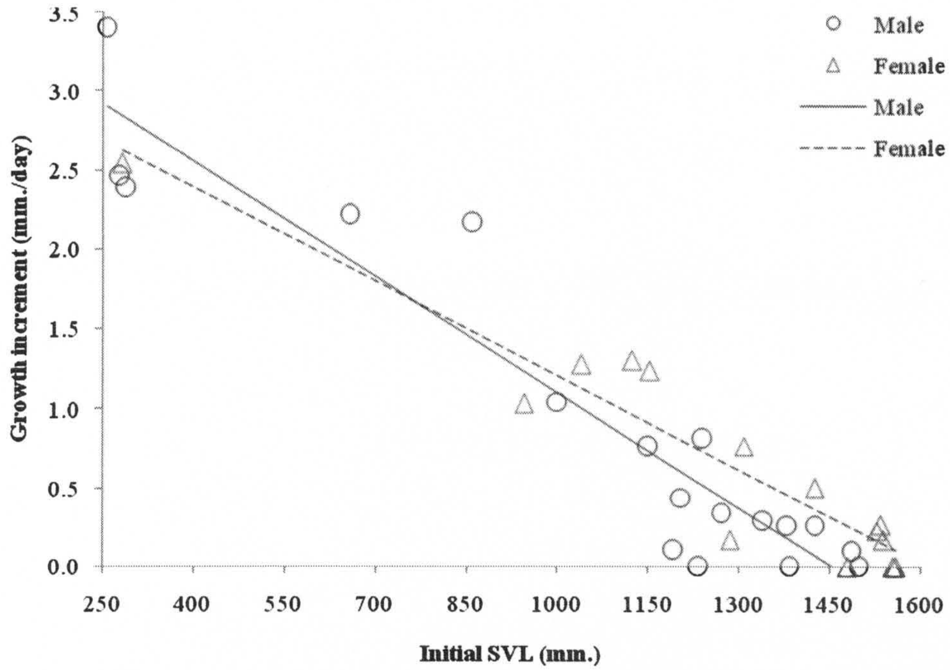

Figure 15. Relationship between snout-vent length (SVL) and growth increment and SVL of *N. kaouthia*.

Based on the capture records of all individuals, three groups of cobras were apparent: first year snake, juvenile (second year), and larger snakes (third year and older) (Figure 16). Snakes in the first year of life have a very different growth rate than snakes more than one year of age ($F_{2,241}$=1702.2, $p< 0.0001$, n= 247). Gains in mass are consistent with increases in length, slopes of mass are significantly different among three age classes ($F_{2,231}$=824.7, $p< 0.0001$, n= 237). The data suggests that first year snakes are typically 80-90 cm long at the end of their first year of growth and weigh 200-300 grams. This is approximately a 2.5-fold increase in SVL from birth and a 15-fold increase in mass from the birth weight. First year snakes have a slender body in comparison to juveniles and adults and successive years will see a more pronounced increase in mass than in length. At the end of their second year of life, individuals were typically 90-100 cm in SVL and 400-600 grams in mass. The age of larger snakes will be difficult or impossible to infer by using size alone. Because the adult age class is comprise of snakes ≥3 years of age, SVL ranges from 105.5 to 162.3 cm (mean = 133.36±12.88 cm.), and mass ranges from 689 to 2680 gram (mean = 1344±420 gram). Individuals having an SVL of approximately 100 cm. (95-105 cm.) includes individuals in their second year and third year of life, but mass is more distinct among age classes. Thus, mass is a more important indicator for determining the likelihood of sexual maturity.

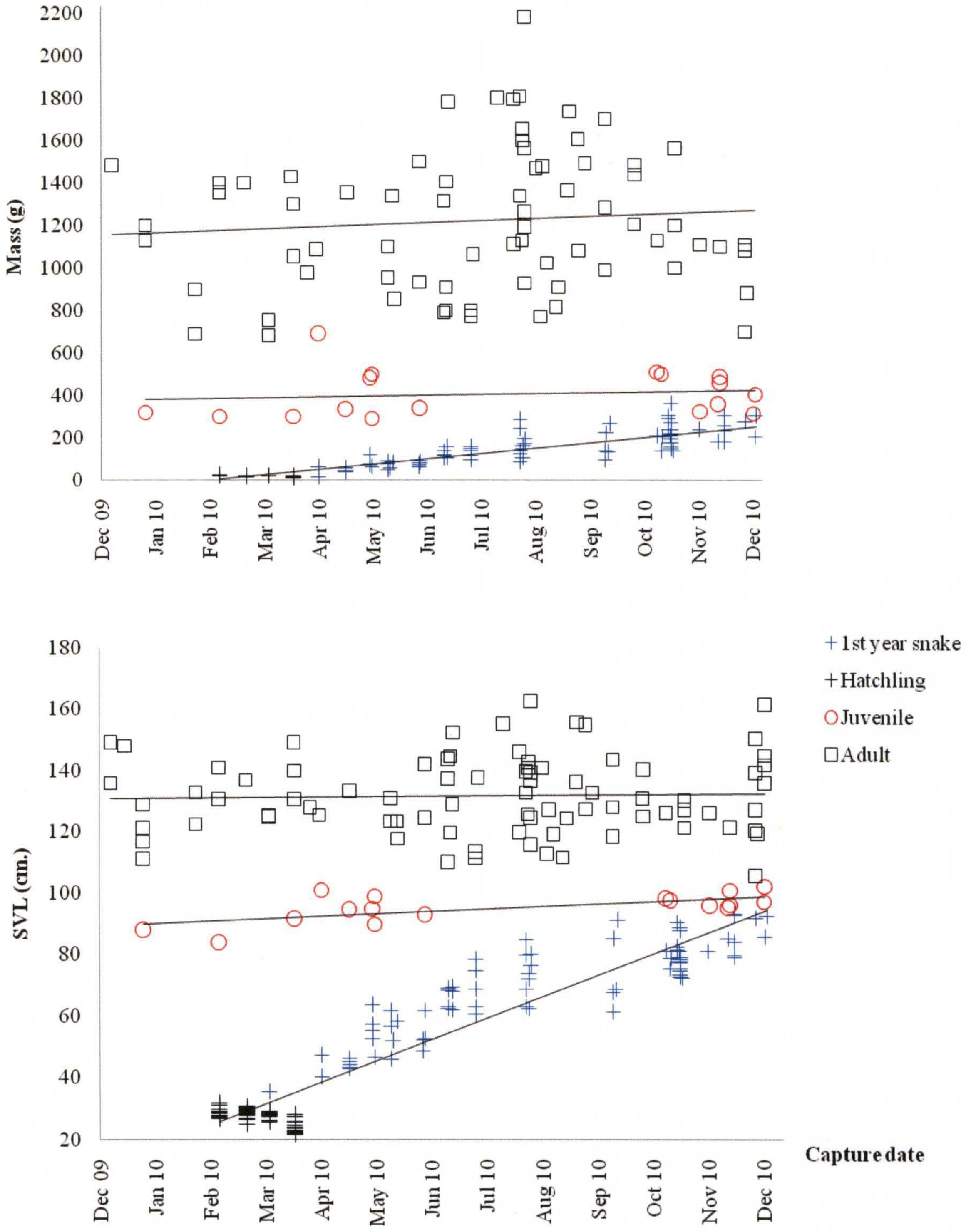

Figure 16. Body size of *N. kaouthia* in relation to capture dates.

Sexual size dimorphism

I evaluated sexual size dimorphism in *N. kaouthia* using all available data from adult males and females. There is no significant difference in SVL between the two sexes (t= -0.68, p=0.4956), however, other dimensions are intersexually different. Monocled cobras exhibit male-biased sexual size dimorphism in mass ($F_{1,163}$=5.53, p=0.0048), head length ($F_{1,173}$=9.71, p=0.0021), and tail length ($F_{1,155}$=7.89, p=0.0056) (Table 5). For mass, the slopes of the regression lines of male and female are not significantly different ($F_{1,163}$=2.01, p=0.1583). However, the Y-intercepts are significantly different ($F_{1,163}$=5.53, p=0.0048), which indicates that male cobras of a given length have a significantly greater mass than females. The least-squares linear regression of best fit for each sex is given by the following equations (Figure 17):

$$\text{Log}_{10}\text{ mass (males)} = 1.036 + 0.015\text{ (SVL)} \qquad (1)$$

$$\text{Log}_{10}\text{ mass (females)} = 1.058 + 0.015\text{ (SVL)} \qquad (2)$$

Table 5. Sexual size dimorphism of *N. kaouthia.*

	Male	**Female**		**df**	***P***
Snout-vent length (cm.)			t= -0.6829	175	0.4956
Mean±SE.	99.1±3.33	102.4±3.63			
N	95	82			
Head length (cm.)			F=9.7079	173	0.0021
Mean±SE.	3.12±0.08	3.03±0.08			
N	95	82			
Tail length (cm.)			F=7.8936	155	0.0056
Mean±SE.	18.09±0.69	17.56±0.63			
N	83	76			
Mass (kg.)			F=5.53	163	0.0048
Mean±SE.	0.69±0.06	0.57±0.07			
N	95	72			

Remark Mass data were log transformed prior to analysis.

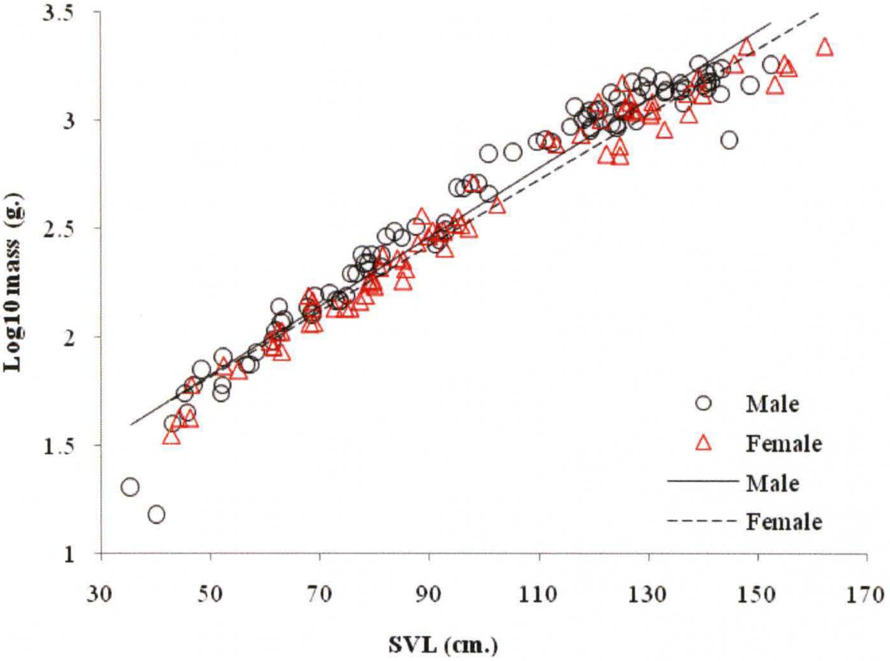

Figure 17. Graph representing body mass relative to snout-vent length (SVL) in *N. kaouthia*. Y axis is $\log_{10}$ transformed.

REPRODUCTION

Reproductive data was obtained from gravid and post-reproductive females from this study and my prior study in 2007. Twenty-seven records (10 from 2007 and 17 from 2009-2010) are shown in Table 6. Only the initial measurement of the recaptured female was used for analysis. Size of reproductive females ranged from 111 cm to 161.4 cm in SVL (mean= 136.7 cm, SD=12.7, n=24), and from 0.69 kg to 2.68 kg of mass (mean=1.43 kg., SD=0.62, n=24) (Table 7).

A pair of individuals, one male and one female, were found together in the same burrow in the middle of October 2010. This male was subsequently recaptured in the middle of December with another female. This suggests that males are polygynous. A couple of individuals were found copulating in a harvester's storage cage in December 2009 (Figure 18). Gravid females were first captured in December in both 2009 and 2010. Eggs were obtained during January-March.

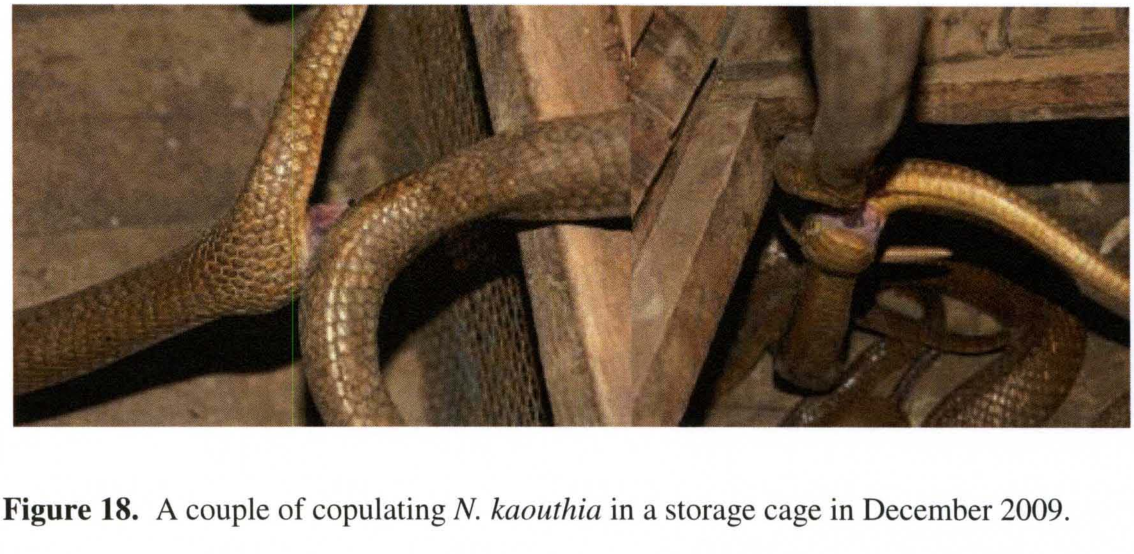

Figure 18. A couple of copulating *N. kaouthia* in a storage cage in December 2009.

Snakes are mostly non-territorial species (Rivas and Burghardt 2005). The majority of snakes live a solitary life, though coexisting individuals may be found during mating season, or period of habitat constraint (CITES TH 2007). From this study, cobras were mostly found alone (97.5% of field-snake encounters, n=203), the five remaining occasions consisted of twice encountering mating couples in breeding season (the same male), two occasions where two snakes were found together in the same tree during flooding, and one encounter with three gravid females occupying the same burrow (Figure 19). Several gravid females living together may suggest social behavior among gravid females or more likely constraints on the number of suitable burrows. The burrow containing three gravid females was located at the corner of a raised earthen dike above the water table, with woody plants providing shade and hiding locations, and the soil inside the burrow was hard and stable. Multiple females found together during the egg-laying period was also observed in the prior study. Three females, each with a separate clutch of eggs, were found in an abandoned midden pile. Each clutch of eggs was laid in its own chamber or hole inside the burrow.

Figure 19. Three-gravid females occupying one burrow

Table 6. Size measurement and reproductive data of reproductive females.

No.	SVL (cm.)	Weight (kg.)	Reproductive condition (gravid/egg number)	No. of neonates hatched	Hatching rate (%)	Year of Data
1	148	2.18	gravid	-	-	2009
2	149	2.3	gravid	-	-	2009
3*	128.5	1.25	gravid	-	-	2010
4	129	2.31	gravid	-	-	2010
5	111	0.93	gravid	-	-	2010
6	139.1	1.75	gravid	-	-	2010
7	150.3	2.68	gravid	-	-	2010
8*	146.6	2.025	gravid	-	-	2010
9	142.1	1.81	gravid	-	-	2010
10	145	1.59	gravid	-	-	2010
11	161.4	2.355	gravid	-	-	2010
12	135.8	1.63	gravid	-	-	2010
13	156.6	1.775	gravid	-	-	2010
14	145	1.95	gravid	-	-	2007
15	125	1.1	12	-	-	2007
16	128	0.75	15	-	-	2007
17	141	1	30	-	-	2007
18	116	0.72	25	-	-	2007
19	136.5	1.07	17	-	-	2007
20	132	0.8	34	-	-	2007
21	150	1.1	28	-	-	2007
22	123.5	0.8	17	-	-	2007
23	131.5	0.9	19	-	-	2007
24	133	0.9	49	16	32.65	2010
25	122.55	0.69	18	17	94.44	2010
26	-	-	18	17	94.44	2010
27	-	-	24	24	100.00	2010

Remark * indicates the same female found gravid in two consecutive year.

Table 7. Summary reproductive data of *N. kaouthia.*

	Mean ± SD	**Range**	**n**
Reproductive female SVL (cm.)	136.7 ± 12.7	111 - 161.4	24
Reproductive female Weight (kg.)	1.43 ± 0.62	0.69 - 2.68	24
Egg-laid Female SVL (cm.)	145.8 ± 12.6	116 - 150	11
Egg-laid Female Weight (kg.)	1.42 ± 0.62	0.69 - 1.1	11
Clutch size (eggs)	23.5 ± 10.0	12 - 49	13
Neonate SVL (cm.)	27.5 ± 2.4	21.5 - 31.6	74
Neonate Weight (g.)	17.34 ± 2.77	8.02-21.29	74
Hatching rate (%)	80.4 ± 16.0	32.65 - 100	4

Remark Only the first record used for the recaptured gravid female.

Among recaptured females, only one female was recaptured during the reproductive season in two consecutive years. This female was found in gravid condition in the 2009 breeding season and in the 2010 breeding season. Thus, at least some wild individuals can produce a clutch of eggs in consecutive years.

The most accurate method for quantifying breeding frequency is continually observing the same females over a lifetime. However, the proportion of reproductive age females that are reproductively active in a given year can also be used to estimate the mean interbirth interval for a species/population. The proportion of reproductive females in each of the plots used in this study is nearly identical (33% versus 36%) (Table 8). I estimate that 36% of total mature females of *N. kaouthia* breed in a given year in these two study areas. This would imply that females breed on average once every three years.

Thus, either the single female that was recaptured being reproductively active in consecutive breeding seasons was an anomaly or I have not been able to fully account for the true proportion of females breeding in the population.

Table 8. Proportion of reproductive females in two study areas.

	Reproductive female (RF)	**Non-reproductive female (NF)**	**% reproductive**
Plot 1	3	6	33.3
Plot 2	8	14	36.4
Total	11	20	35.5

Clutch size and relationship with maternal body size

I collected four egg clutches in 2010. Here, I combine these four clutches with nine clutches from my prior study (2007), to examine possible relationships between maternal mass and clutch size. In the present study, two clutches of eggs were found in Plot 2 with the female inside the burrow, whereas the other two clutches were obtained outside the study areas when the females were harvested and the harvesters left eggs in the burrows (Table 6). Clutch size of *N. kaouthia* ranged from 12 to 49 eggs, with a mean clutch size of 23.5 eggs (SD=10.0, n=13). Average hatching rate of the eggs in captivity was 80.4% (SE= 16.0%, n=4). Regression analysis indicated no significant linear relationship between maternal SVL and fecundity ($F_{1,9}$=1.14, p=0.31, r^2=0.11, Figure 21).

Figure 20. Egg clutches of *N. khaouthia*.

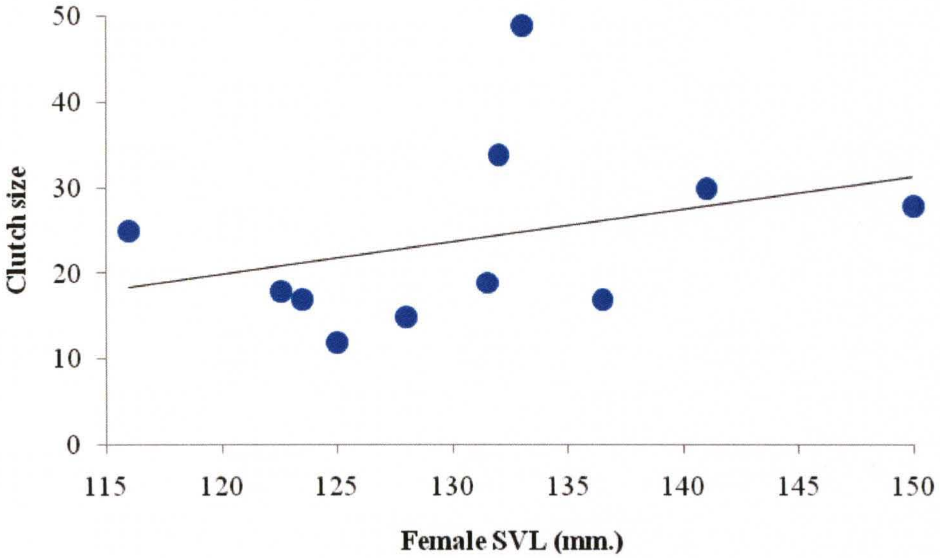

Figure 21. A regression with maternal snout-vent length as the independent variable and clutch size as the dependent variable.

Discussion

GROWTH RATE

Based on data of recaptured individuals of *N. kaouthia*, the growth rate (snout-vent length) of first year snakes is 1.9 times and 7.5 times that of juvenile and adult snakes, respectively. First year snakes typically increase 250% in length during the first year, perhaps attaining 80% of the length attained at sexual maturity. Individuals increase 15 fold in mass, but only attain about 30% of their mass at sexual maturity. There are no data on growth rates of other cobra species in the wild. However, this growth increment is similar to a tropical, similar-sized Elapid, *Pseudodechis porphyriacus* (Shine 1978). The growth rate of *N. kaouthia* differs significantly among age classes, but no difference was detected between the sexes. Rapid growth of hatchlings is common among snakes, for example, Madsen and Shine (2002) observed rapid growth of hatchlings of python (*Liasis fuscus*), and growth declines with increasing body size. They also found intersexual difference in growth, but only in pythons having intermediate size.

Based on the data, it appears that growth might stop when individuals reach approximately 150 cm of SVL. The longest individual obtained during the present study is 162.3 cm SVL. However, the maximum size record for *N. kaouthia* is 230 cm. in length (Vogel 2006). Thus, I conclude that the growth of *N. kaouthia* is not likely to stop when individuals reach 150 cm. Our data is based on a small number of field recaptures, growth rates of large individuals will be very small, and a relatively short period of time elapsed between two capture occasions. A much longer study would be required to accurately estimate age-specific growth patterns in adults of this species.

According to data from captive breeding, cobras can breed when they reach the third year of life and are at least one meter in length. A study on ovarian histology of *N. atra* (mentioned as *N. naja*) by Lance and Lofts (1978) estimated that development time of oocytes from primary to mature stages probably takes three years. This is the first study on growth rates of wild *N. kaouthia*. Based on timing of annual reproduction, *N. kaouthia* may attain sexual maturity in either its third or fourth year of life. Since this species hatches during February-April, and starts breeding in October, the age at first breeding will not be a simple multiple of 12 months. Some individuals may reach maturity between the ages of 31-34 months, similar to individuals reared in captivity. Male snakes may reach sexual maturity earlier than conspecific females due to the lower energetic cost of producing spermatocytes. However, if this species has direct male:male competition for mates, males are unlikely to actually obtain mates until much older. A longer term study is needed to explore these aspects of reproductive effort.

I found no significant difference between two sexes in snout-vent length (SVL), but other body dimensions i.e. head length, tail length, and mass of males are greater than females. These finding are similar to other cobra studies in aspect of longer head and tail of males in comparison to females (Shine *et al.* 2007; Boeadi *et al.* 1998). Likely larger size and other dimorphic morphology has evolved in males via natural selection for male-male combat (Shine 1994).

REPRODUCTION

Knowledge concerning the timing of reproduction is well documented for *N. kaouthia* in Cox (1991) and Chanhome *et al.* (2001). It breeds during October to January, eggs hatch in February to May. Findings obtained from this field study generally support these previous records. Based on the literature from captive rearing, individuals are believed to reach sexual maturity during their third year of age and about 100 cm. in length. The smallest reproductively active female found in this study was 111 cm. SVL and 690 gram in mass.

One male of *N. kaouthia* found with two females in two different occasions during breeding season in this study. Similar observation recorded in a wild male of *N. siamensis* found with two females (CITES TH 2007). However, multiple mating in females with several males was recorded in captivity (Kopczynski, 1993). Observations of a female mated with several males may not be able to conclude multiple mating since some snake species have re-mating prevention mechanism (Shine et al, 2000). With few direct observations available, I tentatively conclude that males of *N. kaouthia* are polygynous, however, it is not clear whether females mate with multiple males in this species. Genetic data on egg clutches could determine this conclusively.

With regard to breeding frequency, at least, some adult females of *N. kaouthia* are capable of breeding in successive years. I recaptured only one female in successive breeding seasons (2009 and 2010) and she was gravid both seasons. However, based on the proportion of reproductive females, I estimate that *N. kaouthia* only breeds once every 2.8 years on average. There are problems with using palpation to estimate reproductive activity. Small follicles within the female's body are difficult to detect, thus some females are likely to be classified as non-reproductive, underestimating the true proportion of females that actually become gravid during the breeding season. Reproductive frequency can vary in response to food resource availability, female fat reservation, and population structure (Seigel and Ford 1987). As one example, breeding frequency in a population of *Crotalus viridis oreganus* ranged from annual to triennial, and the number of reproductive females correlated to prey density in prior year (Diller and Wallace 2002). With the abundance of prey and year round foraging, cobras in agricultural areas likely can accumulate enough energy to reproduce once every year or two. Data compiled by Seigel and Ford (1987) indicated that percentage of gravid females for Australian elapids are generally much higher than the estimates for *N. kaouthia* from this study. As few data are available and the palpation method's accuracy unknown, breeding frequency of *N. kaouthia* may also range from annual to triennial.

Average clutch size of *N. kaouthia* is 23.5±10.0 eggs. I failed to detect a significant positive relationship between maternal body size and clutch size in this species. The result differs from a large number of other snake studies which almost always find a significant and positive relationship between maternal body size and clutch size (*e.g.* Shine 1977; Greene *et al.* 1999; Todd *et al.* 2008). All previous studies for this group of snakes found that fecundity of cobras is correlated with maternal snout-vent lenght (African cobras (*Naja* spp.), *N. melanoleuca*, *N. nigricollis* and an Asiatic cobra species *N. atra* (Luiselli and Angelici, 2000; Ji and Wang, 2005; Shine *et al*, 2007). I assume a similar relationship exists for *N. kaouthia*. Likely the small regression coefficient and non-significant result in this study is due to small sample size and one individual of average size with an unusually large clutch.

The 49 eggs represent an unusually large clutch, with 41 eggs in a single clutch being the second largest recorded clutch from a captive *N. kaouthia* (Kopczynski 1993). Multiple females often occupy the same burrow. Eggs from a single clutch usually adhere together and cannot be separated, but for the clutch of 49 eggs, there was a small group of eggs laid separate from the other eggs. Thus, the very large clutch was probably from more than one female, though only single female was found with the eggs.

Similarly, I observed similar nest site sharing in *N. siamensis* (CITES THA 2007). Elapid snakes exhibit aggregation of gravid females and communal nestling. Possible explanations include suitable nest constraint, lowered nest predation with multiple guardians, and/or thermoregulatory control (Covacevich and Limpus 1972; Shine 1979; Graves and Duvall 1995).

CHAPTER III

DEMOGRAPHICS AND POPULATION SIZE

Introduction

Demography involves the study of population size, age- and size-specific birth and mortality rates, and population dynamics (Dorcas and Willson 2009). Among the various biological aspects of tropical snakes, population demography is probably the least known. Yet, demographic information is essential for understanding snake population biology and to facilitate their conservation and management (Siegel and Mullin 2009).

N. kaouthia is abundant and widely distributed throughout Thailand, and is not considered threatened (*e.g.* Wüster 1998; Chanhome *et al.* 1998; Humphrey and Bain 1990; Nabhitabhata and Chan-ard 2005). However, there are no estimates of density from wild populations of this species. It is a habitat generalist (Cox *et al.* 1998; Chanhome *et al.* 1998), but its preferred habitat seems to be low lying and wet areas (Cox 1991; Wüster 1992). *N. kaouthia* adapts well to human altered landscapes, thriving in agricultural areas and near human settlements (Cox *et al.* 1998; Wüster 1998).

Cobras (*Naja* spp.) have been harvested extensively in Thailand. Cox (1991) reported a large domestic market for snake meat and skins, as well as large numbers of live snakes being exported. Larger size, high abundance, and a lack of ability to spit venom causes *N. kaouthia* to be favored for harvesting over the other two species of

Thai cobras (*N. siamensis* and *N. sumatrana*). Harvested stock for domestic trade was estimated at 10,000 – 15,000 individuals of *N. kaouthia* during 2005-2006 (CITES TH 2007). Stocks of harvested *N. kaouthia* show biased selection for larger-sized snakes, similar to that found in other cobra species, *e.g. N. sputatrix* in Central Java (Boeadi *et al.* 1998).

N. kaouthia is not a protected species under the wildlife law (Department of National Parks, Wildlife, and plant Conservation 1992), however, it is listed under CITES Convention (Convention on International Trade in Endangered Species of Wild fauna and Flora) as Appendix II species that are allowed to be traded under proper control (CITES Secretariat 2011). Export of live cobras has been prohibited in Thailand since 1990. Currently trade consists of domestic consumption and uses, export of skin and skin products, and illegal export of live specimens. The central and southern provinces of Thailand are the primary harvest areas for cobras, with central Thailand being the most active. Rice fields and abandoned agricultural areas are the main harvest sites. Harvest activities are driven by market demand and harvest intensities vary temporally and spatially both due to economic reasons and climatic conditions. Harvesting is more intense during certain times of the year. Flooding periods are the most important harvesting time, because the snakes' burrows are often flooded and this forces the snakes to climb trees or gather at high densities in elevated areas.

A sex ratio of 1:1 is an evolutionarily stable trait (Fisher, 1930). Most snake studies have found the sex ratio not to differ from 1:1 (*e.g.* Brown and Weatherhead 1999; Luiselli and Angelici 2000; Hill and Beaupre 2008). Iverson (1990) observed seasonal variation in the sex ratio of the Bullsnake (*Pituophis melanoleucus*), with male-biased ratio found during the season that males are more active than females. This is not a true sex ratio bias, but rather a capture bias based on the differential activity patterns of males and females at different times of the year. Reproductive activity can increase aboveground activities and mortality risk. Adult males of *Tantilla coronata* tend to be found more frequently than females during mating periods (Todd *et al.* 2008).

Not surprisingly the activity pattern of snakes is often highly seasonal and correlated with weather conditions (Groombridge and Luxmoore 1991). A study conducted by Luiselli and Angelici (2000) observed that records of two Afrotropical cobras (*N. melanoleuca* and *N. nigricollis*) varied among seasons. Record of encountered snakes peaked during the wet season, and was considerably reduced in hottest period. This finding is consistent with a field record of cobras in India, where cobras reach peak aboveground activity during the rainy season (Whitaker, 1978).

Here, I provide estimates for demographic parameters in two wild population of *N. kaouthia*: age-specific mortality and sex ratios. I also use temporal changes in capture rate to speculate on behavior of this species. Demographic rates and their variance provide the backbone for any management plan.

Methods

DATA COLLECTING

Captured snakes were processed in the field and released at the capture site after processing. Detail of study species, study area and snake collection were detailed in Chapter I.

Figure 22. Snakes were processed before releasing to the capture site: PIT tag injection (a), tag identification (b), scale clipping (c), sexing (c), tailbase of female-above, and male -below (e), and releasing captured snake (f).

ANALYSIS

Body size, size class distribution, and sex ratio

Data from field-caught snakes were used to determine sex ratio and size class distribution of *N. kaouthia* at each plot. All captive-hatched snakes were excluded from analysis. Snout-vent length and body mass of snakes were compared between sexes and plots using t-test. Snakes were grouped into one of twelve classes using 10-cm SVL intervals. I used a Log likelihood Ratio Test to determine whether sex ratio and size class distribution differed between the two study sites.

Estimates of survival rate and population size

Capture-mark-recapture data of in-plot snakes over the entire study period are used for analysis in program MARK 6.0 (White and Burnham 1999). Owing to small sample size of juvenile snakes, juveniles (2nd year snake) and adults were pooled for data analysis. I used the POPAN (open population) formulation in program MARK for estimating population size and survival rates. This decision was based on the fact that captive-hatched neonates were released into the populations, births and deaths occurred during the study period, and the results of a closure test (Stanley and Richards 2004) suggested that both populations were open (Plot 1: χ^2=67.5, df=21, p=0.000; Plot 2: χ^2=130.216, df=26, p=0.000).

Parameters estimated by POPAN are: φ, the probability of survival; p, the probability of capture; b, the probability of a new animal entering the population; and N, total of all animals that entered the study site. Population size N is a derived parameter of the model. Parameters can be allowed to be constant (.) or vary by temporally (t), by age class (a), and vary by temporally and by age class (a*t). However, due to only having 26 sampling occasions, I did not test all possible models (Pollock *et al.* 1990).

The survival parameter, φ, was fixed to be time-constant within age class but differ between classes- $\varphi_{(a)}$. The recapture probability, p, was allowed to vary between age classes $p_{(a)}$ or be constant $p_{(.)}$ to avoid inestimable parameters when p is modeled with time dependency-$p_{(t)}$ within POPAN (Schwarz and Arnason 2011). Probability of entry (b) was allowed to vary over time- $b_{(t)}$ and by age class and time-$b_{(a*t)}$, based on the assumption that entrance into the population by individuals of a given age class is likely to be concentrated in certain times of the year, *e.g.* increases of neonate entrants during hatching season.

Each data set was tested for Goodness of Fit (GOF). Due to insufficient data to test GOF using POPAN, I evaluated GOF by using a bootstrap procedure embedded in program MARK for the general model ($\varphi_{(a)}$, $p_{(a*t)}$) for each data set (Cooch and White, 2011). The GOF tests were not statistically significant in both Plot 1 (p=0.26), and Plot 2 (p=0.15), therefore no adjustment was needed for the estimations. Appropriate models are selected by using Akaike Information Criterion (AIC). Model averaging was used among weighted models to accommodate uncertainty of model selection (Cooch and White 2011). Ninety-five percent confidence intervals of the survival rates are compared between sites. Population size was derived from the same models used for estimating survival rates.

Variation in capture probability

Total records of field-caught snakes, excluding lab-born snakes, were grouped with respect to sex and season. Seasonal period of the study areas are divided into three seasons which are dry season (February-April), wet season (May-October), and cold season (November-January) (Singburi provincial office 2011). I used log-likelihood ratios to examine whether males and females differed in their capture probability among seasons; such a difference would suggest a relationship between an individual's sex and their seasonal behavior patterns.

Results

The total number of cobras captured was 247, consisting of 216 in-plot snakes and 31 individuals captured outside the plots. In Plot 1, I marked 86 snakes; 45 field-caught snakes and 41 captive-hatched neonates. In Plot 2 I marked 130 individuals, 97 field-caught snakes and 33 captive-hatched neonates.

Of 216 in-plot individuals captured and marked, twenty-five were recaptured (11.6%). Most snakes were recaptured one time and the maximum number of recaptures was three times for one individual. Table 9 summarizes data from the population survey of *N. kaouthia* for twenty-six occasions over the period of study.

Table 9. Summary number of *N. kaouthia* caught during December 2009- December 2010.

	Adult		**Juvenile**		**1st year snake**	
	Capture	**Recapture**	**Capture**	**Recapture**	**Capture**	**Recapture**
Plot 1 (n=86)	14	10	3	-	56(38)	3(3)
Plot 2 (n=130)	41	5	9	4	68(32)	3(1)
Subtotal (n=216)	**55**	**15**	**12**	**4**	**124(70)**	**6(4)**
Off-plot 1 (n=21)	6	-	3	-	12	-
Off- plot 2 (n=10)	4	-	1	-	5	-
Subtotal (n=31)	**10**	**-**	**4**	**-**	**17**	**-**
Total (n=247)	**65**	**15**	**16**	**4**	**141**	**6**

Remark Parentheses indicate number of captive-hatched snakes.

BODY SIZE, SIZE CLASS DISTRIBUTION, AND SEX RATIO

Individuals in the two plots did not differ in body length or mass (SVL, t=-0.0026, p=1.00; mass, t=-0.80, p=0.42) (Table 10).

For size class distribution, snout-vent length of wild-caught snakes were placed in 10-cm. size classes and viewed as relative frequency distribution as shown in Figure 23. Generally, both plots showed two peaks of frequency at SVL of small (≤70 cm.) and large snake (≥130 cm.), and low frequency of newborn (≤40 cm). Distribution of size classes differed significantly between plots (χ^2=24.39, df=12, *p*=0.018).

In Plot 1, I captured 26 females and 19 males of *N. kaouthia*; and in Plot 2, I captured 51 females and 46 males. Chi-square test indicated no significant difference in sex ratio between the two plots (χ^2=0.410, df=1, *p*=0.522); and for both plots combined, the sex ratio of *N. kaouthia* is not significantly different from 1:1 (χ^2=0.285, df=1, *p*=0.593).

Table 10. Summary data on body size of *N. kaouthia* at two studied plots

		Male	**Female**	**Total**
SVL (cm.)				
Plot 1	Mean±SE	101.6±7.9	102.8±9.5	102.1±6.0
	n	19	26	45
Plot 2	Mean±SE	101.8±4.1	102.4±4.223	102.1±2.9
	n	50	47	97
Body mass (g)				
Plot 1	Mean±SE	765.3±118.7	683.2±168.5	732.9±96.9
	n	26	17	43
Plot 2	Mean±SE	730.4±76.3	556.2±70.6	650.9±53.0
	n	50	42	92

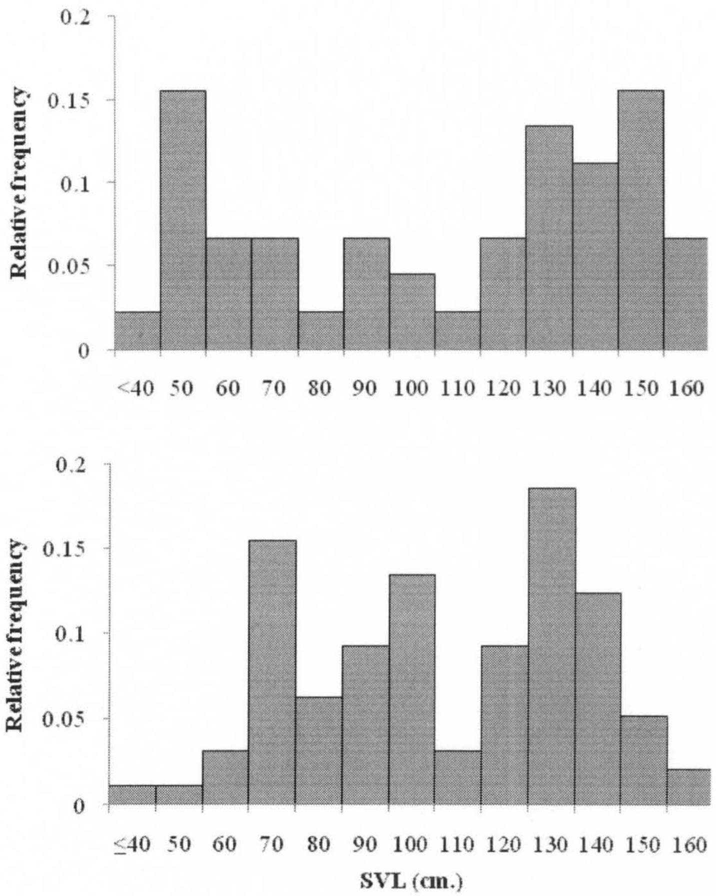

Figure 23. Proportional distribution of snout-vent length –SVL(cm) of *N. kaouthia* in Plot 1 (above) and Plot 2 (below).

ESTIMATES OF SURVIVAL RATES AND POPULATION SIZE

Based on survival rates estimated by POPAN, first year snakes in both plots have lower rates of survival than did larger *N. kaouthia*. Survival rates of first year snakes and older snakes (juveniles and adults, from here on simply adults) in Plot 1 were 0.387±0.085 (95% CI = 0.239 to 0.559) and 0.974±0.021 (95% CI = 0.8809 to 0.995), respectively. For Plot 2, survival rates of first year snakes and adults were 0.557±0.065 (95% CI = 0.428 to 0.679) and 0.893±0.036 (95% CI = 0.799 to 0.946), respectively.

For population size, I used estimates derived from the best model (with lowest AIC score) for each plot. Model averaging is not possible because population size is a derived parameter for the POPAN. Additionally, the best-fit model was at least five times as strongly supported as the next best model for both plots. The best-fit model for Plot 1 and Plot 2 was: $\varphi_{(a)} p_{(.)} b_{(t)}$. Population size for Plot 1 was estimated as 935±293 first year snakes and 48±10 adults in one km^2 area. Population size for Plot 2 was estimated as 1200±411 first year snakes and 289±79 adults in a two km^2 area.

Table 11. POPAN estimates of age-specific survival rates and population sizes of *N. kaouthia*.

Model	AICc	AICc Weights	Age class (yr)	Survival estimates	SE	95% confidence interval	Population Size	SE	95% confidence interval
Plot1									
$\varphi_{(a)}\,p_{(.)}b_{(t)}$	421.189	0.861	1	0.390	0.084	0.242 - 0.561	935.281	293.394	360.229 - 1510.333
			2 and over	0.974	0.021	0.882 - 0.995	47.895	10.129	28.042 - 67.749
$\varphi_{(a)}\,p_{(a)}b_{(t)}$	424.829	0.139	1	0.371	0.084	0.226 - 0.545	662.151	372.468	-67.886 - 1392.188
			2 and over	0.975	0.021	0.875 - 0.995	48.947	10.764	27.849 - 70.045
Modeled average			1	0.387	0.085	0.239 - 0.559			
			2 and over	0.974	0.021	0.8809 - 0.995			
Plot 2									
$\varphi_{(a)}\,p_{(.)}b_{(t)}$	439.708	0.837	1	0.557	0.065	0.428 - 0.679	1200.134	410.604	395.351 - 2004.918
			2 and over	0.893	0.036	0.799 - 0.946	288.451	78.913	133.781 - 443.120
$\varphi_{(a)}\,p_{(a)}b_{(t)}$	442.983	0.163	1	0.556	0.067	0.425 - 0.680	1166.006	662.609	-132.709 - 2464.720
			2 and over	0.894	0.037	0.796 - 0.947	290.227	84.585	124.440 - 456.014
Modeled average			1	0.557	0.065	0.428 - 0.679			
			2 and over	0.893	0.036	0.799 - 0.946			

OBSERVED MORTALITY

The carcass of a marked first year snake and a juvenile snake were found in Plot 2. Two dead adults (one in Plot 1 and one in Plot 2) were also discovered. We could not determine cause of death in any of the cases due to the fact that the carcasses were substantially decayed or were only partial carcasses. Cobras were harvested for trade in these two plots. Snake harvesters mostly visit the site during the last three months of the year, because the sites were usually flooded during these months. To escape the flood waters, snakes may be found in trees up to six meters in height or in burrows located within elevated dikes (Figure 24). One team of harvesters claimed to have harvested 10 adults from Plot 2 in 2009 (the year prior to this study) and at least three adults were collected from Plot 1 during the year of this study (2010).

Cobras are subject to human-caused mortality, both as a result of being killed on sight by many agricultural workers reluctant to share their field with cobras and also occasionally for food (Cox 1991). Agriculture workers mentioned killing *N. kaouthia* encountered during the study period. A brood of newly-hatched neonates was apparently killed as they emerged from the burrow at the beginning of year 2010 in Plot 1. Rat hunters and fisherman also hunt cobras opportunistically.

Figure 24. *N. kaouthia* found on trees and bundle of grass during flooding period.

VARIATION IN CAPTURE PROBABILITY

I grouped total field-caught snakes by sex and capture season. Of 206 individual encounters, most individuals were found in the wet season (n=118), 68 encounters were in the cold season, and only 20 encounters were in the dry season (Table 12). The absolute number of males encountered is greater than females in both the dry season (M:F=12:8) and the wet season (M:F= 69:49). Females were encountered more frequently during the cold season (M:F=29:39). However, log-likelihood ratios indicates no strong seasonal differences between the proportion of males and females encountered (χ^2 =4.74, p=0.09).

Table 12. Variation in seasonal capture probability of *N. kaouthia*.

	Dry season **(Feb-Apr)**	**Wet season** **(May-Oct)**	**Cold season** **(Nov-Jan)**
Male	12	69	29
Female	8	49	39
Total	20	118	68

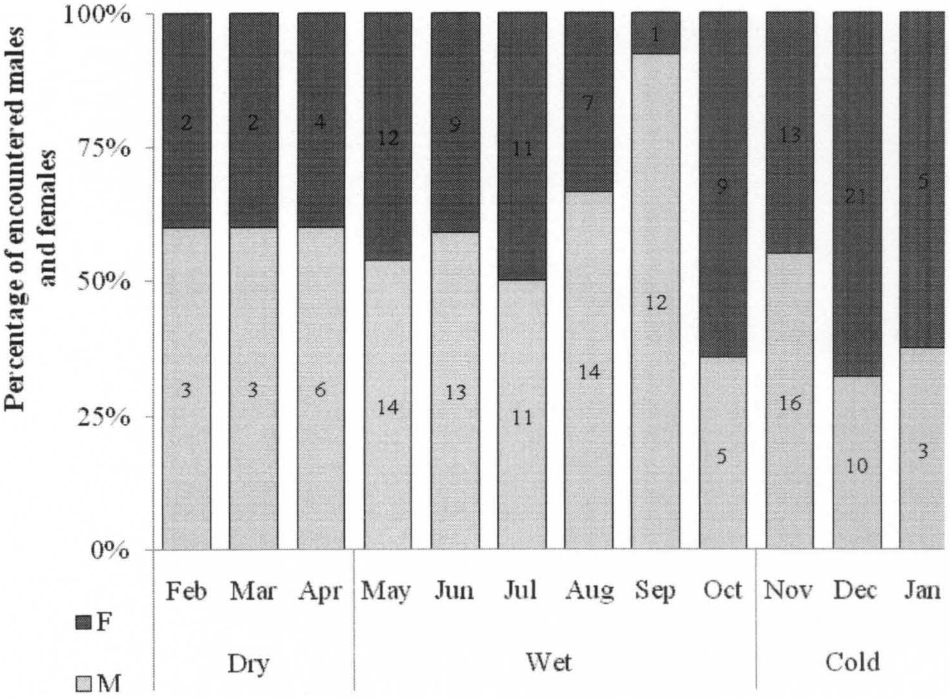

Figure 25. Percentage of males and females *N. kaouthia* encountered in monthly basic (number label indicates encounter frequency)

Discussion

BODY SIZE, SIZE CLASS DISTRIBUTION, AND SEX RATIO

The distribution of size classes differed significantly between the two plots. However, both plots have similar features with regard to the size class distribution: a low frequency of very small individuals (<40 cm SVL); and a bimodal distribution with one peak occuring at 50-70 cm of SVL and another peak at 130-150 cm of SVL. The difference between plots was not consistent and the snakes in one plot were not larger on average than the other. The differences probably reflect asynchromous perturbations (*e.g.*, harvesting) in the two populations.

The distribution itself is likely to reflect biased sampling, in particular with respect to small snakes. The low encounter frequency with the smallest snakes was probably due to their small size, agility, and cryptic behavior (Shine *et al.* 2007). Small snakes (<70 cm of SVL) were found only during April-July while searches were conducted at night and when the fields were clear after harvesting. Cleared paddy fields allowed for a more effective search. Further, juvenile snakes were mostly caught during night searches, when snakes were outside of their hiding places. Conversely, most individuals taken from burrows were adults. This is probably the result of track and sign from large snakes being more easily observed than sign from small snakes. Juvenile snakes also probably live outside of a burrow, as their small size may allow them to easily find a hiding place under clumps of grass, tree roots/cavities, or in soil cracks.

The sex ratio within each plot did not differ from 1:1 and the plots did not differ from each other. This result is consistent with the equal adult sex ratio reported in *N. melanoleuca* and *N. nigricollis* (Luiselli and Angelici 2000). However, a study by Shine *et al.* (2007) suggested a male-biased sex ratio among adults of six African congeners. However, it was difficult to determine in these cases whether the apparent bias was due to a higher mortality rate among females or due to intersexual diference in detectability.

ESTIMATES OF SURVIVAL RATES

As expected, adults had higher survival rates than did first year snakes. Estimated survival rates of first year snakes and adults were 38.7% and 97.4%, respectively for Plot 1. In Plot 2, estimates of annual survival were 55.1% and 89.3% for first year snakes and adults, respectively. Despite fairly large differences in estimated survival rate for first year snakes between the two plots, there were no statistically significant differences due to plot for first year snakes or adults.

The combined estimates for adult survivorship, averaged across plots, was approximately 0.93. This seems somewhat high, but without any estimates of among year variation in survival it is completely plausible. Survivorship this high suggests that about half of the individuals that survive their first year will still be living 9-10 years later. This seems at odds with, but not incompatible with other data. Longevity of wild cobras is unknown, but a still living captive specimen of *N. kaouthia* is fourteen- years old (L. Chanhome, pers. comm.), which is similar to maximum ages in captivity provided by Perkins (1955) for similar-sized Asiatic congeners (*N. atra* and *N. naja*) that lived up to 10 and 12 years, respectively. Further, given the growth rates of adults estimated in Chapter 2, the largest individual in this study (162.3 cm.) is estimated to be 12-14 years of age.

Cobra survival rates are also a bit higher than survivorships estimated from long-term studies on two elapids in Australia. The small-eyed snake (*Rhinoplocephalus nigrescens*) had an estimated annual survival of 0.74 in adults and 0.31 in juveniles; while juvenile survival was 0.55 and adult survival 0.82 in adults of the broad-headed snake (*Hoplocephalus bungaroides*) (Webb *et al.* 2003). These two elapids were collected for pet trade. Webb *et al.* (2002) compared survivorship of the snakes between heavily disturbed years and earlier years and found significant effect on female survival of *Hoplocephalus bungaroides*. However, no effect was observed in *Rhinoplocephalus nigrescens*. The authors suggested that female vulnerability of *Hoplocephalus bungaroides* due to size selective collection that bias to adult female, since females are larger than males in this species. The survivorship of *N. kaouthia* estimated in this study is also slightly higher than survivorship estimates from long-term studies on a couple of rattlesnake species (*Crotalus* sp) (Parker and Brown 1974; Keenlyne 1978; Brown 1991; Martin 1993) and copperheads (*Agkistrodon contortrix*) (Vial *et al.* 1977), which were 0.75-0.85 (Reed *et al.* 2003). However, it is not at all certain how similar survivorship should be between North American snakes of family Viperidae, or even sub-tropical Australian snakes in same family, and tropical snakes of family Elapidae. Thus, I provide the first estimate of adult mortality rates for a true tropical snake in the wild.

The combined estimates for survival of first year snake, averaged across plots, was approximately 0.47. This seems very high, but again I have no estimate of among year variation. If one allows that adult cobras reproduce for the first time at three years of age, live on average until 10 years of age, reproduce every other year, produce 25 eggs per clutch, that 80% of the eggs hatch, and that half the nests are destroyed by predators; then the average female produces 40 neonates during her life. In a stable population (λ=1.0), 2 of those 40 (5%) neonates should reach reproductive age. While the uncertainty around the assumptions concerning life history assumed above, it is hard to imagine that 47% survival during the first year could be typical of this species. Any estimate of first year snake survival not made exclusively from newborn individuals is going to bias survival upwards, as the survivorship of a three month old individual surely differs greatly from that of a three day old individual. An estimate of annual survival using only the first year snakes born in captivity was 0.36.

ESTIMATES OF POPULATION SIZE

Gross population estimates of Plot 1, with an area of 1-km^2, were 935 individuals of first year snakes and 48 adults. For Plot 2 (2 km^2), population sizes were 1200 first year snakes and 288 adults, respectively. Population estimates were based on POPAN open population model, that would allow new animals to enter the area (by birth or immigration) and animals to leave (by death or emigration) (Schwarz and Arnason 2011). Though, I found no in-plot marked snake outside the study area from occasional survey done at surrounding areas, our study habitat was contiguous and relatively homogeneous, so that migration into and out of the sites were possible or even likely. Because the snake population was considered to be open in this study, the effective trapping area is unknown and accurate estimates of density cannot be obtained. Accurate population estimates of snakes have been considered difficult to obtain due to obstacles associated with detectability and sampling bias (Dorcas and Willson 2009). For example, Bonnet and Naulleau (1996) noted that substantial variation in capture probability is based on sex and age.

VARIATION IN CAPTURE PROBABILITY

High capture rates in the wet season and low rates of capture in the dry months of *N. kaouthia* is consistent with a study by Luiselli and Angelici (2000) that found that aboveground activity of *N. melanoleuca* and *N. nigricollis* peaked during the wet season and was reduced during the hottest months of dry season. Over a smaller temporal scale, it was noted that individuals were often encountered outside of their burrows during daylight hours in the dry season just after the rare rain events.

Females of *N. kaouthia* have been reported previously to engage in egg guarding behavior, thus female tend to stay with her eggs in a burrow during the egg-laying and incubation season. Additionally, more than one gravid female was able to be found within the same burrow. High numbers of male snake encountered during August-November is likely related to the breeding season and males actively seeking females to mate with. Bonnet *et al* (1999) found that females of oviparous species are more vulnerable to mortality, as well as capture, during the egg-laying period. Whereas males tend to move frequently, and over longer distances, while searching for a mate, and that leads to high risk of capture and mortality during this period for males.

MANAGEMENT RECOMMENDATIONS

Being a fatally venomous snake sharing habitat with humans puts *N. kaouthia* at a high-risk for human-caused mortality. A study by Whitaker and Shine (2000) suggested that about one-third of snakes approached by people were killed. Because *N. kaouthia* is not pretected by law for domestic exploitation unless the hunting occurs in protected areas, the harvesting of cobras, including the other two species distributed in Thailand (*N. siamensis* and *N. sumatrana*) is enabled. Harvesting mostly takes place in rice fields, especially in central Thailand, which is the largest rice growing area. Commercial cobra harvesting does not occur uniformly over the country. Intense harvesting areas are in the central region and certain areas of the south. Climate condition is a factor facilitating harvesting level, with harvesting activities concentrated :

1) during the rainy season (at the end of the year) when snakes are in good body condition and snake searching is less labor-intensive, i.e, snakes are gathered in small elevated areas or on trees due to flooding and snake tracks were easily detected on surface of moist soil.

2) during the dry season, night hour searchess were conducted during the hottest periods of dry season. This period corespond to clearance period of paddy field after crop harvesting, which facilitates detection of snakes.

This study, and others, suggest a high capture (mortality) rate of females of oviparous species during the egg-laying season. Brooks *et al.* (2007) noted that temporal overlap between the breeding period and harvesting season increased the vulnerability of water snakes havested in Tonle Sap Lake. Cobra harvesting is typically size-selective, large invidividuals were prefered for trade. Response of size selective harvest may involve a shift in age at maturation (Weatherhead and Madsen 2009). With long-term monitoring we might see this trend in harvested populations of cobras.

Life history traits of tropical snakes may alleviate the effects of harvesting. Shine *et al.* (1999) suggest that rapid growth, early maturation, relatively high reproductive output, as well as flexibility in diet and habitat use, probably allow substantial harvesting to be sustainable, however, careful monitoring is needed. Webb *et al.* (2002) compamared snake collecting effects on of two elapids, and found that *Hoplocephalus bungaroides* tend to be more vulnerable to collecting than *Rhinoplocephalus nigrescens*. Beside large-size selective collecting bias to female snakes of *Hoplocephalus bungaroides*, its ecological characteristics such as slow growth rate, later maturation, infrequent reproduction, as well as specialized diet and habitat, causes *Hoplocephalus bungaroides* to be highly vulnerable to harvesting (Webb and Shine 1998; Webb *et al.* 2002; Webb *et al.* 2003). *N. kaouthia* are probably able to withstand harvesting with appropriate management. This species is capable of preying on a variety of amphibians, birds, mammals and reptiles and is distributed broadly thoughout the country. Clutch size of *N. kaouthia* (24 eggs in average) is relatively high, however, nest success in wild populations is unknown, though hatching success is quite high in captivity. Growth rate of *N. kaouthia* in the wild is rapid, which is a likely response to plentiful food (rats) distributed fairly evenly throughout the year in paddy fields. As is true with most species of conservation concern, more data on the demographics and causes of mortality for this species are needed in order for accurate estimates of sustainable harvest rates to be made.

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APPENDIX

Appendix 1. Snout-vent length (SVL) and weight growth increment of *N. kaouthia*

Scale ID	Sex	Age	SVL (mm)	Weight (g)	Elapsed days	SVL		Weight	
						Difference (mm)	Increment (mm/day)	Difference (g)	Increment (g/day)
94	M	N	256	15.93	127	432	3.4	109.07	0.86
32	M	N	278	20.21	78	192	2.46	39.79	0.51
50	M	N	288	21.29	116	277	2.39	53.71	0.46
83	M	N	657	120	138	306	2.22	363	2.63
24	M	J	860	350	83	180	2.17	260	3.13
27	M	J	1000	530	243	254	1.05	485	2
52	M	A	1150	950	110	84	0.76	230	2.09
52	M	A	1234	1180	64	0	0	-80	-1.25
70	M	A	1192	1055	78	8	0.1	105	1.35
4	M	A	1205	1080	226	100	0.44	10	0.04
89	M	A	1240	1320	75	61	0.81	310	4.13
20	M	A	1270	950	44	15	0.34	50	1.14
44	M	A	1340	1280	147	43	0.29	390	2.65
44	M	A	1383	1670	68	0	0	-230	-3.38
29	M	A	1380	1550	175	45	0.26	260	1.49
29	M	A	1425	1810	62	16	0.26	-430	-6.94
7	M	A	1485	1400	137	13	0.09	25	0.18
7	M	A	1498	1425	32	0	0	35	1.09

Appendix 1. Snout-vent length (SVL) and weight growth increment of *N. kaouthia* (Continued)

Scale ID	Sex	Age	SVL (mm)	Weight (g)	Elapsed days	SVL		Weight	
						Difference (mm)	Increment (mm/day)	Difference (g)	Increment (g/day)
43	F	N	282	18.72	106	270	2.55	51.28	0.48
147	F	J	945	345	27	28	1.04	-40	-1.48
71	F	J	1040	670	121	155	1.28	285	2.36
28	F	A	1123	700	85	111	1.31	300	3.53
56	F	A	1152	685	201	249	1.24	795	3.96
6	F	A	1285	1250	137	23	0.17	-150	-1.09
6	F	A	1308	1100	205	158	0.77	925	4.51
53	F	A	1425	1315	137	69	0.5	965	7.04
5	F	A	1480	2180	15	0	0	0	0
55	F	A	1528	1430	30	7	0.23	110	3.67
55	F	A	1535	1540	15	4	0.27	-70	-4.67
55	F	A	1539	1470	158	27	0.17	305	1.93
61	F	A	1560	1700	30	0	0	-50	-1.67
61	F	A	1555	1650	136	0	0	130	0.96

Remark Weight increments in bold indicate gravid condition.

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Oct 2-14, 2004	CITES Thirteenth meeting of the Conference of the Parties, Bangkok, Thailand
Nov 17-25, 2004	IUCN Third World Conservation Congress, Bangkok, Thailand
Nov 28-30, 2006	The 4th meeting of ASEAN CITES Experts Group on CITES, Manila, Philippines
May 9-11, 2007	The 5th meeting of ASEAN CITES Experts Group on CITES, Singapore
June 3-16, 2007	CITES Fourteenth meeting of the Conference of the Parties, Hague, Netherlands

Invited presentations:

- CITES implementation of Thailand at the 4th meeting of ASEAN CITES Experts Group on CITES, Manila, Philippines.

Research Experience and Papers:

- The Field Assessment of the population of Cobra (*Naja* spp.) in Thailand.