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Snake prices and crocodile appetites: Aquatic wildlife supply and demand on Tonle Sap Lake, Cambodia

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ABSTRACT

Commercial trade is a major driver of over-exploitation of wild species, but the pattern of demand and how it responds to changes in supply is poorly understood. Here we explore the markets for snakes from Tonle Sap Lake in Cambodia to evaluate future exploitation scenarios, identify entry points for conservation and, more generally, to illustrate the value of multi-scale analysis of markets to traded wildlife conservation. In Cambodia, the largest driver of snake exploitation is the domestic trade in snakes as crocodile food. We estimate that farmed crocodiles consume between 2.7 and 12.2 million snakes per year. The market price for crocodiles has been in decline since 2003, which, combined with rising prices for their food, has led to a reduced frequency of feeding and closure of small farms. The large farms that generate a disproportionate amount of the demand for snakes continue to operate in anticipation of future market opportunities, and preferences for snakes could help maintain demand if market prices for crocodiles rise to pre 2003 levels. In the absence of a sustained demand from crocodile farms, it is also possible that alternative markets will develop, such as one for human snack food. The demand for snakes, however, also depends on the availability of substitute resources, principally fish. The substitutability and low price elasticity of demand offers a relatively sustainable form of consumerism. Given the nature of these market drivers, addressing consumer preferences and limiting the protection of snakes to their breeding season are likely to be the most effective tools for conservation. This study highlights the importance of understanding the structure of markets and the behaviour of consumer demand prior to implementing regulations on wildlife hunting and trade.

1. Introduction

The globally expanding domestic and international trade of wild species is now a multi-billion dollar business (Roe et al., 2002) and a major driver of over-exploitation (Broad et al., 2003). Trade statistics have been widely used to explore sustainability of exploitation, either by overlaying levels of capture with elements of species' biology (Robinson and Redford, 1991; Reynolds et al., 2001; Jerozolimski and Peres, 2003; Clarke et al., 2006), or assessing trends in quantity and price (Pinnegar et al., 2002; Cowlishaw et al., 2005). However, the factors that determine patterns of demand, elasticity to price and the co-evolution of supply and demand are key for predicting how trade may continue in the future (Wilkie and Godoy, 2000), and therefore for the design of regulatory responses to meet conservation aims.

In globalized markets, large disturbances in supply and demand of commodities lead to highly volatile prices (Kroner et al., 1993), and therefore new commodity chains can form and fracture rapidly. This is a major challenge when the product is biodiversity and its trade can lead to irreversible consequences through the sequential loss of species (Huitric, 2005; Berkes et al., 2006). In the bushmeat trade, studies of consumption patterns, preferences and the role of substitution of resources have advanced our understanding of the interplay between demand for and supply of exploited resources (Wilkie and Godoy, 2001; Fa et al., 2002; East et al., 2005; Rowcliffe et al., 2005). These studies have, however, been rare elsewhere and for other types of wildlife. Particularly in Asia, where there has been massive growth in the export of wild plant and animal resources, there have been few analyses of the economic context shaping market drivers, in order to predict potential outcomes to inform conservation.

In Southeast Asia, where significant populations of wild species remain and contribute to sustaining livelihoods of large rural populations, the increasing level of exploitation for trade has become a

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major concern for conservationists and natural resource managers (Yiming and Dianmo, 1998; Brukner, 2001; Stuart, 2004; Zhou and Jiang, 2004; Cheung and Dudgeon, 2006; van Mulekom et al., 2006). Cambodia is a case in point. As it emerged from a long history of conflict and isolation with a wealth of natural resources, it has become a source of wildlife trade for regional and international markets (Yiming and Dianmo, 1998; Stuart and Platt, 2004). While these markets can bring short-term benefits in terms of raised incomes, they can also lead to loss of species and a depleted resource base for future generations.

The Tonle Sap Lake is one of Cambodia's most important natural resources, supporting over one million people: it is the largest wetland in Southeast Asia and seasonal inundation of the floodplain makes it highly productive (Lamberts, 2001; Kummu et al., 2006). The monsoon season each year causes the water level in the Mekong River to rise and the Tonle Sap River to reverse direction, creating seasonally flooded forests, grasslands and rice fields, which are rich in nutrients and wildlife. The abundance of fish and wildlife have attracted people to the area throughout history for subsistence living, but the intensity of exploitation has escalated following Cambodia's recent shift into a market-based economy (Bonheur and Lane, 2002).

There are indications that the current natural resource use of the Tonle Sap ecosystem, particularly fishing, has exceeded sustainable levels (Lim et al., 1999; Lamberts, 2006), and growth in aquaculture, fish export and crocodile farming have increased the demand for resources from the lake. The extreme exploitation of snakes as a food source for crocodiles and to supply international markets is thought to be leading to a severe decline in capture rates of snakes (Brooks et al., 2007). An estimated 6.9 million snakes of seven species, including one that is endemic to the lake, are estimated to be removed from Tonle Sap lake annually, representing the world's largest exploitation of any snake assemblage (Brooks et al., 2007). While there are international markets for snakes as exotic leather, luxury food and traditional medicine (Shine et al., 1999; Stuart, 2004; Zhou and Jiang, 2004, 2005), the domestic market for snakes in Cambodia is the most significant. This is dominated by the crocodile farm industry, which uses snakes as a food supply (Stuart et al., 2000; Brooks et al., 2007).

Commercial farming of the native and critically endangered Siamese Crocodile, *Crocodylus siamensis*, became a lucrative business in Cambodia in the late 1980s when the country began to initiate a free market economy (Thouk, 1998; IUCN/SSC, 2004). The industry in Cambodia was originally proposed to CITES (Convention on the International Trade in Endangered Species) to export skins of captive-bred individuals, but the trade so far has been almost entirely based on live export of hatchling and juvenile crocodiles to Thailand, Vietnam and China. Approximately 1000 crocodile farms operate in Cambodia, which are largely clustered around the floodplain of Tonle Sap (IUCN/SSC, 2004). Adult and sub-adult crocodiles are fed freshwater fish and snakes, marine fish, rodents, and animal slaughter waste (So et al., 2005) and, in recent years when local resources have been scarce, imported fish have also been used (Lamberts, 2006).

This paper explores the dynamics of supply and domestic demand for Tonle Sap snakes. In order to assess how price responds to supply, how the markets are evolving and how demand responds to price and market changes, we: (1) examine trends in the price and supply of snakes traded for crocodile and human consumption, (2) assess the role of fish (a substitute resource) in determining the price of snakes as crocodile food, and therefore as a major driver of snake hunting intensity, (3) identify the farm characteristics that determine the demand for snakes, and (4) identify current market changes in the crocodile farm industry and the response of crocodile farmers. We then develop predictions about future demand for snakes and explore how these can be used to anticipate and guide required conservation and resource management responses. The insights that we gain from this case study demonstrate the value of using research in market dynamics as a core element of conservation research on exploited wildlife species.

2. Methods

The qualitative and quantitative methods used in this study are listed in Table 1 and further details are provided below.

2.1. Consumption by crocodile farms

Surveys of crocodile farms took place in 1998, 2001 and 2003. In 1998, the Cambodian government's application to register six farms with CITES necessitated a total stock count of all farms in Cambodia. In 2001, the Wildlife Conservation Society Cambodia Program surveyed a sample of floating farms (those using floating pens in which the crocodiles are moved onto the land during the dry season for egg laying and hatching) in Battambong province. This program also surveyed land-based farms (those with permanent land-based structures) in four of the provinces surrounding the lake in 2003. Surveys recorded the number of adult and sub-adult (older than 2 years but not yet mature) crocodiles and whether snakes were fed to the crocodiles. Farmers informed us that crocodiles reach maturity between 6 and 8 years and that sub-adult crocodiles are fed half the quantity given to adult crocodiles. Farm size was therefore calculated as the number of adults + (0.5 $\times$ number of sub-adults) to reflect food requirements. In 2003, estimated quantities of fish and snakes fed per time period were recorded. These data on farm size and consumption were log 10 transformed for analyses to estimate overall consumption. Data on farm size were also used in a logistic regression to determine the effect of farm size on the likelihood of feeding snakes. The frequency and months of feeding and the age of each farm were also recorded. Crocodile hatchlings are not fed snakes and are therefore not included in our analyses.

2.2. Trade monitoring at landing sites

We recorded quantities of snakes landed and prices paid by traders during a trade monitoring program conducted over 24-h periods for a total of 160 days, from June 2004 until February 2008 at Chong Khneas landing site (Fig. 1; details in Brooks et al. (2007)). This survey captured 1169 and 194 transactions for snakes sold domestically for crocodile and human food (sold live), respectively, from which daily quantities of snakes traded and average snake prices were calculated. We also obtained trading records from two of the main large-scale crocodile food traders, which included prices and quantities of all species (snakes, fish and rats) traded as crocodile food between July 2005 and March 2006.

2.3. Catch monitoring at hunting sites

Snakes sold domestically are typically caught using gillnets and sold per kg on a daily basis. Between June 2004 and March 2008, we recorded 2455 fishers' daily catches over 270 days within the flooded forest of Battambong province (Fig. 1; further details in Brooks et al. (2007)), from which mean daily snake capture rates were calculated.

2.4. Farmer and trader information on snake markets

We conducted semi-structured interviews with four traders operating at Chong Khneas landing site and three at Kampong

Table 1
Description of the types and dates of surveys of snake supply and demand carried out in the study and the data provided by each survey.

	Dates	Data provided
Consumption by crocodile farms		
Crocodile farm surveys	1998 (Total stock count), 2001 (Floating farm survey), 2003 (land farm survey)	Demand pattern for snakes
Trade monitoring at trade sites		
Trade monitoring programme	June 2004–February 2008 (160 sample days)	Price and quantity of snakes traded at key sites
Trader records	July 2005–March 2006	Price and quantity of snakes and fish bought and sold by traders
Catch monitoring at hunting sites		
Catch monitoring programme	June 2004–March 2008 (270 sample days)	Price and quantity of snakes traded at hunting sites
Farmer and trader information on snake markets		
Semi-structured interviews and informal discussions with traders	June 2004–March 2006	Qualitative understanding of the snake market
Ad-hoc visits to markets and trade sites	June 2004–August 2008	Observation of the snake market
Follow up discussions with hunters and traders	Aug 2008	Changes in the market and hunter behaviour
Semi-structured interviews with crocodile farmers	April 2005–March 2006	Qualitative understanding of consumer demand
Semi-structured interviews with officials from the government Fisheries Administration	April 2005–March 2006	Market changes in the crocodile farm industry

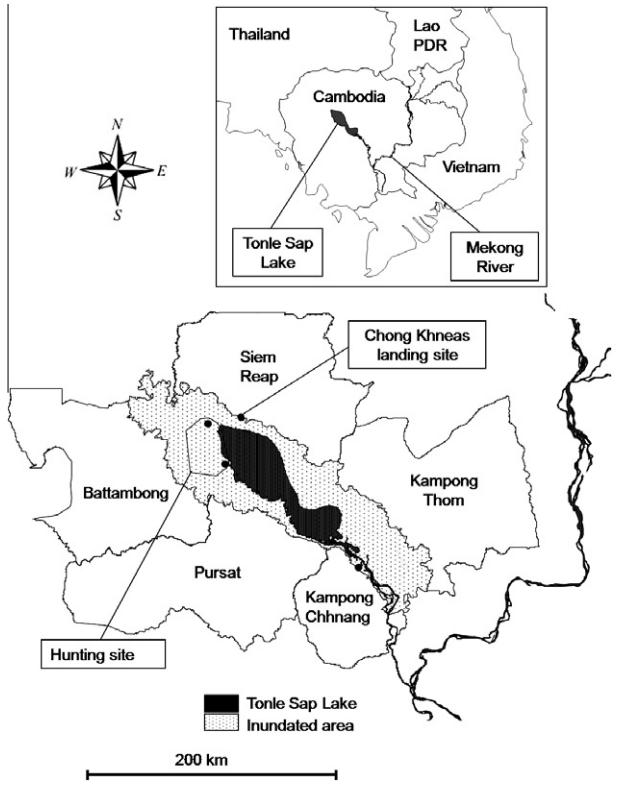

Fig. 1. Tonle Sap (The Great Lake) and the surrounding flood zone. This shows the location and boundaries of the five provinces surrounding the lake and the locations of the major hunting site where catch monitoring was carried out, and the landing site where trade was monitored (Chong Khneas).

Chhnang landing site, as well as informal discussions with 12 other traders operating at trading sites around the lake, between June 2004 and March 2006. These interviews included questions on snake trading locations and markets, changing patterns of demand, and traders' views on future trends and options. Market operations were also recorded at trading sites during the trade monitoring and through ad hoc visits to landing sites and markets. Informal discussions with hunters and traders in Battambong and Siem Reap province were held during a follow-up visit in 2008 to establish recent changes in market demand for snakes and the quantities caught and traded.

We also conducted semi-structured interviews with nine crocodile farmers in Siem Reap Province in 2005 and 2006, one of whom was the head of the Crocodile Farming Development Association of Cambodia (a government-supported group of crocodile farmers who work with CITES and the Crocodile Specialist Group of IUCN). These interviews provided information on farm sizes and crocodile food preferences, farmer perceptions of and responses to changes in market price, future plans for their farm and for the industry in Cambodia generally. We also interviewed two officials from the government Fisheries Administration concerning the current state of the crocodile farming industry in Cambodia and future plans.

2.5. Statistical analyses of supply

Annual trends in price and quantity of snakes traded were explored with general linear models that control for seasonal variation and we include regression beta coefficients (β) when reporting these results. Correlations were used to explore the associations between: (i) the price and quantity of snakes traded at landing sites and (ii) the quantity of snakes traded and catch size at hunting grounds. The effect of fish price on the price of snakes was explored with general linear models of data obtained from trader records. As the distribution of the snake quantity data was skewed over orders of magnitude, these data were $\log_{10}$ transformed to provide a distribution of residual variance appropriate for these analyses.

3. Results

3.1. Structure of the Tonle Sap snake trade

Snakes are hunted by fishers within the flooded forests of Tonle Sap Lake and sold to intermediary traders who transport a variety of aquatic resources to landing sites at the edge of the lake. At these sites, snakes are sold to traders specializing in crocodile food, human food, or large snakes for international markets for skins and live trade. In Chong Khneas landing site in Siem Reap province (Fig. 1), where 46% of the estimated 6.9 million snakes traded from Tonle Sap are landed, 96% of the snakes landed are small (25–

86 cm snout-vent length SVL), primarily of seven species (*Enhydris enhydris, Enhydris longicauda, Homalopsis buccata, Enhydris bocourti, Erpeton tentaculatus, Xenochrophis piscator* and *Cylindrophis ruffus*) and traded mostly for crocodile food (Brooks et al., 2007). The remaining 4% are larger snakes (56–135 cm SVL) of the species *H. buccata* and *E. bocourti*, which are traded through a separate marketing chain. The high value of these species means that individuals longer than 75–80 cm are always sold for skins or live export and will only be used as crocodile food after the skins have been removed. Based on mean monthly averages of price and quantity between 2004 and 2007, the total value of all snakes at the point of landing at Chong Khneas was USD220,897 ± 47,086 (SE) per annum.

3.2. The price of snakes

The domestic market for snakes is predominantly for crocodile food. However, live caught and fresher individuals are separated and used for human food, primarily as snack food. The price of snakes traded domestically varies seasonally and annually (Fig. 2). Linear models of daily prices, including year as a covariate and controlling for month, indicated small but significant price increases in both the crocodile ($F_{1,168} = 23.46$, β (year) = 0.024, $P < 0.0001$) and human food trade ($F_{1,75} = 21.22$, β (year) = 0.061, $P < 0.0001$) over the 4 years. These analyses are based on non-inflated price data and show an annual increase in price of USD 0.02 and 0.06 for the crocodile and human food trade respectively, which is equivalent to increases in price of 6% and 10%, based on the average prices for this period. This exceeds the national inflation rate for this period, which ranged between 1.7% and 5.8% (National Institute of Statistics of Cambodia).

3.3. Supply of snakes

The quantity of snakes traded domestically declined significantly between 2004 and 2008, as indicated by linear models of $\log_{10}$ transformed quantity values, controlling for month, with year as a covariate and an interaction term between month and year ($F_{4,14} = 22.81$, β (year) = −0.91, $P < 0.0001$, Fig 3). Based on weekly averages, the price of snakes is negatively correlated with the quantity traded (crocodile food: $r = -0.45$, $n = 121$, $P < 0.0001$, human food: $r = -0.28$, $n = 85$, $P < 0.01$) and the quantity traded is positively correlated with catch size ($r = 0.4$, $n = 86$, $P < 0.0001$). While these univariate relationships support an understanding of the system, there is insufficient sample size and statistical power to use multivariate models which could incorporate the seasonal and annual variation in price.

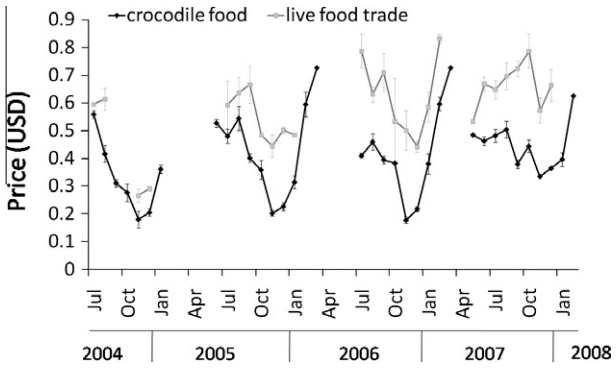

Fig. 2. Seasonal and annual variability in the price (USD) for snakes sold as crocodile food and live for human food, from July 2004 until February 2008. SE bars represent variation within each month.

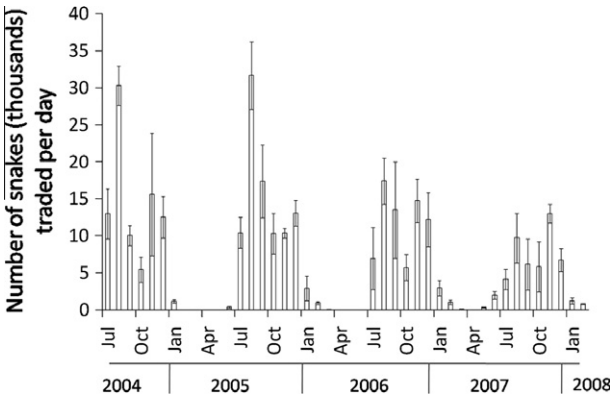

Fig. 3. The mean ± SE number (thousands) of snakes traded per day for the domestic trade for crocodile and human food.

The records of two large-scale traders of crocodile food in Siem Reap province between July 2005 and February 2006 indicate that snakes comprised *c.* 21% of crocodile diet, but varied from 0% in February to *c.* 49% in July (Fig. 4). Fish and snakes are substituted for one another depending on the season, but given the dominance of fish in the market, it is expected that fish, rather than snake price is the dominant factor, and that the price of snakes is influenced by the price of fish. The records of two large-scale crocodile food traders operating in Chong Khneas port from July 2005 until March 2006 showed that, while snake price did not vary significantly with the quantity of snakes sold as crocodile food ($F_{1,43} = 3.32$, $P = 0.075$), it increased with an increase in fish price ($F_{1,43} = 12.60$, $P < 0.001$). In addition, during the trade monitoring program in October 2005, we observed people struggling to sell snakes due to the low price and high abundance of fish available. Fig. 5 shows that, when fish price is high, the price of snakes is higher than would be expected given the quantity of snakes being traded but, at low fish prices, snake price varies considerably, possibly as a result of additional markets for snakes, such as human consumption that may operate independently of fish price.

Hunter behaviour also influences the supply of snakes. In August 2008, a large proportion of live snakes traded in Chong Khneas was, according to traders in the area, a consequence of more hunters using traps, rather than gillnets, to catch fish and live snakes that can be sold at a higher price as human food. Changing hunter behaviour may be part of the reason for the recent declines in

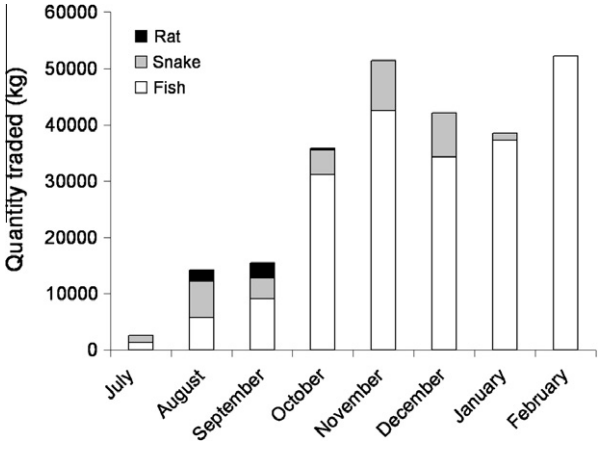

Fig. 4. Monthly variation in the total quantity of crocodile food (fish, snakes and rats) traded by two of the principal large-scale traders in Chong Khneas from July 2005 until February 2006.

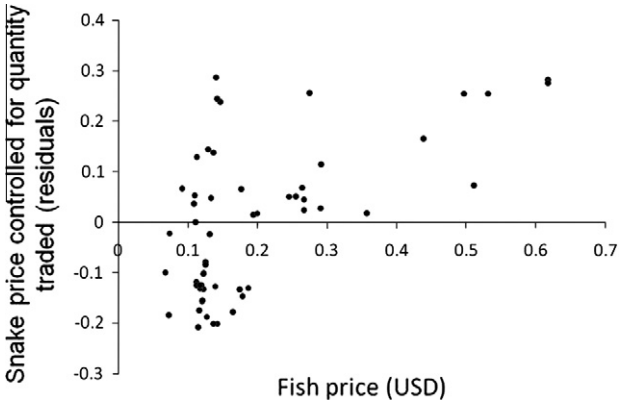

Fig. 5. The relationship between the unstandardized residuals of the daily price–quantity regression (snake price = 0.64–0.07 log (number snakes traded), $R^2 = 0.07$, $df = 53$, $P = 0.06$), and the price of fish traded at Chong Khneas between July 2005 and March 2006 ($y = 0.66x + -0.13$, $R^2 = 0.37$, $P < 0.0001$).

snake trade (Fig. 3), although declines in catches do suggest that population sizes have declined over a longer time period (Brooks et al., 2007).

3.4. Demand for snakes

Both the number of crocodile farms and average farm size have increased dramatically over the last decade. In 1998, the largest farm in the complete stock survey of 391 farms held 530 crocodiles, and only 5% of farms held >100 crocodiles. By 2003, a sample of 103 farms (approximately 10% of the total) recorded nine farms holding >500 crocodiles, and 47% holding >100 crocodiles. Farm size (no. adults + 0.5 no. sub-adults) has increased significantly and exponentially with the number of years that they have been in operation ($\log_{10}$(farm size) = 0.04 farm age + 1.34, $R^2 = 0.26$, $P < 0.0001$). In 2004, 949 farms were recorded by the Department of Fisheries, which equates to between 32,999 and 159,376 captive crocodiles in Cambodia (excluding hatchlings).

Both fish and snakes are fed to crocodiles in these farms, and the quantities consumed increase significantly with farm size (Fig. 6). In 2001, all 100 floating farms used fish as crocodile food and 58% also fed snakes. In 2003, all 103 farms fed fish and 79% also used snakes. The farms that use snakes as food are significantly larger (Fig. 7, Table 2), with virtually all farms containing more than 100 crocodiles feeding snakes in addition to fish.

The size distribution of farms that feed snakes (Fig. 7) and the relationship between farm size and quantity of snakes fed to the crocodiles per year (Fig. 6b), together provide an estimate of the total quantity of snakes fed to the 103 farms included in the 2003 survey (141,344 kg year^{-1}). There were approximately 920 farms in the provinces surrounding Tonle Sap Lake in 2004 and, assuming that the distribution of farm sizes in this sample is representative of the whole area, approximately 1300,369 kg of snakes (12.2 million snakes) would have been fed to crocodiles in 2003. However, the 2003 survey excluded the smaller floating farms. The proportion of floating farms among the 920 farms is not known but they are certainly in the minority. Estimates of quantities of snakes consumed using the 2001 floating farm survey extrapolated to all 920 farms gives an estimate of 292,624 kg snakes (2.7 million snakes) per year. Thus the true figure is likely to lie between these two estimates of 2.7 and 12.2 million snakes and towards the upper end of the range (as land-based farms are far more common).

In every month of the year, the price of snakes on Tonle Sap is consistently higher than that of fish, indicating a preference for snakes (paired t-test, $t_9 = 3.35$, $P < 0.008$). Of the six crocodile farmers interviewed who stated preferences, four preferred snakes and two preferred fish. Reasons given for snakes being of higher quality include their higher bone content compared to that of fish, which is considered of benefit for breeding success and skin production, as well as the slower rate at which they are digested by crocodiles, which reduces the frequency of feeding. Reasons for preferring fish include their lower price, high abundance and the perception that they are the natural food of the crocodile.

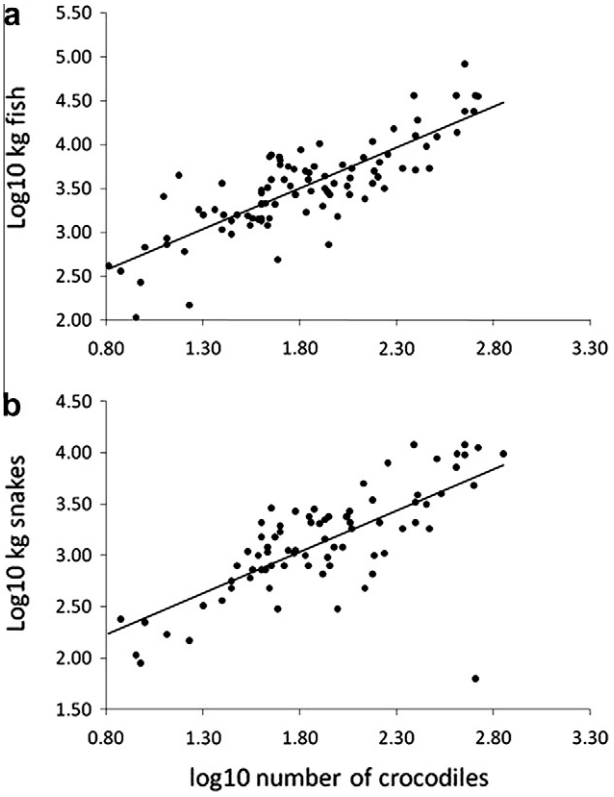

Fig. 6. Relationships between farm size (number of crocodiles) and quantities of: (a) fish and (b) snakes consumed per farm per year recorded from interviews with crocodile farmers in 2003 (fish: $y = 0.93x + 1.82$, $R^2 = 0.67$, $P < 0.0001$, snakes: $y = 0.80x + 1.59$, $R^2 = 0.52$, $P < 0.0001$).

3.5. Market changes in the crocodile farm industry

The Cambodian crocodile market is currently undergoing a decline in demand and the mean (±SE) market price of hatchling crocodiles has fallen from USD37 ± 0.5 in 2003 to USD16 ± 1.2 in 2005. In 2008, the price was anecdotally reported as being as low as USD11. Additionally, a substantial increase in the price of all types of crocodile food was reported between 1990 and 2005 (So et al., 2005). Four of the crocodile farmers interviewed in 2005 informed us that they have reduced the frequency of feeding due to the decline in price of crocodiles and the high price of food. Both of the large-scale crocodile food traders informed us that crocodile farmers are requesting snakes less frequently in response to these market changes. Based on these six reports, feeding frequency is now 56.9 ± 6.0 (SE)% of the rate prior to the market crash occurring around 2003. The interviewed farmers were all from relatively large farms, with six of the nine holding over 100 adult crocodiles. All except one had no plans to stop farming as they could afford to continue feeding their crocodiles while they wait for market prices to rise. They did not believe that the market would disappear completely as, throughout recent history, market prices for Cambodian crocodiles have always fluctuated. The one crocodile farmer who

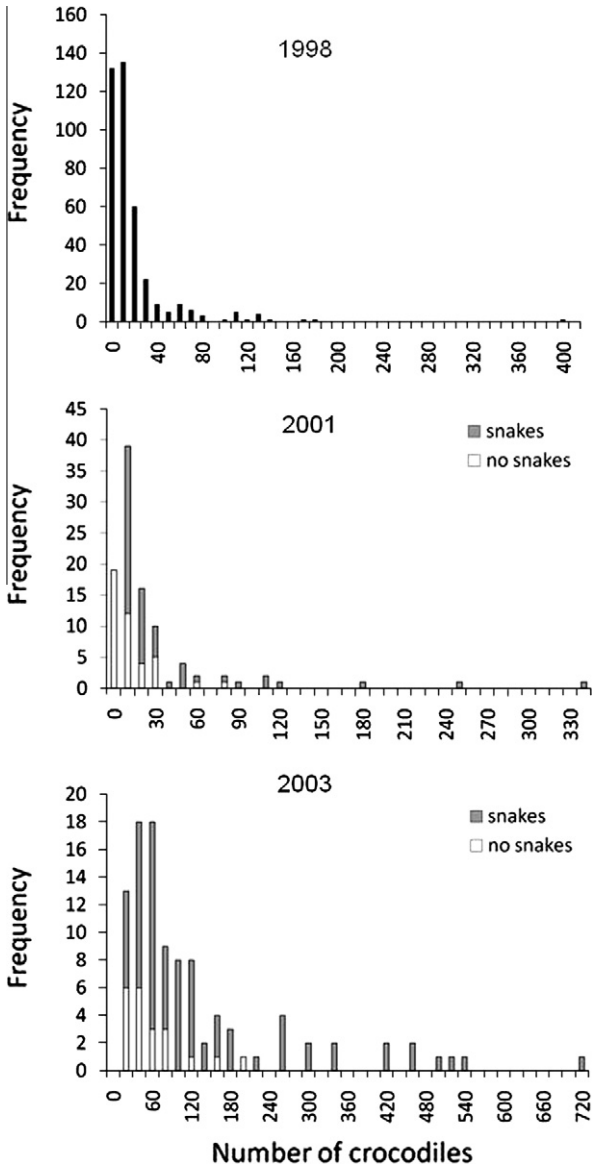

Fig. 7. Size distribution of crocodile farms in 1998 (all 396 farms in Cambodia), 2001 (sample of 100 floating farms) and 2003 (sample of 103 land farms), that did and did not feed snakes (2001 and 2003 only). The number of crocodiles is calculated as the number of adult crocodiles + (0.5 × number of sub-adult crocodiles).

wanted to close down the farm because of the low market price of crocodiles and high price of food, owned the smallest of all the farms we interviewed, with 22 adults and 35 sub-adults.

Interviews with crocodile farmers, including the head of the Crocodile Farming Development Association of Cambodia, and officials from the Fisheries Administration, indicated that the recent decline in price of crocodiles in Cambodia is the result of a decline in demand from neighbouring countries. Thailand and Vietnam previously purchased hatchling crocodiles from Cambodia to be reared for their skins but are now successfully breeding crocodiles, and China no longer trades directly with Cambodia, due to the high export tax set by the Cambodian government. As it can take 6–7 years for Siamese crocodiles to reach maturity (Thouk, 1998), it is possible that many of the hatchling crocodiles exported to Vietnam and Thailand in the 1990s are now breeding adults. In response to these changes, the Fisheries Administration and the Crocodile Farming Development Association are attempting to convert crocodile farms from producing hatchlings to producing skins, for which markets are thought to exist. Of the six crocodile farmers interviewed in Siem Reap Province, five have attended meetings and training workshops to aid in this conversion, but we encountered only one crocodile farmer who was developing the farm to rear crocodiles suitable for sale of their skin. The anticipated cost of such conversion is high and only the very large farms thought that this may be an option for the future if the market price for hatchlings does not increase.

3.6. Snakes as snacks

The quantity of snakes sold as human food is unknown but the practice is more common in the south of the lake where there are fewer crocodile farms. This is principally a snack food market, as snakes are not typically a major source of people's protein in the area. One of the main traders in Chong Khneas (interview ID: MM18) informed us that the demand for snakes as human food is too small to be worth trading if the demand from crocodile farms crashed. However, two traders informed us that human consumption of snakes was increasing and we encountered new traders travelling to the lake from other provinces to collect snakes for sale as human food in upland urban areas. According to one of the main snake traders in this area, people only started to come from other provinces to buy snakes to sell as human food in 2003 (interview ID: MM18). Human consumption of snakes may therefore become more substantial in the future.

4. Discussion

Tonle Sap Lake is a globally significant productive wetland situated amid the rapidly developing and increasingly market-orientated Southeast Asian region. As a result, seven snake species in Tonle Sap Lake are hunted to supply a range of international and domestic markets including exotic leather, live export, animal feed, and snack food. The largest driving force of snake exploitation is, however, the domestic trade in snakes as food for farmed crocodiles. This set of circumstances pertains to many ecosystems around the world, which supply a variety of goods and services to both domestic and international markets (MEA, 2005). In both forested and aquatic ecosystems, for example, there is often exploitation of both common and abundant species of low value for domestic food markets, as well as higher value species for export markets, which may include niche-markets for high-value products derived from rare and endangered species (Roe et al., 2002).

Table 2
Results of a logistic regression analysis of the effect of farm size (the number of crocodiles) on the probability that snakes are used as a food supply in the 2001 survey of floating farms and the 2003 survey of land farms.

Year of survey	Predictor variable	*B* (SE)	*P*	Log likelihood	Chi-squared	% Predicted correctly
2001	Farm size	2.04 (0.46)	0.0001	108.4	27.6	71.6
	Constant	−1.40 (0.44)	0.001			
2003	Farm size	1.96 (0.65)	0.003	92.4	10.9	76.2
	Constant	−2.07 (1.1)	0.06			

In such contexts, wildlife trade studies tend to be focused on one commodity, or one particular value chain (e.g. mahogany, wild orchids, bushmeat, seahorses, live reef fish) and few studies have explored the key linkages with related markets where the exploitation involves the same people (e.g. Brashares et al., 2004). A greater attention to the immediate context of wildlife trade industries is therefore likely to benefit conservation managers and policy advisors by providing them with information on the likely consequences of alternative management actions. We illustrate this here with reference to the snake and crocodile trade case study.

4.1. Conservation implications of the domestic snake market

Captive rearing of crocodiles for international trade is regarded by many as an effective conservation tool for the protection of exploited and threatened crocodilians (Blake and Loveridge, 1975; Revol, 1994; Thorbjarnarson, 1999), yet little consideration has been given to the conservation implications of the domestic demand it creates for a source of food. We estimate that domestic crocodiles in Cambodia consume between 2.7 and 12.2 million snakes per year, spanning the estimated 6.9 million traded annually (Brooks et al., 2007).

This market demand is responsible for the world's largest snake hunt and is likely to lead to severe population declines of several species. Decreases in snake catches have been reported between 1995 and 2005 (Brooks et al., 2007), which correspond with reported increases in the price of snakes (So et al., 2005). Of particular concern is the endemic species, *E. longicauda*, which represents between 16% and 39% of the overall catch. There is also likely to be a higher impact on *H. buccata* and *E. bocourti*, both of which are becoming increasingly rare in catches and thought to be more vulnerable due to their larger size and lower fecundity (Brooks et al., 2007). As has been highlighted in the bushmeat trade and in many fisheries, scarce and vulnerable species may still be driven to extinction as long as more abundant species continue to make generic hunting profitable (Wilkie and Godoy, 2001; Dulvy et al., 2003).

4.2. The effect of market changes on consumer demand

Crocodile farming suffers from typical boom and bust cycles that are dictated by economic situations in consumer countries and unpredictable fashion trends (Thorbjarnarson, 1999). Cambodia's role of maintaining a breeding stock to supply crocodile farms in other countries, rather than direct integration in the product market, creates additional instabilities for Cambodian crocodile farmers. The price of crocodiles in Cambodia peaked in the mid 1980s and has since been in decline as a result of market saturation following privatization of the production sector (Thouk, 1998; Jelden et al., 2005). Despite the unstable market and falling prices for crocodiles, the number and size of farms continued to increase throughout this period, leading to the high levels of demand for snakes shown in this study.

More recently, however, declines in demand from neighbouring countries have caused crocodile prices to drop below the margin of profit, which, in combination with rising prices for their food, is causing many crocodile farms to reduce feeding frequency. The demand for snakes is therefore responding to this combined effect, implying that while the price elasticity of demand for snakes is high, such elasticity depends upon the market price of crocodiles. This is similar to the sensitivity of fish and bushmeat consumption in South and Central America to changes in both household income and price (Wilkie and Godoy, 2001), indicating the importance of understanding both the preferences and economic situation of consumers when evaluating present and future demands in wildlife trade.

4.3. Future market trajectories

If the market for Cambodian crocodiles does not resume it is likely that many small crocodile farms will close. However, the large established farms that generate much of the overall demand for snakes and have invested and profited though the industry, are likely to continue in anticipation of future market opportunities. New market opportunities may emerge, including the currently-considered shift from production of hatchlings in Cambodia to production of crocodile skins for international export (IUCN/SSC, 2004). Thus, a high overall demand for snakes may be maintained by the large farms, particularly given the perception by farmers that snakes are a better source of food than fish for the production of high quality crocodile skin. We can also expect the use of snakes as human food to continue, and perhaps increase further, if demand from crocodile farms falls. However the importance of fresher snakes for this market is likely to limit quantities and therefore this demand is unlikely to replace that of the crocodile farms.

4.4. The role of substitutes in consumer behaviour

The price and demand for snakes as crocodile food is strongly influenced by the price of fish. Despite a slight quality premium on snakes as indicated by their higher price, the predominance of fish on the market indicates that fish is the main driver of the price of crocodile food. The price of snakes sold as a snack food is also likely to be subject to the price of alternatives snack food commodities such as fish, birds and insects, as well the more conventional packaged snack foods. The role of substitute resources in the relationship between demand and supply has been previously recognized, with consumers often substituting one protein source for another, depending on availability and price (Wilkie and Godoy, 2001; Brashares et al., 2004; Rowcliffe et al., 2005; Wilkie et al., 2005). The market response to availability of resources and their substitutes can introduce a level of sustainability into the system, whereby the availability of substitutes prevents price incentives driving exploitation at low population densities (Hall et al., 2008).

4.5. Points of conservation intervention

While restriction of access to this resource or trade bans could benefit snake populations, it could harm other species through the re-direction of exploitative pressure, and would probably lead to strong opposition from local communities. In the event of a continued market for Cambodian crocodiles, conservation action could address the consumer preference for snakes shown by some farmers, to prevent perverse price incentives. The development of an alternative food supply for crocodiles would not only aid in the conservation of Tonle Sap snakes, but would also relieve much of the pressure on the fisheries of Tonle Sap. The potential shift towards the use of snakes as human food is of less concern due to substitutability and the higher quality premium and lower quantities required. It does, however, highlight the volatile nature of the markets that dictate the exploitation of natural resources. In light of shifting and uncertain markets, the domestic trade in snakes could be controlled through a no-hunting season that corresponds to the main breeding season of the species caught and traded (Brooks et al., 2007). This management strategy would allow the hunting and trade to continue at the time of year when it is most important to fishers, traders and consumers. Given the importance of snakes to the local economy, this option may be the most likely to be accepted by local communities (Brooks et al., 2008).

4.6. Conclusion

Measures to regulate trade often focus on species endangerment, either at the global, national or population level, and are initiated in a precautionary manner. CITES is the most influential instrument for regulating international trade, but there are often national instruments that can control domestic trades to some degree. Such approaches typically operate irrespective of the nature of consumer demand, and often fail to consider the linkages between different markets for natural resources.

The Cambodian snake markets illustrate how a range of consumer demands in a segmented market can influence sustainability. The domestic snake trade described in this study is one that, despite extreme trade figures, is likely to be more aligned with ecosystem sustainability goals, as a result of the substitutability and low price elasticity of demand. This differs considerably from the international snake market that is present in Cambodia, where end market prices for such luxury goods are often less constrained and value may even increase further in response to rarity, as has been shown for a number of rare species (Courchamp et al., 2006). This understanding not only allows us to predict future exploitation scenarios, but also to evaluate current and future need for conservation intervention, and to advise on its implementation.

Regulatory trade measures have received criticism for both their impacts on local populations as well as being ineffective in conserving species threatened by trade (Roe et al., 2002; Dickson, 2003). One of their failings is the lack of flexibility and adaptability to the specific context in which trade is occurring. Asian wildlife markets are evolving quickly, thus necessitating adaptive and responsive forms of management for sustainable use that are based, in part, on information regarding the behaviour of consumer markets driving the exploitation.

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References

Berkes, F., Hughes, T.P., Steneck, R.S., Wilson, J.A., Bellwood, D.R., Crona, B., Folke, C., Gunderson, L.H., Leslie, H.M., Norberg, J., Nyström, M., Olsson, P., Österblom, H., Scheffer, M., Worm, B., 2006. Globalization, roving bandits, and marine resources. Science 311, 1557–1558.

Blake, D.K., Loveridge, J.P., 1975. The role of commercial crocodile farming in crocodile conservation. Biological Conservation 8, 461–472.

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.

Brashares, J.S., Arcese, P., Sam, M.K., Coppolillo, P.B., Sinclair, A.R.E., Balmford, A., 2004. Bushmeat hunting, wildlife declines, and fish supply in West Africa. Science 306, 1180–1183.

Broad, S., Mulliken, T., Roe, D., 2003. The nature and extent of legal and illegal trade in wildlife. In: Oldfield, S. (Ed.), The Trade in Wildlife: Regulation for Conservation. Earthscan Publications, London, pp. 3–23.

Brooks, S.E., Allison, E.H., Reynolds, J.D., 2007. Vulnerability of Cambodian water snakes: initial assessment of the impact of hunting at Tonle Sap Lake. Biological Conservation 139, 401–414.

Brooks, S.E., Reynolds, J.D., Allison, E.H., 2008. Sustained by snakes? Seasonal livelihood strategies and resource conservation by Tonle Sap fishers in Cambodia. Human Ecology 36, 835–851.

Brukner, A.W., 2001. Tracking the trade in ornamental coral reef organisms: the importance of CITES and its limitations. Aquarium Sciences and Conservation 3, 79–94.

Cheung, S.M., Dudgeon, D., 2006. Quantifying the Asian turtle crisis: market surveys in Southern China, 2000–2003. Aquatic Conservation: Marine and Freshwater Ecosystems 16, 751–770.

Clarke, S., McAllister, M.K., Milner-Gulland, E.J., Kirkwood, G.P., Michielsens, C.G.J., Agnew, D.J., Pikitch, E.K., Nakano, H., Shivji, M.S., 2006. Global estimates of shark catches using trade records from commercial markets. Ecology Letters 9, 1115–1126.

Courchamp, F., Angulo, E., Rivalan, P., Hall, R.J., Signoret, L., Bull, L., Meinard, Y., 2006. Rarity value and species extinction: the anthropogenic allee effect. Plos Biology 4, 2405–2410.

Cowlishaw, G., Mendelson, S., Rowcliffe, J.M., 2005. Evidence for post-depletion sustainability on a mature bushmeat market. Journal of Applied Ecology 42, 460–468.

Dickson, B., 2003. What is the goal of regulating wildlife trade? Is regulation a good way to achieve this goal? In: Oldfield, S. (Ed.), The Trade in Wildlife: Regulation for Conservation. Earthscan, London, pp. 23–33.

Dulvy, N.K., Sadovy, Y., Reynolds, J.D., 2003. Extinction vulnerability in marine populations. Fish and Fisheries 4, 25–64.

East, T., Kümpel, N.F., Milner-Gulland, E.J., Rowcliffe, J.M., 2005. Detreminants of urban bushmeat consumption in Río Muni, Equatorial Guinea. Biological Conservation 126, 206–215.

Fa, J.E., Juste, J., Burn, R.W., Broad, G., 2002. Bushmeat consumption and preferences of two ethnic groups in Bioko Island, West Africa. Human Ecology 30, 397–416.

Hall, R.J., Milner-Gulland, E.J., Courchamp, F., 2008. Endangering the endangered: the effects of perceived rarity on species exploitation. Conservation Letters 1, 75–81.

Huitric, M., 2005. Lobster and Conch fisheries of Belize: a history of sequential exploitation. Ecology and Society 10, 21.

IUCN/SSC, 2004. Siamese Crocodile Conservation in Cambodia, Crocodile Specialist Group, Siamese Crocodile Working Group.

Jelden, D., Manolis, C., Giam, C.H., Thomson, J., Lopez, A., 2005. Crocodile Conservation and Management in Cambodia: a Review with Recommendations. Summary Report of the IUCN – SSC Crocodile Specialist Group Review Mission to Cambodia.

Jerozolimski, A., Peres, C.A., 2003. Bringing home the biggest bacon: a cross-site analysis of the structure of hunter–kill profiles in Neotropical forests. Biological Conservation 111, 415–425.

Kroner, K.F., Kneafsey, D.P., Claessens, S., 1993. Forecasting Volatility in Commodity Markets. The World Bank, International Economics Department.

Kummu, M., Sarkkula, J., Koponen, J., Nikula, J., 2006. Ecosystem management of the Tonle Sap Lake: an integrated modelling approach. International Journal of Water Resources Development 22, 497–519.

Lamberts, D., 2001. Tonle Sap Fisheries: a Case Study on Floodplain Gillnet Fisheries. Food and Agriculture Organization, Bangkok.

Lamberts, D., 2006. The Tonle Sap Lake as a productive ecosystem. Water Resources Development 22, 481–495.

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.

MEA, 2005. Ecosystems and Human Well-Being: Current State and Trends. Millennium Ecosystem Assessment. World Resources Institute.

Pinnegar, J.K., Jennings, S., O'Brien, M., Polunin, N.V.C., 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. Journal of Applied Ecology 39, 377–390.

Revol, B., 1994. Crocodile farming and conservation, the example of Zimbabwe. Biodiversity and Conservation 4, 299–305.

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

Robinson, J.G., Redford, K.H., 1991. Neotropical Wildlife Use and Conservation. University of Chicago Press, Chicago.

Roe, D., Mulliken, T., Milledge, S., Mremi, J., Mosha, S., Grieg-Gran, M., 2002. Making a Killing or Making a Living, Biodiversity and Livelihood Issues No. 6. IIED and TRAFFIC.

Rowcliffe, J.M., Milner-Gulland, E.J., Cowlishaw, G., 2005. Do bushmeat consumers have other fish to fry? Trends in Ecology and Evolution 20, 274–276.

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

So, N., Tong, E., Norng, S., Hortle, K., 2005. Use of Freshwater Low Value Fish for Aquaculture Development in the Cambodia's Mekong Basin. Department of Fisheries and Mekong River Commission, Phnom Penh, Cambodia.

Stuart, B.L., 2004. The harvest and trade of reptiles at U Minh Thuong National Park, Southern Vietnam. Traffic Bulletin 20, 25–34.

Stuart, B.L., Platt, S.G., 2004. Recent records of turtles and tortoises from Laos, Cambodia, and Vietnam. Asiatic Herpetological Research 10, 129–150.

Stuart, B.L., Smith, J., Davey, K., Din, P., Platt, S.G., 2000. Homalopsine watersnakes: the harvest and trade from Tonle Sap, Cambodia. Traffic Bulletin 18, 115–124.
Thorbjarnarson, J., 1999. Crocodile tears and skins: international trade, economic constraints, and limits to the sustainable use of crocodilians. Conservation Biology 13, 465–470.
Thouk, N., 1998. Current Status of Crocodile in Cambodia in Captivity and in the Wild. In: Contribution to the 14th Working Meeting of the Crocodile Specialist Group in Singapore, 14–17 July, Phnom Penh, Cambodia.
van Mulekom, L., Axelsson, A., Batungbacal, E.P., Baxter, D., Siregar, R., de la Torre, I., 2006. Trade and export orientation of fisheries in Southeast Asia: under-priced export at the expense of domestic food security and local economies. Ocean & Coastal Management 49, 546–561.
Wilkie, D.S., Godoy, R.A., 2000. Economics of bushmeat. Science 287, 973.
Wilkie, D.S., Godoy, R.A., 2001. Income and price elasticities of bushmeat demand in Lowland Amerindian societies. Conservation Biology 15, 761–769.
Wilkie, D.S., Starkey, M., Abernethy, K., Nstame Effa, E., Telfer, P., Godoy, R., 2005. Role of prices and wealth in consumer demand for bushmeat in Gabon, Central Africa. Conservation Biology 19, 268–274.
Yiming, L., Dianmo, L., 1998. The dynamics of trade in wildlife across the Guangxi border between China and Vietnam during 1993–1996 and its control strategies. Biodiversity and Conservation 7, 895–914.
Zhou, Z., Jiang, Z., 2004. International trade status and crisis for snake species in China. Conservation Biology 18, 1386–1394.
Zhou, Z., Jiang, Z., 2005. Identifying snake species threatened by economic exploitation and international trade in China. Biodiversity and Conservation 14, 3525–3536.