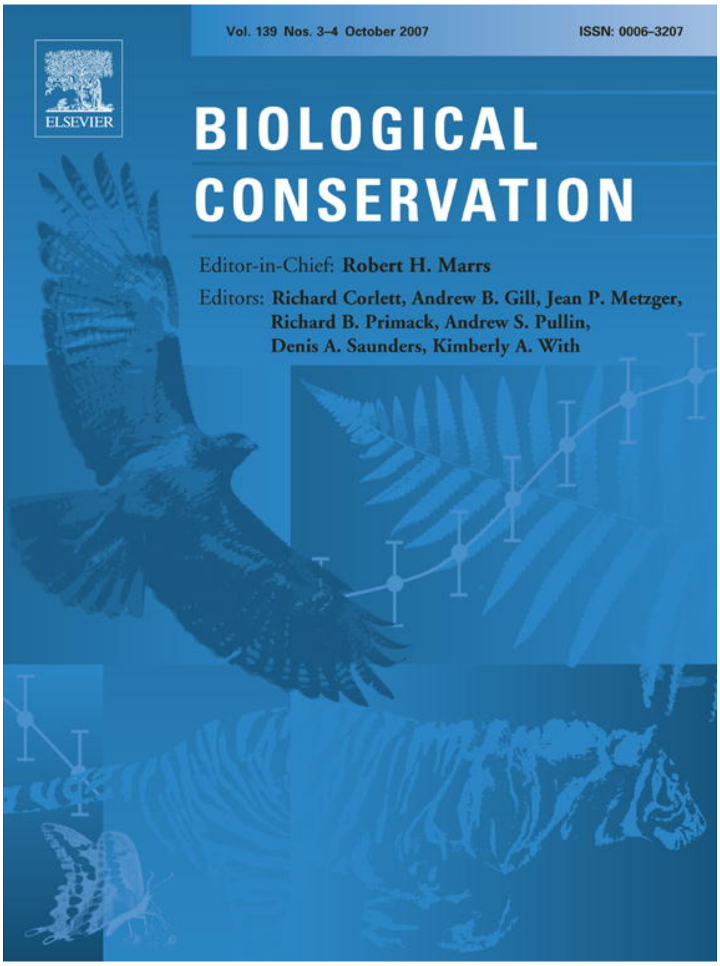
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# Vulnerability of Cambodian water snakes: Initial assessment of the impact of hunting at Tonle Sap Lake

*Sharon E. Brooks*[a,*], *Edward H. Allison*[b], *John D. Reynolds*[c]

[a]School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK
[b]The Worldfish Center, P.O. Box 500, GPO, 10670 Penang, Malaysia
[c]Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada V5A 1S6

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ABSTRACT

This paper documents the emergent snake 'fishery' occurring on Tonle Sap Lake where an estimated 6.9 million snakes (mostly homalopsids) are removed annually, representing the world's largest exploitation of a single snake assemblage. Based on interviews with hunters, we found that snake catches declined by 74–84% between 2000 and 2005, raising strong concerns about the sustainability of this hunting operation. A combination of experimental trials to estimate population sizes and extensive catch and trade monitoring programs indicated that population density varies both spatially and temporally, largely due to the seasonally fluctuating environment of Tonle Sap Lake. The quantity of snakes captured mirrors the lake's seasonal fluctuations, due to temporal changes in both catch per unit effort and the number of people hunting. Through interviews with hunters we scored the seven exploited species for perceived changes in catch size. All species were reported as declining and their scores match their predicted vulnerability based on a combination of timing of exploitation relative to breeding, proportion of catch consisting of mature females and large fecund females, fecundity, body size, size at maturity, and vulnerability to capture by gill nets. This information can inform conservation decisions for the long-term preservation of this snake assemblage. We propose emphasis should be placed on the snake skin trade that is targeting the largest, highly fecund females, and that any efforts to reduce hunting should focus on the peak in trade that occurs during the main breeding season.



## 1. Introduction

Sustainability of exploitation has become a central issue in conservation, due to growing demands on biological resources for food, shelter, fibre and medicines (Milner-Gulland and Mace, 1998; Reynolds and Peres, 2006). The extent of exploitation that can be sustained depends on the biology of the species and the intensity of the activity. For wild animals, there has been extensive research in both the fisheries domain and in studies of the bush meat trade, which has yielded a range of models for estimating sustainable rates of exploitation (Milner-Gulland and Akcakaya, 2001; Reynolds et al., 2001a). Many of the assessment approaches used are very data intensive, which precludes their use in most situations, particularly in many tropical regions where heavy exploitation occurs with little knowledge of the species involved and the extent of exploitation occurring. However, a range of indicators can be used to provide initial assessments based on basic features of life histories in relation to capture statistics (Reynolds et al., 2001a; Dulvy et al., 2004; Froese, 2004).

* *Corresponding author:* Tel.: +44 7941 871662.
E-mail addresses: s.brooks@uea.ac.uk (S.E. Brooks), e.allison@uea.ac.uk (E.H. Allison), reynolds@sfu.ca (J.D. Reynolds).
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Many snake species around the world face heavy exploitation pressure (Keogh et al., 2001; Zhou and Jlang, 2004), yet this is rarely studied. This means that impacts of hunting on snake populations are largely undocumented. Snakes have been captured throughout history for medicinal products, meat, leather, objects of worship and decoration. Within China, the commercial trade in snakes became large-scale domestically in the 1980s, and more recently regional trade has expanded (Klemens and Thorbjarnarson, 1995; Zhou and Jlang, 2004). For some species such an expansion in trade had led to concerns about the ecological sustainability of exploitation (Shine et al., 1999; Keogh et al., 2001).

In recent years, snake hunting has become a prevalent feature of the Tonle Sap Lake in Cambodia (Stuart et al., 2000). Although this ecosystem holds one of the most productive inland fisheries in the world, since the lake became securely accessible again in the 1990s, there has been gross overexploitation of many fish species and substantial decreases in the catch per unit effort (Lim et al., 1999; Bonheur and Lane, 2002). There has also been extensive exploitation of the other wildlife of the lake such as birds, turtles and snakes which are also being depleted (Bonheur and Lane, 2002).

Concurrently, within the Tonle Sap basin there has been a substantial boom in the local crocodile farm industry, which is breeding and rearing the native Siamese crocodile, *Crocodylus siamensis*, and the non-native Cuban crocodile, *Crocodylus rhombifer* for commercial purposes (Campbell et al., 2006). This has added considerable pressure to the demands for protein from the lake which, in recent years, has been partly provided by the exploitation of water snakes (Stuart et al., 2000). There are also international markets for the snakes of Tonle Sap, including skins are used for fashion products, as well as live animals used for human consumption, often in expensive restaurants (Stuart et al., 2000; Bonheur and Lane, 2002).

Tonle Sap Lake is the largest lake in SE Asia and one that exhibits a unique hydrological system. Each year, as a result of the increased flow of the Mekong River during the SW monsoon, the Tonle Sap river changes direction and floods the lake, increasing its area from 2500 $km^2$ to between 10,000 and 16,000 $km^2$ (Lim et al., 1999). This creates a highly dynamic ecosystem, with seasonally fluctuating water levels and areas of flooded habitat. This in turn provides an array of seasonally available resources, shaping patterns of fishing, wildlife exploitation and other livelihood activities.

The majority of snakes living within Tonle Sap are semi-aquatic homalopsid water snakes, previously known as homalopsines (Saint Girons and Pfeffer, 1972; Voris et al., 2002; Lawson et al., 2005). Despite their abundance, they are seldom seen in the wild, as they spend most of their time beneath the surface of the water, where they are vulnerable to capture by gill nets. Therefore, in response to the market demand for snakes from the crocodile farm industry, Tonle Sap fishers have recently begun to target these snake species (Stuart et al., 2000). This has led to large numbers of snakes being captured, yet the true extent of the exploitation and the impact on snake populations was previously unknown. Of the species involved, only the pythons (*Python* spp.) and cobras (*Naja* spp.) are listed under the Convention on International Trade in Endangered Species (CITES), and protected by Cambodian law. Species that breed in water currently fall under the jurisdiction of the Department of Fisheries, which has made no provision for the protection of water snakes.

Following on from the work provided by Stuart et al. (2000), this paper provides a detailed documentation of the emergent snake 'fishery' occurring on Tonle Sap Lake. We provide the first statistics of capture rates and trade quantity that are based on year round sampling. By overlaying catch data with biological data, we assess the relative vulnerability of different species based on the timing of exploitation relative to their breeding season, proportion of catch consisting of mature females and the large fecund females, fecundity and body size, including size at maturity. Through interviews with local hunters, we present the perceived rate of decline in catches over recent years, and obtain scores of the relative declines of the various species involved, which we then relate to intrinsic life history traits and capture statistics in order to make preliminary inferences regarding the sustainability of snake hunting.

## 2. Methods

### 2.1. *Assessment of trade*

We used a combination of methods to assess the trade in the five provinces that surround Tonle Sap Lake. The study was carried out between June 2004 and March 2006, with estimates of annual trade based on a hunting season that extends from June until March. For some sites we have obtained data for two hunting seasons and in these cases the mean was taken as our annual estimate. In all five provinces we identified landing sites where snakes were sold by both hunters and lake-based intermediary traders to land-based traders. In some provinces landing sites are clearly defined areas through which the majority of trade passes, whereas in others, trade occurs over an undefined area. In the latter situation trade is more difficult to monitor and is therefore likely to be underestimated. In addition to the large-scale trade, snakes that are caught as by-catch are often consumed within the household or sold in small local markets in numerous villages both on and around the lake. These activities have not been quantified but are likely to be small-scale in comparison to the targeted catch.

We identified major landing sites in Siem Reap, Battambong and Kampong Chhnang province where large quantities of snakes were sold. The Chong Khneas landing site in Siem Reap province was chosen as the principal site to monitor the trade, based on the known high level of trade that occurs there as a result of the high density of crocodile farms, and hence high demand for snakes for food. We monitored this landing site intensively from July 2004 until March 2006. Monitoring occurred over 24 h periods on a weekly basis throughout the hunting season and additional shorter visits were made opportunistically. When our monitoring periods lasted for less than 24 h, we used correction factors to estimate the total for a 24 h period based on average quantities of snakes being landed for each hour of the day for that month. For each boat that arrived, we recorded the weight of snakes landed in kg. We divided the snakes into two categories according to the way they were sold: (1) small-bodied snakes of mixed species normally sold dead for crocodile food and occasionally for human consumption; (2) large-bodied, high value snakes of two species, sold separately by weight or by number depending on their size, and sold for skins and live export. For each landing the boat owner was asked the origin of the catch. This information was gathered by an assistant who has lived in the local village all his life, and has a good rapport with the people involved in the trade, minimising potential bias from dishonest replies. We also used this method at Battambong landing site in 2004 on two occasions. At these trading ports the mean number of snakes traded per day in each month was used to calculate the estimated total number of snakes traded for that month. This information was then used to estimate the total quantity traded through each port.

At Kampong Chhnang and Battambong province landing sites, we identified the traders that purchase the majority of the snakes landed at these sites. We asked them to retain records of the quantities they traded on a daily basis. While we acknowledge the potential for dishonest recordings, these traders record this information under normal circumstances and would have little reason to write false records. We estimated the remaining quantity of snakes traded at these sites from regular visits and interviews with other traders who purchased their snakes directly from the landing sites.

We spent 12 days visiting sites within Siem Reap, Kampong Thom, Kampong Chhnang and Pursat province to quantify previously unidentified trade. We derived estimates of annual trade through several sites from interviews with various traders. Much of this trade, particularly within Kampong Thom, occurs directly from trader to trader and no clearly defined landing site exists. This method is the most limited and potentially biased as it does rely on honesty. However, through interviewing several traders, we were able to triangulate our findings and discard interviews that did not concur with others. Only the trade that could be quantified was included in our estimates and there are likely to be more trade routes than those we have identified.

Conversion factors based on repeated counts of known weights of snakes taken from major landing sites were used to convert weight into number of snakes. Our estimates of trade quantity of the high value large-bodied snakes are based on those traded at Chong Khneas port, although this trade does exist at various localities around the lake.

### 2.2. *Catch species composition*

We haphazardly sampled catches at landing sites to record species composition. From the crocodile food trade we counted and recorded the species of a total of 62,230 snakes from 162, 18 and 5 separate samples in Siem Reap, Kampong Chhnang and Battambong province respectively. In Siem Reap this was carried out throughout the season on a weekly basis, as far as possible, providing a time series of the relative proportions of each species in the catch. We estimated the species composition of the large-bodied snakes traded at Chong Khneas in Siem Reap from the trade monitoring data, whereby people were asked how many of each species were in each landing.

### 2.3. *Catch per unit effort*

We had 1475 encounters with snake hunters located out on the lake who we intercepted at trading points before they sold their catches to the traders. These locations were recorded using a Geographical Positioning System (GPS) and were typically less than 3 km from the areas where hunting occurs. We identified, counted and where possible weighed each species in their catch to obtain the quantity of each species caught. We then conducted a short questionnaire with each hunter regarding their effort (gear type and size and duration set in water), habitat where hunting occurred (water depth and colour, habitat type and distance from current location) and whether they were targeting snakes. Of the 1475 catches recorded, 1335 were caught using a gill net. The area of each gill net was calculated from the length and height provided in the questionnaire. We then calculated the catch per unit effort from the number of snakes per 1000 $m^2$ of gill net per day, for snakes overall and for each species separately. For the comparisons of catch per unit effort with trade quantity we converted this into kg per 1000 $m^2$ per day based on the average weights of each species measured at landing sites. When testing for the effect of different variables on catch per unit effort, we $\log 10 + 1$ transformed the data and excluded zero values for individual species to provide a normal distribution for parametric statistics. The removal of zero values removed cases where species were not present, but had no effect on their relative abundances in the areas where they were encountered.

### 2.4. *Size–frequency of snake catches*

From the catches landed at Chong Khneas we randomly selected, measured, weighed and sexed 8826 snakes: 4244 *Enhydris enhydris*, 1599 *Enhydris longicauda*, 1600 *Homalopsis buccata*, 141 *Enhydris bocourti*, 869 *Erpeton tentaculatus*, 234 *Xenochrophis piscator* and 139 *Cylindrophis ruffus*. No data are available for the other species that we recorded in the hunters' catches as they did not appear in the trade. Using these size–frequency data we applied simple fisheries indicators to assess the potential for sustainability of this snake 'fishery' for each species involved. Using the length at which 50% of the female population is mature (Brooks, unpublished data), we calculated the proportion of mature females in the catch. In order to assess the proportion of females that were in the upper size ranges, we calculated the proportion of captured females above 85% maximum length. We calculated the fecundity at mean length of capture and maximum body length for females, using the linear regressions of clutch size and body length (Brooks, unpublished data), which we used to express the proportion of potential reproductive output realised prior to capture. In our calculations using maximum length, we used the maximum observed length at the 99th percentile as this was found to remove sample size biases. In our comparisons of life histories, the maximum mass was estimated from the mean of the largest 10% of the distribution, to remove sample size biases between the species. Such biases would have been particularly apparent in some species, where many of the larger females contained eggs and were therefore removed from the sample when using mass.

### 2.5. Interviews with local hunters

We interviewed 60 snake hunters between June 2004 and December 2005 in Battambong province. These interviews were independent of those carried out during the catch monitoring and were conducted in people's households. We asked each person to estimate the quantity of snakes that they caught in the current year, the previous year and in the year they started hunting. All estimates were given for both the high season, when people target snakes and obtain high catches, and the low season when snakes are generally caught as a by-catch. Additionally, we asked hunters which months of the year they hunt snakes. Using picture cards of the main seven species we see in the trade, we asked people to score each species for changes in their abundance. We applied the scores to the categories as follows:

| | |
|---|---|
| +2 | Increase |
| 0 | No change |
| −1 | Small decline |
| −2 | Medium decline |
| −3 | Large decline |

For each species we multiplied the proportion of people who described changes in each category by the score for that category, and then calculated a total score from the sum of these scores. A high negative score thereby reflects a large decline. Increases were seldom reported and therefore only a single grade was included. More often, species were recorded as declining and therefore it was necessary to scale decline scores into three grades. An alternative scoring system, in which an increase in abundance was given a value of +1, did not change any conclusions.

### 2.6. Population estimates

We conducted two preliminary depletion experiments to estimate snake densities in the flooded forest of Battambong province. One was carried out in August and one in November 2005. The experimental design consisted of three replicates. Three circles, each 700 m circumference, of gill net were set to act as a barrier closing off areas of flooded grassland dominated with the woody legume species *Sesbania javanica*; a common habitat in the floodplain. The circles were set a minimum of 100 m apart from each other. We used three small circles instead of one large one because it was easier for the hunters to set nets in smaller circles. Inside each circle a further 350 and 700 m of gill net was set in the two experiments, respectively. The location of the experimental areas was recorded using a GPS so that we could calculate each area accurately using Arcview GIS. Six hunters were hired to carry out the experiment and those responsible for the barrier nets identified the direction from which each snake had entered the net, in order to record snakes caught from inside and outside the experimental area separately. Although the snakes become very tangled in the nets, it was possible to determine the direction of entry from the side where the tail was, as the entire body of the snake was not able to pass through the net due to the small mesh-size. The nets were checked daily and we recorded the numbers of each species caught in each net for seven days. Data from the three circles were combined. The population estimate was derived from the standard fisheries depletion method (Jennings et al., 2001) whereby the number of snakes caught in each sampling period, $N_i$, was regressed against the cumulative number caught, $X_i$:

$$N_i = a - bX_i,$$

where $a$ is a constant and $b$ is the slope of the regression. The total number in the population, $N$, is calculated as

$$N = -a/b.$$

Confidence intervals were set at 95% and calculated from the standard formula used to estimate confidence limits on estimates derived from linear regressions.

**Table 1 – Estimated quantity of snakes traded in the five provinces around Tonle Sap Lake and the species composition for three of these provinces**

| Province | Trade quantity per annum (kg) | Species composition | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Number counted | *Enhydris enhydris* | *Enhydris longicauda* | *Homalopsis buccata* | *Enhydris bocourti* | *Erpeton tentaculatus* | *Xenochrophis piscator* | *Cylindrophis ruffus* |
| Siem Reap | | | | | | | | | |
| Crocodile food trade | 311,959 ± 56,559 | 57,038 | 71.0 | 16.2 | 3.1 | 0.6 | 6.9 | 1.5 | 0.8 |
| Skin trade | 46,496 ± 9143 | 22,867 | | | 97.6 | 2.4 | | | |
| Kampong Thom | 162,195 ± 19,655 | | | | | | | | |
| Kampong Chhnang | 139,402 ± 50,233 | 4114 | 56.1 | 39.3 | 1.2 | 0.2 | 3.2 | 0.1 | 0.02 |
| Pursat | 88,286 ± 45,607 | | | | | | | | |
| Battambong | 28,511 ± 15,035 | 1178 | 71.6 | 17.0 | 3.0 | 0.4 | 6.1 | 1.5 | 0.4 |
| Total | 776,849 ± 196,232 | | | | | | | | |

Estimates for the two distinct trades that occur in Siem Reap province are given separately. Species composition data indicate the total number of snakes counted and the percent of these belonging to each species.

## 3. Results

### 3.1. Trade quantity

The quantity of snakes traded in Siem Reap includes both those traded for crocodile food and those for the international skin trade (Table 1). Species composition for the skin trade at Chong Khneas is taken from the monitoring data whereby people were asked how many of each species were in each landing. Species composition for the crocodile food trade was taken from direct counts of samples in the three provinces; Siem Reap, Battambong and Kampong Chhnang.

We found that a total of at least 777 tonnes of snakes are traded at various destinations around the lake per year, which equates to 6.9 million individuals (Table 1). Although there are potential biases where our methods rely on being told the truth by traders, in areas where we have both quantities recorded by traders and quantities we recorded, they are of the same magnitude, indicating that this bias is minimal. The actual number removed may be considerably higher as this estimate does not include those used for human and crocodile consumption on the lake (i.e. not landed at ports), nor smaller unidentified trade routes.

Of the trade we identified, 46% occurred in Siem Reap province, where we focused our efforts on trade monitoring. Of the landings in this province, 98% came from traders from various locations who used motorized boats to collect snakes from multiple hunters. Our trade monitoring program showed that 93.4%, 3.2% and 2.8% of the quantity of these snakes originated from the forests of Battambong, Siem Reap and Pursat province, respectively. Of all trade identified, 49% of the snakes were therefore caught within the flooded forests of Battambong province, where we focused our catch monitoring program to quantify the catch per unit effort of hunter's catches.

The quantity of snakes traded at Chong Khneas port in Siem Reap province shows a strong seasonal fluctuation, as did the catch size per area of net per day (Fig. 2). However, the quantity of snakes traded is affected not only by catch per unit effort, but also by the proportion of hunters that are hunting in any given month (Fig. 3). The total number of people who hunt snakes is unknown. At low values of both

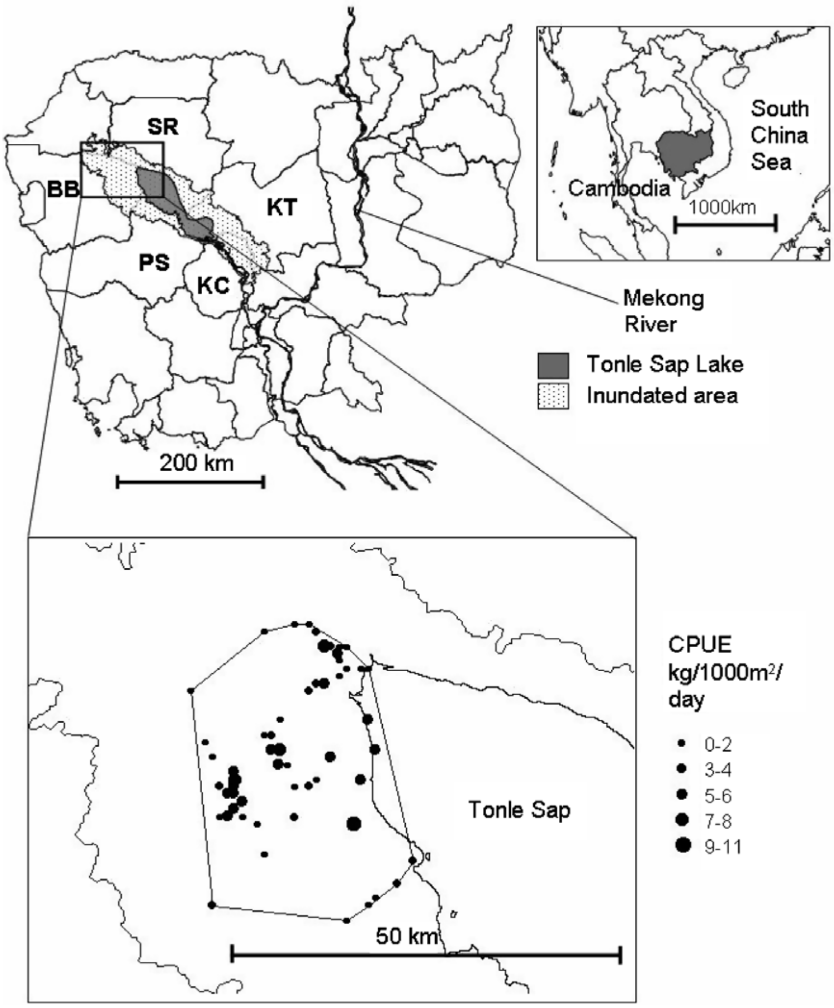


**Fig. 1 – Map of Cambodia showing the location of Tonle Sap Lake and the surrounding flood zone. The five provinces surrounding the lake are labelled [Siem Reap (SR), Kampong Thom (KT), Kampong Chhnang (KC), Pursat (PS) and Battambong (BB)]. The inset shows the study site and the black markers represent locations of catch per unit effort (CPUE) data. The size of each marker indicates the mean catch per unit effort at each location, ranging from 0–2 to 9–11 kg/1000 m$^2$/day.**

catch per unit effort and proportion of hunters hunting, no trade occurred because too few snakes were caught to transport to landing sites. The low trade quantity at the two highest catch per unit effort values is driven by the low proportion of hunters that hunt in the months of November and December when most (but not all) hunters are excluded from fishing lots (see Section 4). A multiple regression shows that while both catch per unit effort and proportion of hunters who are hunting are significant predictor variables, the latter explains more of the variation in trade quantity than catch per unit effort (model $R^2 = 0.66$, $P < 0.001$, partial correlations (catch per unit effort) $r = 0.50$, $P = 0.59$ (proportion of hunters hunting) $r = 0.73$, $P < 0.001$).

### 3.2. *Catch per unit effort (catch size per area of net per day)*

Mean catch per unit effort taken at various sites showed both spatial (Fig. 1) and temporal variation (Fig. 2). The water depth

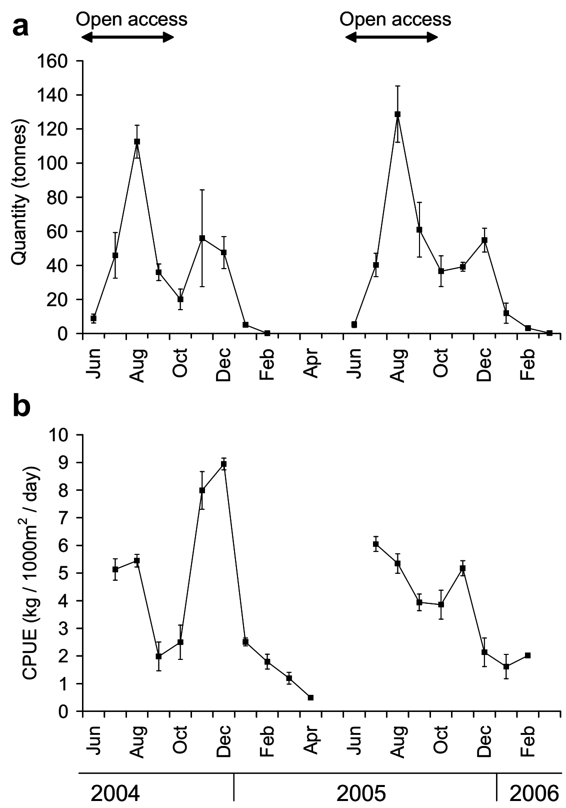


**Fig. 2 – (a) Estimated quantities of snakes traded over two hunting seasons at Chong Khneas port in Siem Reap province, based on mean values of quantity traded per day multiplied by the number of days in each month in which trading occurred. The standard error bars represent the variation between sample days. (b) The mean monthly catch per unit effort (CPUE) measured from gill net catches in the flooded forest of Battambong province over the same time period. Standard error bars represent the variation between hunters' catches. The arrows above the figures show the time of year when the resource is open access. At all other times access is restricted due to the operation of the private fishing concessions.**

at hunting sites also fluctuated with seasonal changes in the overall lake level (Fig. 4). We therefore controlled for these seasonal effects when analysing the effects of other variables on catch per unit effort. A two-factor ANCOVA showed that habitat type and water colour each had significant effects on catch per unit effort after controlling for water depth and month ($F_{5,932} = 8.44$, $P < 0.0001$, $F_{6,392} = 5.87$, $P < 0.0001$ for habitat and colour, respectively). The highest catches per unit effort occurred in shallow water (standardized $\beta = -0.07$, $P < 0.0001$). Bonferroni corrected *post hoc* analyses showed that the differences lay in the low catch per unit effort of open water compared to all other habitats, with the highest catches in flooded grassland and forest habitats compared with those along channels and in habitat dominated with *Sesbania javanica* ($P < 0.05$). Catch per unit effort also tended to be higher in the darker black and red coloured water than in the lighter blue, green and brown coloured water.

Unsurprisingly, the catch per unit effort was significantly higher when hunters were targeting snakes, rather than taking snakes as a by-catch ($t = -5.25$, d.f. = 209.5, $P < 0.0001$). The fishing gear used to catch fish and snakes is identical. In order to target snakes, hunters set their net in darker shallow water among vegetation, rather than the clear open water where they are able to catch fish. This therefore concurs with our result of a decrease in catch per unit effort with depth and open non-vegetated water. The hunters do not remove small fish that become caught in the net as these fish serve as a lure for snakes.

We recorded 11 species of snake in the catches. These vary considerably in their catch per unit effort, with *Enhydris enhydris* dominating the catch (Table 2). Some species occur in the catch that are undetectable in the trade. *Enhydris plumbea*, a non-venomous homalopsid, is believed by local people to be venomous and is therefore often killed and discarded. The cobras and pythons (*Naja kaouthia*, *N. siamensis* and *Python molurus*), which are more terrestrial than the homalopsids, are also sold. However, this is often done secretly as the trade in these species is illegal and can incur heavy fines.

For eight of the species recorded in the catches, habitat had a significant effect on catch per unit effort, after controlling for depth (Table 3). In all species except for *Erpeton tentaculatus* and *E. plumbea* the catches were highest in flooded grassland habitats. Most of the species do not occur in the open lake, but are restricted to the vegetated areas. Individuals of *E. enhydris* and *Cylindrophis ruffus* were very occasionally caught in the open water of the lake. Only three individual granulated file snakes, *Acrochordus granulatus*, were recorded during this study, and they were found in the open lake. Whereas *E. plumbea* had the highest catch per unit effort in deeper water, all of the other species that showed significant relationships between catch per unit effort and depth were caught most often in shallower water (Table 3).

### 3.3. *Population density*

The population estimates obtained from the two preliminary depletion experiments varied both between species and between experiments, which were conducted at different times and places (Table 4). Although these were preliminary trials, they give the first indications of possible densities in the wild

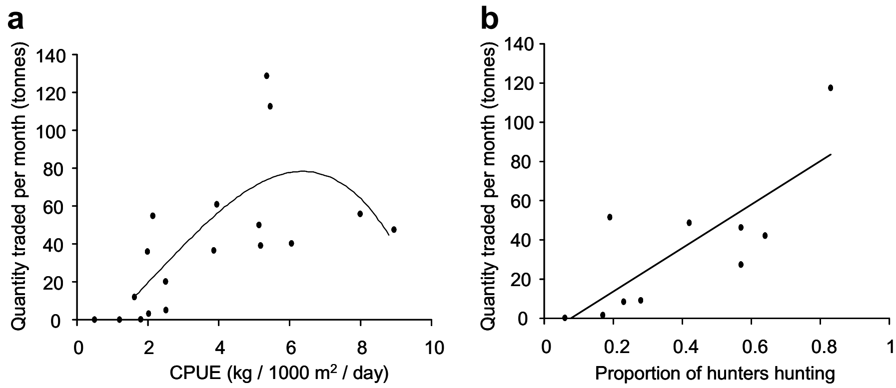


**Fig. 3 – Relationship between quantities of snakes traded at Chong Khneas port and (a) catch per unit effort (CPUE) and (b) the proportion of hunters that are hunting. In (a) each data point represents mean values for 18 separate months. In (b) the proportion of hunters hunting is based on an estimate independent of year and has therefore been plotted against a mean quantity of snakes traded in each month of the year taken over 2 years. (a) Cubic model: $R^2 = 0.47$ ($y = -578.6 + [476.9x] + [72.8x^2] + [-11.4x^3]$) and (b) linear model: $R^2 = 0.61$ ($y = 110{,}983x - 8598.8$).**

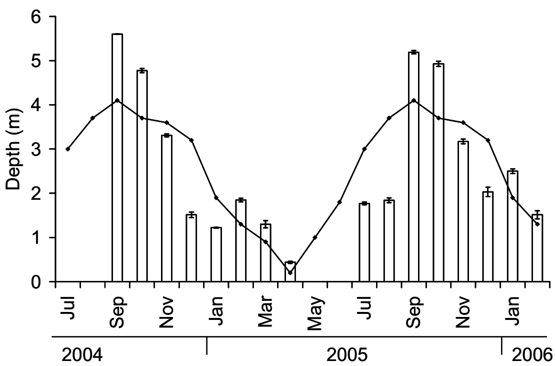


**Fig. 4 – Mean water depth taken from various hunting sites in Battambong province (bars) and at Prek Kdam hydrometric station, Tonle Sap Lake (line). The former is taken from our hunting monitoring program and shows standard error bars, and the latter from continual monitoring by the Mekong River Commission (MRC).**

for these species, depending on how good the assumptions prove to be. *E. enhydris* and *E. tentaculatus* both showed significant depletion regressions (i.e. number caught declining with time) in the August and November trials. Both of these species had much higher densities in November. Although the experiments were carried out at the same depth (4 m) and in the same habitat type (flooded grassland dominated with *Sesbanea javanica*), they were carried out at different locations. Therefore, the differences in densities could be due to either temporal or spatial effects.

Table 3 shows the average rank abundances between the two trials for each species. These ranks match perfectly with the species compositions in the trade at Siem Reap (Table 1), except for the fact that *E. longicauda* and *E. tentaculatus* were ranked equally in these trials, and in the trade *E. longicauda* was more abundant. As a "back-of-the-envelope" calculation, we scaled up these preliminary results for snake densities to the entire study area, encompassing all areas of data collection shown in Fig. 1. This gave preliminary estimates

**Table 2 – The exploited species and their catch per unit effort, measured as the number of snakes per 1000 m$^2$ gill net per day, and the mean weight of each species caught using gill nets**

| Family | Species | Catch per unit effort ± SE | Mean weight per snake (g) ± SE |
|---|---|---|---|
| Homalopsidae | *Enhydris enhydris* | 23.03 ± 0.78 | 100.8 ± 3.9 |
| | *Enhydris longicauda* | 4.36 ± 0.21 | 147.5 ± 6.9 |
| | *Homalopsis buccata* | 2.34 ± 0.08 | 195.9 ± 11.3 |
| | *Erpeton tentaculatus* | 1.75 ± 0.10 | 107.3 ± 4.45 |
| | *Enhydris bocourti* | 0.41 ± 0.03 | 187.9 ± 9.8 |
| | *Enhydris plumbea* | 0.02 ± 0.005 | 189.6 ± 18.1 |
| Colubridae | *Xenochrophis piscator* | 0.88 ± 0.05 | 180.3 ± 10.0 |
| | *Cylindrophis ruffus* | 0.39 ± 0.03 | 269.4 ± 13.4 |
| Elapidae | *Naja kaothia/siamensis* | 0.004 ± 0.007 | 500.0 ± 100.0 |
| Boidae | *Python molurus* | 0.01 ± 0.005 | 250.0 ± 150.0 |
| Acrochordidae | *Acrochordus granulatus* | 0.002 ± 0.001 | 100.0 ± 0.0 |

**Table 3 – The effect of depth and habitat type on the catch per unit effort (number snakes per 1000 m$^2$/day) of seven snake species based on a one-factor ANCOVA with depth as the covariate**

| Species | Depth ($\beta$) | Habitat ($P$) | Habitat type (all aquatic) | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Grassland | Forest | Grass/forest | Channel | *S. javanica* mix | Open lake |
| *E. enhydris* | −0.09*** | *** | $1^{a}$ | $2^{b}$ | $3^{ab}$ | $5^{c}$ | $4^{c}$ | $6^{d}$ |
| *E. longicauda* | −0.07*** | * | 1 | 2 | 5 | 3 | 4 | |
| *H. buccata* | −0.07*** | *** | $1^{a}$ | $3^{b}$ | $4^{b}$ | $2^{ab}$ | $5^{c}$ | |
| *E. bocourti* | −0.02* | *** | $1^{a}$ | $3^{b}$ | $5^{b}$ | $4^{b}$ | $2^{ab}$ | |
| *E. tentaculatus* | −0.04** | *** | $2^{ab}$ | $4^{bc}$ | $5^{c}$ | $3^{b}$ | $1^{a}$ | |
| *X. piscator* | −0.004** | * | $1^{a}$ | $2^{ab}$ | $4^{ab}$ | $3^{ab}$ | $4^{b}$ | |
| *C. ruffus* | −0.007 | * | $1^{a}$ | $3^{b}$ | $5^{ab}$ | $4^{ab}$ | $2^{ab}$ | $6^{ab}$ |
| *E. plumbea* | 0.03* | * | $2^{b}$ | $1^{a}$ | | | $3^{b}$ | |
| *Naja* spp. | | | | 1 | | | | |
| *P. molurus* | 0.03 | | 2 | 1 | | | | |
| *A. granulatus* | | | | | | | | 1 |

Standardized $\beta$ values and their significance levels are provided for depth and significance of the habitat effect is given (*$P < 0.05$; **$P < 0.001$; ***$P < 0.0001$). The rank order of catch per unit effort in different habitat types is given, with significant differences between them based on the Bonferroni corrected post hoc analyses, denoted by different superscript symbols (a, b and c).

**Table 4 – Population densities of snake species from depletion experiments conducted in August and November 2005**

| Species (mean rank abundance) | Experiment 1 – total area = 85897 m$^2$ August 2005 | | | | | | Experiment 2 – total area = 83122 m$^2$ November 2005 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Nb | Regression coefficients | | | $P$ | Density snakes 10 m$^{-2}$ (95% CI) | Nb | Regression coefficients | | | $P$ | Density snakes 10 m$^{-2}$ (95% CI) |
| | | $b$ | $a$ | $R^2$ | | | | $b$ | $a$ | $R^2$ | | |
| *E. enhydris* (1) | 89 | −0.009 | 1.010 | 0.63 | <0.05 | 0.13* (0.05–0.70) | 403 | −0.005 | 3.581 | 0.56 | 0.05 | 0.84* |
| *E. longicauda* (2) | 37 | −0.002 | 0.268 | 0.15 | 0.38 | 0.14 | 58 | −0.006 | 0.552 | 0.53 | 0.06 | 0.10* |
| *H. buccata* (3) | 50 | −0.011 | 0.625 | 0.83 | <0.01 | 0.07* (0.04–0.12) | 5 | | | | | |
| *E. tentaculatus* (2) | 21 | −0.021 | 0.427 | 0.87 | <0.01 | 0.02* (0.01–0.04) | 90 | −0.018 | 1.516 | 0.83 | <0.01 | 0.10* (0.06–0.18) |
| *X. piscator* (4) | 3 | | | | | | 42 | −0.005 | 0.371 | 0.32 | 0.18 | 0.08 |
| *E. bocourti* (6) | 8 | | | | | | 0 | | | | | |
| *C. ruffus* (5) | 8 | | | | | | 6 | | | | | |

Linear regression coefficients ($a$ and $b$), $R^2$ values and significance levels are given for the depletion plots for each species. Confidence intervals are provided only for those with significant regressions. The total number of each species caught (Nb) is given for each experiment, along with the mean rank of abundance between the two experiments.

of population sizes with 95% confidence intervals for all species combined of 3.5 (2.5–9.4) and 10.5 (10.1–11.2) million snakes from the August and November trials, respectively. The confidence intervals provided here are based only on the species for which they are known and therefore a wider range of densities is possible. Given the estimate of nearly 3 million snakes traded from this area each year, we would expect the actual population density to be in the upper range of what we have shown here.

### 3.4. *Sustainability*

The estimates of catch per hunter over the last 25 years, based on the recall of hunters, show considerable variation, but there has been a distinct decline over the last 5 years. Between the years of 2000 and 2005, high season catches have declined by 74% and low season catches by 84% (Fig. 5).

### 3.5. *Maturity and reproductive potential of exploited females*

In all species except *H. buccata* and *E. bocourti*, the mean length of captured females is at or above the length of maturity, with the proportion of females above maturity ranging from 45% to 92% (Table 5). Due to the large size at maturity of *H. buccata* and *E. bocourti*, most of the females captured

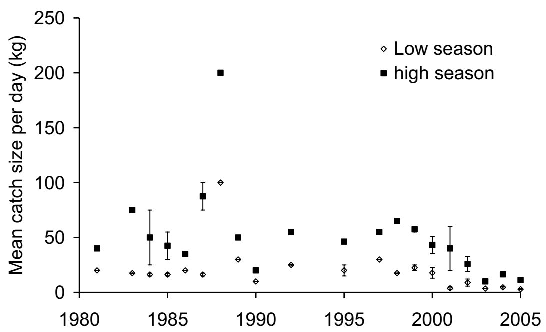


**Fig. 5 – Temporal changes in catch sizes of snakes per hunter, based on the perceptions of 60 hunters in Battambong province. Data are shown for both the high and low season; times of year when snake catches are typically high and low, respectively. The sample size for each year ranges from 1 to 46 and standard error bars show the variation between these estimates.**

**Table 5 – The proportion of captured females above the mean length of maturity and above 85% maximum length for seven snake species**

| Species | Mean SVL of captured females ± SE (*n*) | % captured females mature | % captured females above 85% max length | Fecundity at mean size of capture ($F_{mean}$) | Potential fecundity at maximum size ($F_{max}$) | $F_{mean}$ as a % of $F_{max}$ |
|---|---|---|---|---|---|---|
| *E. enhydris* | 50.5 ± 0.2 (1723) | 56.1 | 16.1 | 10.1 | 20.3 | 49.9 |
| *E. longicauda* | 48.7 ± 0.2 (866) | 72.4 | 21.5 | 16.1 | 29.2 | 55.1 |
| *H. buccata* | | | | | | |
| Crocodile food trade | 58.5 ± 0.8 (273) | 3.3 | 1.5 | 0 | 20.2 | 0 |
| Skin trade | 81.1 ± 0.4 (603) | 48.6 | 11.9 | 8.7 | 20.2 | 43.3 |
| *E. bocourti* | | | | | | |
| Crocodile food trade | 45.7 ± 1.6 (50) | 2.0 | 0 | 0 | 19.4 | 0 |
| Skin trade | 86.2 ± 2.7 (20) | 95.0 | 30.0 | 12.9 | 19.4 | 66.4 |
| *E. tentaculatus* | 50.1 ± 0.3 (366) | 65.3 | 12.6 | 11.8 | 18.9 | 62.6 |
| *X. piscator* | 60.7 ± 1.0 (112) | 44.6 | 12.5 | 29.0 | 64 | 45.3 |
| *C. ruffus*[a] | 71.5 ± 0.8 (78) | (92.3) | 41.0 | 9.1 | 13.4 | 67.5 |

Fecundity at mean length of capture is shown for each species and expressed as a proportion of fecundity at maximum body length.
a The size at maturity was insignificant ($P = 0.1$) and the result derived from this parameter is therefore bracketed.

using the size-selective gill net technique are immature. In the skin trade, however, where individuals are caught using traps and baited hooks, the mean lengths are equal to and above the mean length of maturity for *H. buccata* and *E. bocourti*, respectively, with a much higher proportion of mature individuals in the catch of *E. bocourti* than *H. buccata* (Table 5).

For comparative purposes we have calculated size-based reference points for each species at 85% maximum body length. Of the females occurring in the skin trade, 30% are above this reference point in *E. bocourti*, compared to 12% in *H. buccata*. Of the other species occurring in the crocodile food trade, 41% of caught *C. ruffus* are above this size-based reference points, with all other species ranging from 13% to 22% (Table 5).

The fecundity of captured individuals, expressed as a percentage of the potential fecundity of that species at 90% body length, indicates the reproductive output that has been realised, as a proportion of the potential that could have been possible in the absence of fishing mortality. Immature individuals, such as those of *H. buccata* and *E. bocourti* which enter the crocodile food trade, have therefore achieved 0% of their reproductive potential. Of those occurring in the skin trade, the individuals of *E. bocourti* are closer to their maximum fecundity than *H. buccata*. Of the individuals of the other species caught for crocodile food, those of *E. enhydris*, *E. longicauda* and *X. piscator* have realised approximately half of their reproductive potential and those of *E. tentaculatus* and *C. ruffus* are much closer to their maximum (Table 5).

### 3.6. *Temporal overlap of reproduction and exploitation*

The degree of overlap between exploitation and reproduction provides an indication of population vulnerability based on timing. *E. enhydris*, which exhibits two breeding seasons, as also shown in previous studies (Saint Girons and Pfeffer, 1971; Murphy et al., 2002), shows the greatest degree of overlap, with exploitation peaking just prior to, or at, the peak reproductive periods (Fig. 6). *C. ruffus*, which also breeds during July and August, shows considerable overlap with this first peak in exploitation. All other species show a single reproductive period from December to February and March. Of these species, *E. longicauda* and *E. tentaculatus* show the greatest overlap between reproduction and hunting mortality due to the majority of trade in these species occurring during the second peak in hunting, just prior to their reproductive seasons. *H. buccata* and *E. bocourti* occur in two separate trades that target different sized individuals. While the skin trade is small in comparison to the crocodile food trade overall, it is responsible for half of the total catch of *H. buccata* each year and selects for the larger individuals. During the first peak in trade the numbers caught for crocodile food exceed those caught for skins, but this pattern is reversed in the second trade peak, which shows considerable overlap with the breeding season for this species. Although fewer *E. bocourti* are caught for skins than for crocodile food, this species also shows a peak in trade of large-bodied individuals during their breeding season (Fig. 6). The timing of exploitation of the smaller individuals of these two species for crocodile food is less important as the majority of these individuals are immature.

### 3.7. *Life histories*

The interviews with hunters indicated that catch rates of the seven main species have declined over time (Table 6). Using maximum female body mass, mass at maturity and fecundity at maturity taken from unpublished data, we did not find any clear life history correlates of differences among species in their rates of decline. However, the two species with the strongest declines (*H. buccata* and *E. bocourti*), were the largest, including their mass at maturity, and they had the lowest fecundity next to *C. ruffus* (Table 6).

## 4. Discussion

The scale of exploitation of snakes from Cambodia's Tonle Sap Lake that we have reported here represents the largest documented snake hunting operation in the world, with an estimated minimum of 6.9 million snakes (777 tonnes) captured per year. Although we focused on the region with the greatest

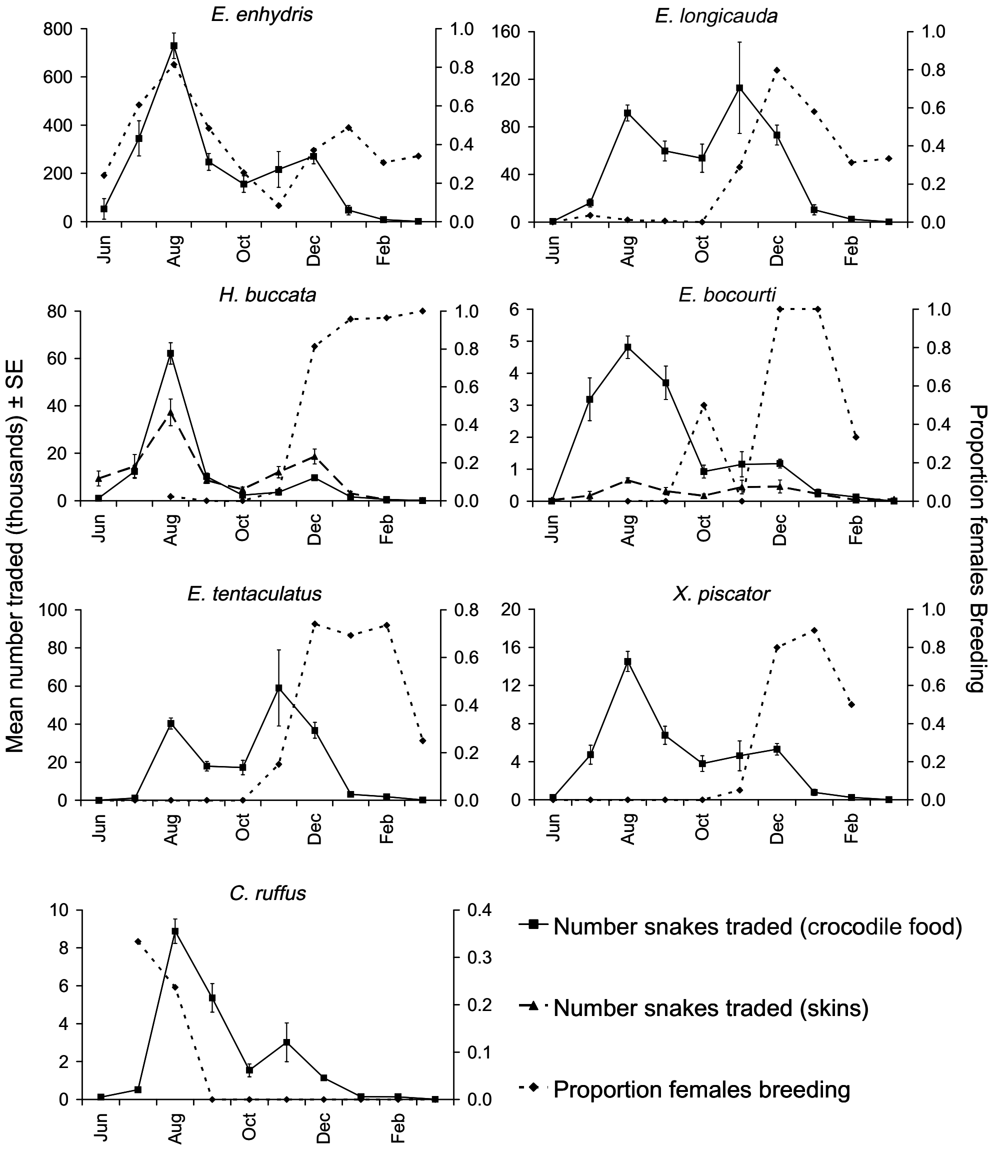


**Fig. 6 – Seasonal patterns of exploitation and reproduction for seven snake species. The two lines for exploitation of *H. buccata* and *E. bocourti* represent the two separate trades in which they occur. The standard error in estimates of trade quantity in each month is derived from the variation in quantity traded between sample days.**

**Table 6 – Scores of relative declines in catch sizes of seven snake species based on hunter interviews, ranked in order of decreasing decline**

| | Score | Rank | Mean maximum female mass (g) ± SE (*n*) | Mass at maturity (g) | Fecundity at maturity (no. eggs per breeding bout) |
|---|---|---|---|---|---|
| *E. bocourti* | −2.36 | 1 | 857.5 ± 70.4 (64) | 418.4 | 7.7 |
| *H. buccata* | −2.29 | 2 | 569.1 ± 27.5 (728) | 310.1 | 8.8 |
| *E. enhydris* | −1.86 | 3 | 200.2 ± 4.2 (1160) | 96.4 | 9.0 |
| *E. longicauda* | −1.77 | 4 | 288.9 ± 6.6 (712) | 119.2 | 12.7 |
| *X. piscator* | −0.59 | 5 | 432 ± 32.1 (103) | 149.4 | 28.8 |
| *E. tentaculatus* | −0.25 | 6 | 188.7 ± 7.2 (322) | 90.6 | 10.6 |
| *C. ruffus* | −0.23 | 6 | 360.3 ± 9.6 (78) | 170.5 | 6.6 |

These are shown in comparison with female life history traits of each species: maximum female mass is taken from the mean of the largest 10% of the sample and the total sample size is shown in brackets. Mass and fecundity at maturity are derived from body length at maturity and relationships of clutch size and body mass with body length (Brooks, unpublished data).

level of exploitation, the true figure is probably much higher, as our calculations do not include local consumption and smaller unidentified trade routes. *E. enhydris*, which represents around 70% of this total quantity, is therefore the most heavily exploited snake species that has been documented. Our estimates of trade quantity are considerably higher than those reported by Stuart et al. (2000) for the same region, mainly due to differences in both the estimated number of snakes per kg. The authors report that *E. enhydris* accounted for a similar proportion of the catch to what was found in this study and it is therefore likely that the discrepancy between the studies is the result of a decrease in average size of snakes and / or a decline in the abundance of the larger species, such as *H. buccata*.

Where possible, estimates of sustainability of exploitation are obtained by combining information on the hunting operation with baseline catch statistics and information on the biology of the species involved (Milner-Gulland and Mace, 1998; Reynolds et al., 2001b). In practise this is rarely possible, with notable exceptions in wealthy countries for commercial fisheries, recreational hunting, and logging (Reynolds and Peres, 2006). We lack long time series of catch and effort data from Tonle Sap Lake, and although known for other populations of some species (Murphy et al., 1999), we lack population parameters such as population size, age at maturity and growth rate for the Tonle Sap populations, thus precluding the use of standard exploitation models to determine whether hunting mortalities are sustainable. However, we do have several lines of evidence, ranging from interviews with hunters to life history variation among snake species, which enable us to rank species according to vulnerability, and provide general guidelines for sustainable hunting methods. These sustainability and vulnerability issues are discussed below, following an initial overview of the hunting operation in this seasonal environment.

### 4.1. *Hunting interactions with habitats*

The homalopsids in this assemblage are semi-aquatic snakes that typically live within mud-root tangle habitat in shallow water (Murphy et al., 1999; Karns et al., 1999–2000). This habitat preference concurs with the higher catch rates in shallower water and in flooded grasslands shown here. Due to the annual flood cycle of Tonle Sap Lake, these shallow areas move several kilometres back and forth each year and we do not know how the snakes respond to the strong seasonality of this environment. Previous studies on *E. enhydris* in Thailand showed they exhibit sedentary periods punctuated by longer movements, with a mean daily rate of movement of approximately 20 m (Karns et al., 1999–2000). These studies were conducted in relatively static environments with little fluctuation in resource availability, vegetation cover, water depth and clarity. The snakes of Tonle Sap may show similar patterns but will travel greater distances gradually over time in order to maintain their association with preferred habitats and food supply. We have shown through preliminary population density experiments and catch monitoring that snake population densities vary both spatially and temporally. Catches are higher both as the water first enters the forest and again as it recedes, which could be the result of a concentration of snakes at low water levels. However, at this stage we cannot separate these density effects from catchability effects, i.e. snakes become more difficult to catch in deeper clearer water. Spatial differences are apparent from our catch monitoring data, through which we often observed snake hunters moving their gill nets until they find a location where catches are sufficient. We have also shown a significant effect of targeting on catch size, which highlights a well-known problem of using catch per unit effort as an index of abundance, as it compounds the behaviour of the hunter with the relative abundance of snakes. The extent of hunting will also depend on accessibility of the habitat. At the end of September each year the commercial fishing lots (publicly auctioned fisheries domains which cover a large areas of Tonle Sap Lake), begin operation and large areas of flooded forest are closed to public access. Therefore, despite the high catches as the water recedes, overall effort is reduced as many of the hunters are refused access to these areas of the forest. This accounts for the drop in trade quantity with high catch per unit effort in Fig. 3.

### 4.2. *Sustainability issues*

The intensity of exploitation experienced by the Tonle Sap snakes gives cause for concern. Despite the fact that tropical snakes are more likely to be able to withstand intensive commercial exploitation than their temperate zone relatives, as a result of faster growth, earlier maturation and higher reproductive output (Shine et al., 1999), their ability to withstand the mortality shown in this study is highly questionable. A large population of hunters with gill nets penetrates all areas occupied by these snakes, concentrating effort along the shallow edge, which appears to be favoured by the snakes, leaving few or no unexploited refuges. This is in contrast with what has been shown for the exploitation of other tropical aquatic snakes. Shine et al. (1995) attributed the inaccessible habitat and low snake population density, as a result of high water depth, to the low vulnerability of file snakes to over-exploitation. The low densities exhibited by many snake species may deter targeted hunts, although even as a by-catch, many sea snakes are showing high susceptibility to over-exploitation, due to intense commercial trawling (Milton, 2001). Therefore, given the combination of the by-catch and targeted exploitation of the Tonle Sap snakes, it is not surprising that severe declines have been reported.

In the absence of temporal data on catch statistics for this trade, we have relied upon recall by hunters to establish rates of decline and differences among the species. The use of interviews to reconstruct recent historical changes in population status is often used in conservation studies (Sadovy and Leung, 2003) and while this technique is far from perfect, the relative declines of each of the species reported in this study do concur with catch statistics and expectations from elements of their biology. Specifically, species differ in their relative abundance, degree of targeting, timing of exploitation relative to their breeding season, proportion of catch consisting of mature females and large fecund females, fecundity and body size, including size at maturity.

### 4.3. *Population size and exploitation rate*

Without knowledge of population sizes we cannot calculate per capita exploitation rates. Differences among species in catch per unit effort reflect a combination of differences in their natural abundance with differences in their vulnerability to capture. *C. ruffus*, *X. piscator* and *E. plumbea* are the only species within this assemblage that are seen swimming on the surface of the water and are probably more terrestrial in nature (Saint Girons, 1972; Voris and Karns, 1996). They are therefore likely to be less vulnerable to capture by gill nets set beneath the water and the low catch per unit effort levels shown here are likely to be a reflection of this. All other species are homalopsid water snakes that are likely to have a higher vulnerability to capture due to the time spent beneath the water. Homalopsids, however, have been shown to exhibit considerable ecological diversity; in particular between *E. tentaculatus* which is a sit and wait predator and the other homalopsids in this assemblage which are active feeders (Voris et al., 2002). We therefore cannot assume that these species will show similar rates of exploitation. Therefore, the relative differences in their catch rates shown in this study are likely to reflect both their differing natural abundances and differences in their ecology and catchability. Our population density estimates provide only a preliminary guideline. Further replication of this method is required in all habitats and throughout the year, to establish the overall density of the various species throughout the Tonle Sap basin. Nonetheless our estimates indicate that a significant proportion of the snake populations may be removed each year.

### 4.4. *Vulnerability based in timing of exploitation*

Not all individuals are equally important to the growth of a population. The reproductive value of an individual, which is a measure of its expected contribution to the population (MacArthur, 1960), changes with age and with season. Thus, the timing of exploitation relative to the timing of reproduction is a likely determinant of vulnerability. Reproductive value increases as an individual approaches its reproductive season, peaks at parturition, and decreases following reproduction, when there is a greater chance that it will die before the next reproductive bout (Kokko et al., 2001). Vulnerability due to timing of exploitation is therefore highest in *E. enhydris*, with peaks in exploitation occurring before and during the peak reproductive periods. Previous studies of fish have shown that the impact of removing an individual before or during the spawning season, can be up to 46% higher than removing one after the spawning season (Matsuda et al., 1994). This may be a significant factor in the reported decline of *E. enhydris*. All species except *C. ruffus* breed during the second peak in trade from October through January. This peak in trade will therefore have a disproportionate impact per individual removed, compared to the first peak, as a result of the high reproductive value of individual females during this time. Such information can be used to inform management choices.

### 4.5. *Size-based determinants of vulnerability*

In fisheries, there is widespread support for the 'let them spawn at least once' policy, to help prevent stock collapse (Die and Caddy, 1997; Myers and Mertz, 1998). Based on this premise, the probability of having bred before capture has been applied to assessments of vulnerability of sea snakes to exploitation (Milton, 2001) and we have applied it here. All species in this study show a positive relationship between clutch size and body size (Brooks, unpublished data) and this has also been shown in other parts of their range (Murphy et al., 2002; Karns et al., 2005). Reproductive output therefore continues to increase with age. Mortality is likely to decrease with age until senescence has an effect. The reproductive value of an individual female to the growth of a population therefore increases with age. Based on this assertion, it has been suggested that, in the case of highly depleted populations, a few successful and highly fecund females can effectively safeguard a population (Caddy and Seijo, 2002). Larger fish often produce larger offspring that will have a greater chance of survival (Aubone, 2004) and a similar trend has been shown for snakes (Madsen and Shine, 1992). It therefore follows that, unless they are close to the end of their lifespan, larger mature females should also be protected. Froese (2004) termed female fish above the optimum length of capture 'mega-spawners' and proposed the implementation of fishing strategies that result in 0% mega-spawners caught. Optimum length of capture is the length of maximum yield per recruit, where the product of the number of surviving individuals multiplied with their average weight results in the highest biomass, usually corresponding to the highest egg production (Froese and Binohlan, 2000). The optimum length is unknown for these snake species and we have therefore set as a benchmark for comparisons, a maximum size limit at 85% maximum length.

In this study, we have presented the proportion of females caught that are above the size at which 50% of the population is mature, as well as above 85% maximum length. *E. bocourti*, followed by *H. buccata*, therefore, show the greatest potential impact on the population per individual removed, due to the high proportion of the catch that is immature and above this size-based reference point. The lower number of large sized individuals in the catch of some species may reflect depletion due to over-hunting (Froese, 2004). However, since hunting snakes for skins has a long history in this area, it is unlikely that the exploitation rate in the upper end of populations is greater for any species, than for *H. buccata* and *E. bocourti*. The trade of large snakes for the skin trade is undoubtedly having a large impact on the population of *H. buccata* and *E. bocourti*. While these species are not CITES listed, a license is required for their transport and export, which is seldom obtained. Greater enforcement against the illegal export of these snakes would therefore be a necessary and feasible step in the protection of these species. As the capture of snakes for crocodile food is indiscriminate to species, it is much harder to devise methods that would reduce the number of immature females of *H. buccata* and *E. bocourti* caught.

### 4.6. *Vulnerability based on intrinsic life histories*

The intrinsic life history traits of species are important determinants of the resilience of populations to exploitation (Reynolds, 2003). Maximum body size, size at maturity and fecundity are likely to be important for persistence or recovery and have been shown to correlate with decline in other taxa (Jennings et al., 1998; Purvis et al., 2000). We found no clear correlates with our scores of decline and any single life history trait, although the two species with the strongest declines were the largest and had relatively low fecundities. It is, however, difficult to disentangle the effects of these intrinsic life history traits from the other factors that could cause population declines, which are highlighted in this paper as having differing effects on each species.

*Enhydris enhydris* was scored as showing the third strongest decline, despite the fact that this species is one of smallest, with a small size at maturity. However, it has a relatively low fecundity and perhaps more importantly shows the greatest overlap of exploitation with its breeding season. *C. ruffus* appears to be an anomaly in this assessment. It has been scored with showing the least decline, yet it is a relatively large-bodied species, with a potentially large size at maturity, low fecundity and a large proportion of captured females are mature. However, this species is more terrestrial than the other species in this assemblage, as supported by our observations of it basking in trees, and therefore is likely to be less susceptible to capture.

## 5. Conclusion

The enormous scale of snake hunting that we have documented for Tonle Sap Lake (at least 6.9 million snakes per year) raises obvious questions about sustainability. While we are unable to use standard exploitation models to produce testable predictions regarding sustainability, we have attempted to answer those questions by showing that variation among species in life history traits as well as the extent and timing of hunting and the size distribution of the affected population, is correlated with differences among species in rates of decline reported by hunters. We propose that any efforts to reduce hunting should focus on the second peak in trade occurring from October to December, in order to protect breeding females. The size ranges of individuals targeted by the two trades described here (crocodile food and snake skin trade) are together causing the greatest declines in the largest species, *H. buccata* and *E. bocourti*. This snake community represents a crucial income source for some of the poorest people in Cambodia and the governance system managing natural resources in this area is weak and under-resourced. Therefore, conservation of this system requires a multifaceted approach to ensure any intervention is both ethical and feasible. The information in this paper highlights priority areas of focus that can feed into assessments of conservation strategies for the long-term preservation of this snake assemblage, and the benefits that local communities derive from them.

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## REFERENCES


Aubone, A., 2004. Loss of stability owing to a stable age structure skewed toward juveniles. Ecological Modelling 175, 55–64.

Bonheur, N., Lane, B.D., 2002. Natural resources management for human security in Cambodia's Tonle Sap Biosphere Reserve. Environmental Science and Policy 5, 33–41.

Caddy, J.F., Seijo, J.C., 2002. Reproductive contributions foregone with harvesting: a conceptual framework. Fisheries Research 59, 17–30.

Campbell, I.C., Poole, C., Giesen, W., Valbo-Jorgensen, J., 2006. Species diversity and ecology of Tonle Sap Great Lake, Cambodia. Aquatic Sciences 68, 355–373.

Die, D.J., Caddy, J.F., 1997. Sustainable yield indicators from biomass: are there appropriate reference points for use in tropical fisheries? Fisheries Research 32, 69–79.

Dulvy, N.K., Ellis, J.R., Goodwin, N.B., Grant, A., Reynolds, J.D., Jennings, S., 2004. Methods of assessing extinction risk in marine fishes. Fish and Fisheries 5, 255–276.

Froese, R., 2004. Keep it simple: three indicators to deal with overfishing. Fish and Fisheries 5, 86–91.

Froese, R., Binohlan, C., 2000. Empirical relationships to estimate asymptotic length, length at first maturity, and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. Journal of Fish Biology 56, 758–773.

Jennings, S., Reynolds, J.D., Mills, S.C., 1998. Life history correlates of responses to fisheries exploitation. Proceedings of the Royal Society of London 265, 333–339.

Jennings, S., Kaiser, M.J., Reynolds, J.D., 2001. Marine Fisheries Ecology. Blackwell Publishing, Oxford.

Karns, D.R., Voris, H.H., Chan-ard, T., Goodwin, J.C., Murphy, J.C., 1999–2000. The spatial ecology of the rainbow water snake, *Enhydris enhydris* (Homalopsinae) in Southern Thailand. Herpetological Natural History 7, 97–115.

Karns, D.R., Murphy, J.C., Voris, H.K., Jerry, S., 2005. Comparison of semi-aquatic snake communities associated with the Khorat Basin, Thailand. The Natural History Journal of Chulalongkorn University 5, 73–90.

Keogh, J.S., Barker, D.G., Shine, R., 2001. Heavily exploited but poorly known: systematics and biogeography of commercially harvested pythons (python curtus group) in Southeast Asia. Biological Journal of the Linnean Society 73, 113–129.

Klemens, M.W., Thorbjarnarson, J.B., 1995. Reptiles as a food resource. Biodiversity and Conservation 4, 281–298.

Kokko, H., Lindström, J., Ranta, E., 2001. Life histories and sustainable harvesting. In: Reynolds, J.D., Mace, G.M., Redford, K.H., Robinson, J.G. (Eds.), Conservation of Exploited Species. Cambridge University Press, London, pp. 301–322.

Lawson, R., Slowinski, J.B., Crother, B.I., Burbrink, F.T., 2005. Phylogeny of the Colubroidea (Serpentes): new evidence from mitochondrial and nuclear genes. Molecular Phylogenetics and Evolution 37, 581–601.

Lim, P., Lek, S., Tana Touch, S., Mao, S.-O., Chhouk, B., 1999. Diversity and spatial distribution of freshwater fish in Great Lake and Tonle Sap river (Cambodia, Southeast Asia). Aquatic Living Resources 12, 379–386.

MacArthur, R.H., 1960. On the relation between reproductive value and optimal predation. Proceedings of the National Academy of Sciences 46, 143–145.

Madsen, T., Shine, R., 1992. Determinants of reproductive success in female adders, *Vipera berus*. Oecologia 92, 40–47.

Matsuda, H., Mitani, I., Asano, K., 1994. Impact factors of purse seine net and dip net fisheries on a chub mackerel population. Research on Population Ecology 36, 201–207.

Milner-Gulland, E.J., Akcakaya, H.R., 2001. Sustainability indices for exploited populations. Trends in Ecology and Evolution 16, 686–692.

Milner-Gulland, E.J., Mace, R., 1998. Conservation of Biological Resources. Blackwell Science Ltd., Oxford.

Milton, D.A., 2001. Assessing the susceptibility to fishing of populations of rare trawl bycatch: sea snakes caught by Australia's Northern Prawn Fishery. Biological Conservation 101, 281–290.

Murphy, J.C., Voris, H.H., Karns, D.R., Chan-ard, T., Suvunrat, K., 1999. The ecology of the water snakes of Ban Tha Hin, Songkhla Province, Thailand. Natural History Bulletin of the Siam Society 47, 129–147.

Murphy, J.C., Voris, H.H., Stuart, B.L., 2002. Female reproduction in the rainbow watersnake, *Enhydris enhydris* (Serpentes, Colubridae, Homalopsinae). The Natural History Journal of Chulalongkorn University 2, 31–37.

Myers, R.A., Mertz, G., 1998. The limits of exploitation: a precautionary approach. Ecological Applications 8, 165–169.

Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society of London 267, 1947–1952.

Reynolds, J.D., 2003. Life histories and extinction risk. In: Blackburn, T.M., Gaston, K.J. (Eds.), Macroecology. Blackwell Publishing, Oxford, pp. 195–217.

Reynolds, J.D., Peres, C.A., 2006. Overexploitation. In: Groom, M.J., Meffe, G.K., Ronald Carroll, C. (Eds.), Principles of Conservation Biology. Sinauer Associates, Sunderland, Massachusetts, pp. 53–291.

Reynolds, J.D., Jennings, S., Dulvy, N.K., 2001a. Life histories of fishes and population responses to exploitation. In: Reynolds, J.D., Mace, G.M., Redford, K.H., Robinson, J.G. (Eds.), Conservation of Exploited Species. Cambridge University Press, Cambridge, pp. 147–168.

Reynolds, J.D., Mace, G.M., Redford, K.H., Robinson, J.G., 2001b. Conservation of Exploited Species. Cambridge University Press, Cambridge.

Sadovy, Y., Leung, W.L., 2003. Near extinction of a highly fecund fish: the one that nearly got away. Fish and Fisheries 4, 86–99.

Saint Girons, H., 1972. Les Serpents du Cambodge, Mémoires du Muséum National d'Histiore Naturelle, Paris, 170 pp.

Saint Girons, H., Pfeffer, P., 1971. Le cycle sexuel des serpents du Cambodge. Annales des Sciences Naturalles 13, 543–572.

Saint Girons, H., Pfeffer, P., 1972. Notes sur l'ecologie des serpents du Cambodge. Zoologische Mededelingen, Rijkmuseum van Natiirlijke Historie, Leiden 47, 65–86.

Shine, R., Harlow, P., Keogh, J.S., Boeadi, 1995. Biology and commercial utlilization of acrochordid snakes, with special reference to Karung (*Acrochordus javanicus*). Journal of Herpetology 29, 352–360.

Shine, R., Ambariyanto, P.S., Harlow, J.S., Mumpuni, 1999. Reticulated pythons in Sumatra: biology, harvesting and sustainability. Biological Conservation 87, 349–357.

Stuart, B.L., Smith, J., Davey, K., Din, P., Platt, S.G., 2000. Homalopsine watersnakes; the harvest and trade from Tonle Sap, Cambodia. Traffic 18, 115–124.

Voris, H.H., Karns, D.R., 1996. Habitat utilization, movements, and activity patterns of *Enhydris plumbea* (Serpentes: Homalopsinae) in a rice paddy wetland in Borneo. Herpetological Natural History 4, 111–126.

Voris, H.K., Alfaro, M.E., Karns, D.R., Starnes, G.L., Thompson, E., Murphy, J.C., 2002. Phylogenetic relationships of the Oriental-Australian rear-fanged water snakes (Colubridae: Homalopsinae) based on mitochondrial DNA sequences. Copeia, 906–915.

Zhou, Z., Jlang, Z., 2004. International trade status and crisis for snake species in China. Conservation Biology 18, 1386–1394.