ELSEVIER

Biological Conservation 87 (1999) 349–357

BIOLOGICAL CONSERVATION

Reticulated pythons in Sumatra: biology, harvesting and sustainability

Richard Shine[a,*], Ambariyanto[a,1], Peter S. Harlow[a], Mumpuni[b]

[a]*School of Biological Sciences A08, The University of Sydney, Sydney, N.S.W. 2006, Australia*
[b]*Centre for Research in Biology, Museum of Zoology, LIPI, Bogor 16122, Indonesia*

Received 26 February 1998; received in revised form 1 May 1998; accepted 2 June 1998

Abstract

Hundreds of thousands of giant snakes (*Python reticulatus*) are taken from the wild to be killed for their skins each year, raising doubts about the longterm sustainability of this offtake. We visited four locations in northern Sumatra (Medan, Seisuka, Rantauprapat and Cikampak) at four times of year and gathered information on the sizes, sexes, reproductive status and food habits of 784 slaughtered pythons. Pythons in northern Sumatra mature at larger body sizes than do those studied previously in southern Sumatra (Palembang). Their seasonal timing of reproduction is shifted appreciably, presumably because the two areas lie on opposite sides of the equator. The slaughtered animals are mainly adult males and adult plus juvenile females. Females attain larger sizes than males, but very large females are rarely captured. This bias may reflect size-related shifts in habitat selection; smaller snakes (including adult males of all sizes, and recently-matured females) feed primarily on commensal rats and hence are abundant in disturbed (agricultural and village) habitats. Female pythons produce large clutches (mean = 24.2) of large eggs (mass > 250 g), but reproduce only once every 2 to 4 years. The apparent ability of reticulated python populations to withstand high levels of offtake may reflect their demography (rapid growth rates, early maturation, high fecundity), their flexibility in diets and habitat use, and their ability to evade detection (because neither foraging nor thermoregulation require extensive movements). © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: Diets; Ecology; Reptile; Reproduction; Snake; Sustainable use

1. Introduction

It is almost always difficult to evaluate the degree of "sustainability" of exploitation of a wild population. For example, fisheries biologists have often failed to achieve this aim, despite intensive effort and complex models (e.g. King, 1995; Roberts, 1997). Even under ideal circumstances, where the resource in question is clearly delimited and easily quantified, it can be difficult to establish the degree of harvesting which will allow indefinite persistence of the resource at levels that are "acceptable" ecologically, economically, aesthetically, or genetically (e.g. Choquenot, 1996). In cases where the exploited species is poorly known biologically, and virtually impossible to survey quantitatively in the field, the problems are greatly exacerbated. Unfortunately, many of the biological resources that are being heavily exploited in tropical regions fall into exactly this category.

Conventional "optimal sustainable yield" approaches rely upon the investigator's ability to quantify the impact of harvesting intensity on population density (e.g. Rothschild, 1983; Roberts, 1997). If this is impossible, we are left with few alternatives other than experimental management or highly conservative recommendations (Grigg, 1995). In either case, the most useful initial step is to characterise the basic ecological attributes of the exploited species. Such information is relatively inexpensive and easy to obtain (by examining harvested animals) and can serve as a basis for inferences on the species' ability to withstand various types and intensities of anthropogenic offtake. Even though it may not provide a basis for quantitative suggestions on offtake levels, knowledge of the species' biology may help to frame management plans that maximise economic returns while minimising the ecological impact of the trade (e.g. by identifying times and places that harvesting should not occur).

We have taken this approach to examine the ecological characteristics of a giant reptile species that is heavily exploited throughout much of southeast Asia. Reticulated pythons are either the largest or second-largest species of snake in the world, with reliable

* Corresponding author. Fax: +61-2-9351-5609; e-mail: rics@bio.usyd.edu.au
[1] Present address: Dipenegoro University, JI. Imam Bardjo SH, Semarang, Indonesia.

PII: S0006-3207(98)00068-8

records of specimens exceeding 9 m in length and 150 kg in mass (Pope, 1975). The skins of this species are highly sought-after for the commercial leather industry, and > 500 000 snakes are taken from the wild every year for this purpose (Groombridge and Luxmoore, 1991; Jenkins and Broad, 1994). The harvesting is concentrated in Indonesia, especially in Sumatra and Kalimantan (Groombridge and Luxmoore, 1991; Jenkins and Broad, 1994). The longterm sustainability of these high offtake levels has been questioned by numerous authorities (e.g. Lim, 1976; Jenkins and Broad, 1994; Roth and Mertz, 1997).

Despite this international concern, the biology of *Python reticulatus* has remained virtually unknown, as is the case for most species of tropical reptiles. Unfortunately, intuition based on the biology of well-studied temperate-zone species may provide a poor basis for inferences about superficially similar tropical species. For example, concerns about the sustainability of the commercial trade in giant Asian pythons are based in part on extrapolation from studies on large crotaline snakes of temperate-zone North America. These animals are typically uncommon, and their life-histories involve several traits (notably delayed maturation, low rates of growth and reproduction, and high survival rates) that reduce their ability to sustain intensive commercial exploitation (e.g. Campbell et al., 1989; Brown, 1991). If these traits are typical of large snakes from tropical as well as temperate-zone environments, then the Asian pythons may be poorly-suited to commercial harvesting.

We set out to clarify this situation some years ago, commencing with examination of > 1000 reticulated pythons brought into skinning premises in southern Sumatra. We used this information to document basic biological attributes of the species (Shine et al., 1998a, 1998b), but have delayed considering the implications for sustainable use until we had obtained equivalent data from slaughterhouses in northern Sumatra. We have now completed this phase of the work also. The present paper compares the northern-Sumatran pythons with their previously-studied southern conspecifics, and uses the combined data set to speculate on the ecological sustainability of the commercial trade in this species.

2. Materials and methods

2.1. Study area

We visited slaughterhouses where snakes and lizards are brought to be killed and skinned, in four cities and towns in northern Sumatra: Medan (3°35′N 98°39′E), Seisuka (3°25′N 99°27′E), Rantauprapat (2°05′N 99°46′E) and Cikampak (1°43′N 100°15′E). The pythons are collected in various parts of northern Sumatra, and are transported alive to the slaughterhouses. We could not reliably determine the origin of most specimens. Reticulated pythons occur in suitable habitat (especially, close to rivers and swamps) throughout low-lying areas of Sumatra (David and Vogel, 1996).

The climate in this area is characterised by consistently high mean temperatures, with little seasonal variation (all months have mean temperatures > 26°C: Arakawa, 1969). Rainfall is high (mean annual precipitation at Medan Polonia = 2174 mm) and relatively uniform, but with two minor peaks in May and November (Arakawa, 1969). Although the climate of Palembang (the site of our previous study in southern Sumatra) is broadly similar to that of Medan, the Palembang climate is more strongly seasonal. The same two peak monsoon periods occur as in the Medan region, but at Palembang they are separated by a more pronounced dry-season.

2.2. Methods

We visited northern Sumatra four times, with our trips spread evenly over the year (March, June, August, December) so that we could evaluate seasonal variation. On each trip we travelled to slaughterhouses in each of the four cities and towns listed above, and examined freshly-killed pythons before and after skinning. We recorded snout-vent length (henceforth = SVL), tail length and body mass, and then examined the snake's carcass to determine sex and reproductive condition (by direct inspection of the gonads). We removed, weighed, counted and measured oviductal eggs, and counted numbers of corpora lutea and vitellogenic ovarian follicles. The testes were measured, and their volumes calculated from these dimensions (James and Shine, 1985). We classed males as adult if they had large turgid testes, and/or opaque thickened efferent ducts. Females were classed as mature if they had oviductal eggs, vitellogenic ovarian follicles (> 10 mm diameter), corpora lutea from previous clutches, and/or thickened muscular oviducts. Any prey items in the alimentary tract were removed for later identification. A subset of these items was identified to species level by microscopic examination (see Shine et al., 1998a for details of methods). We scored fat-body size on a four-point scale to provide an index of energy stores. We also recorded the numbers of large ascarid nematodes evident in the stomachs of many snakes.

3. Results

3.1. Procedures for collecting and processing pythons

Based on conversations with people who had captured pythons and brought them in to be sold, it seems as though the snakes are caught in several ways. Many are captured serendipitously, as people go about their normal activities in the fields, plantations and forests.

Others are captured close to or within villages. Several Palembang snakes had been caught on fishing lines placed under houses after the snake or its tracks had been seen. In such cases, a large hook is baited with a rat or chicken, and left in position until the snake has swallowed the bait. We found such hooks in the stomachs of several pythons. Many of the larger snakes are captured in snares (rope nooses) set near waterbodies, wherever the trails of large pythons are detected (M. Sudirman, pers. comm.). We were told that most pythons are killed when encountered, even if they are not sold to skin-dealers, because of the value of the meat and the advantages of removing nuisance animals that might otherwise devour chickens, dogs or children.

Snakes destined for the skin trade are kept alive in bags, and transported to the traders' premises where they are stored for variable periods of time. They are killed by a variety of techniques in different establishments (a blow to the head, suffocation, or pithing by a wire into the brain) and then suspended by the head. In most establishments the alimentary tract of the snake is then filled with water, to expand the body wall and facilitate separation of the skin from the underlying musculature (Fig. 1). The skin is left on the head and tail, and the remainder of the skin removed in one piece via either a midventral or mid-dorsal longitudinal cut. The skin is then scraped free of adherent tissue, and pegged out in the shade to dry (Fig. 1). The flesh along the snake's lateral surface is dissected away and sold fresh, or dried for human food. The gall bladder is removed and dried for sale as traditional medicine. In one establishment, some of the gravid female pythons were kept alive until they had oviposited their clutches, and were then allowed to incubate the eggs through to hatching before being killed and skinned. Their offspring were sold for the international pet trade.

3.2. Variation among localities

We obtained information on 784 reticulated pythons killed for their skins. Our first analyses looked for differences among samples from the four locations at which we examined pythons. Although snakes from the four different localities did not differ in sex ratios ($\chi^2 = 0.96$, 3 df, $p = 0.81$), the proportion of juvenile snakes among the slaughtered animals showed significant spatial variation ($\chi^2 = 27.95$, 3 df, $p < 0.0001$). This result mostly reflects one location (Seisuka), where

(a) (b) (c) (d)

Fig. 1. Processing techniques used for reticulated pythons killed for the skin industry. After the snakes are killed, they are (a) hung up and (b) filled with water; then the skins are removed, (c) scraped clean, and (d) pegged out to dry.

no juveniles were killed. If attention is restricted to adult snakes, we detected no significant spatial differences in mean body sizes of the slaughtered snakes (two-factor ANOVA with location and gender as the factors, interaction non-significant, location effect $F_{3,521} = 0.43$, $p = 0.73$). However, we detected significant differences among the four locations in numbers of gut parasites ($F_{3,420} = 3.46$, $p < 0.02$; snakes from Seisuka and Cikampak had fewer parasites than snakes from the other sites) and relative fat body sizes ($F_{3,779} = 3.86$, $p < 0.01$; snakes from Medan had lower fat reserves).

3.3. Variation among trips

Table 1 provides information on the numbers of adult and juvenile pythons of each sex examined during each of our four trips at different times of the year. Despite the relatively aseasonal climate, we detected strong differences among the four trips in the sex and age composition of the pythons. The relative numbers of juvenile *versus* adult animals varied among the trips, both in males ($\chi^2 = 11.51$, 3 df, $p < 0.01$) and females ($\chi^2 = 69.33$, 3 df, $p < 0.0001$). The sex ratio also shifted through time, in both juveniles ($\chi^2 = 12.18$, 3 df, $p < 0.01$) and adults ($\chi^2 = 23.50$, 3 df, $p < 0.0001$), as did the proportion of snakes containing prey items in the alimentary tract ($\chi^2 = 24.78$, 3 df, $p < 0.0001$; ranging from 41% in December to 75% in June). Reproductive traits also showed strong seasonality (see below).

3.4. Sexual dimorphism

Female reticulated pythons in northern Sumatra mature at larger sizes than do males (approx. 240 versus 190 cm SVL) and grow to larger sizes (maximum lengths in our sample of approx. 580 versus 460 cm SVL: Fig. 2). Although the body-size distributions of male and female pythons were relatively similar, most of the males were adults whereas about half of the females were juveniles (18% juvenile in males, 49% in females: $\chi^2 = 83.46$, 1 df, $p < 0.0001$; see Fig. 2).

Table 1
Numerical composition of the harvested snakes (*Python reticulatus*) in terms of their sexes and reproductive status (adult *versus* juvenile) on each of our four trips to northern Sumatra.

Trip no.	Dates	Males		Females	
		Juvenile	Adult	Juvenile	Adult
1	22–31 August 1996	0	15	2	23
2	30 November–12 December 1996	14	101	26	71
3	23 February–7 March 1997	36	105	54	61
4	12–25 June 1997	24	118	99	35
Totals		74	339	181	190

Dates shown are actual span of dates when snakes examined, and comprised only part of the overall trip.

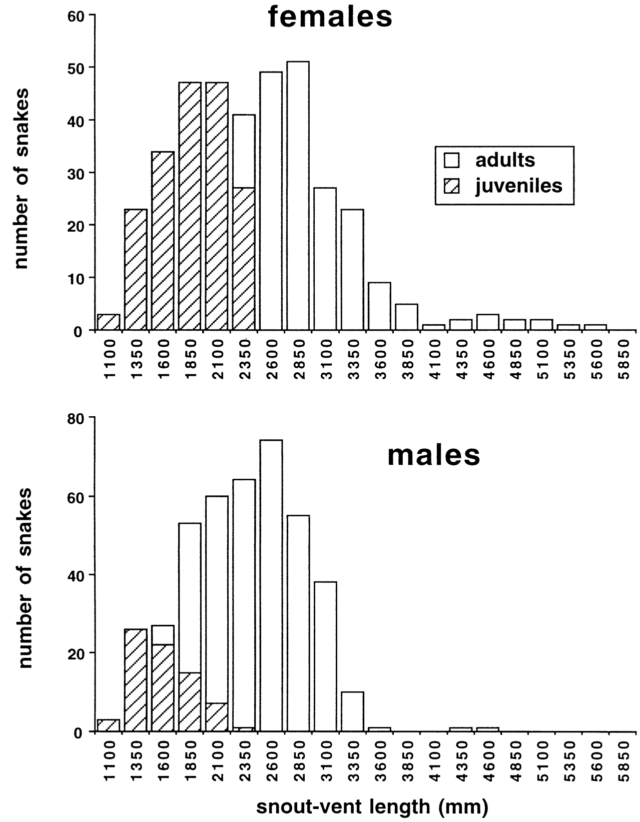

Fig. 2. Body-size distributions of the harvested pythons. Although snout-vent length distributions were relatively similar in the two sexes, differences in size at maturity mean that most of the males were adults whereas many of the females were juveniles.

3.5. Reproductive biology

Reproduction is strongly seasonal in both sexes. Relative size of the testes varied among trips (one-factor ANCOVA with trip number as the factor, SVL as the covariate, and ln combined testis volume of adult males as the dependent variable: slopes homogeneous, intercepts $F_{3,332} = 5.14$, $p < 0.002$), being largest in August and smallest in June. The proportions of adult females that were reproductively active when killed (i.e. were gravid, or had ovarian follicles >20 mm) also varied among trips, with none in August (out of 15), 6 of 48 (13%) in December, 13 of 43 (30%) in March and 1 of 22 (5%) in June. These data enable strong rejection of the null hypothesis of equal proportions of reproductive females during each trip ($\chi^2 = 12.14$, 3 df, $p < 0.01$). Females lay a single clutch of eggs around April–May each year, although many adult females are non-reproductive even at this time (see above).

Clutch sizes averaged 24.2 eggs (SD = 12.9, range = 8 to 71), and increased strongly with maternal body size (Fig. 3; regression of clutch size on maternal SVL—$r = 0.94$, $n = 18$, $p < 0.0001$). Eggs in two fullterm clutches averaged 204 and 300 g, and Relative Clutch

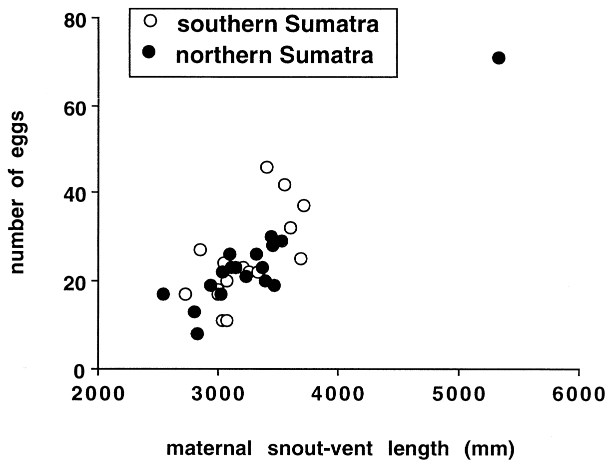

Fig. 3. Clutch sizes relative to maternal body size in reticulated pythons from northern Sumatra (Medan area; this study) and southern Sumatra (Palembang area, from Shine et al., 1998a). Statistical analyses (in text) show that these regressions are not significantly different.

Mass (ratio of clutch mass to maternal carcass mass) of one female was 0.39.

3.6. Energy stores and numbers of gut parasites

A two-factor ANOVA with gender and reproductive maturity/immaturity as factors showed that the relative size of the fat bodies (as indicated by our four-point scale) varied with both of these factors. Fat body scores were consistently higher in females than in males ($F_{1,779} = 25.95$, $p < 0.0001$), and consistently higher in adults than in juveniles ($F_{1,779} = 223.17$, $p < 0.0001$; means of 1.19 for adult females, 0.17 for juvenile females, 0.71 for adult males, 0.08 for juvenile males). Thus, the degree of disparity in fat-body sizes between adult and juveniles also differed between the sexes (interaction $F_{1,779} = 11.96$, $p < 0.001$). In contrast, the same kind of analysis for numbers of ascarid nematodes revealed no significant differences in parasite burdens as a function of gender, reproductive status, or their interaction ($p > 0.40$ for all comparisons).

3.7. Dietary composition

Rats were the most common type of prey found in the alimentary tracts of the dissected pythons, but we also recorded several domestic chickens and a few larger mammals (Fig. 1, Table 2). The proportion of the diet composed of rats did not differ between adult and juvenile pythons within either males (dividing prey into the three categories of "rat", "bird" and "other": $\chi^2 = 0.59$, 2 df, $p = 0.75$) or females ($\chi^2 = 0.13$, 2 df, $p = 0.94$). However, dietary composition differed significantly between male and female pythons (testing rats versus all others—$\chi^2 = 7.01$, 1 df, $p < 0.01$; testing commensal prey items [rats plus chickens] against all others—$\chi^2 = 4.61$, 1 df, $p < 0.04$).

4. Discussion

In combination with our previous work in the Palembang area (Shine et al., 1998a,b), we now have information on the biological attributes of > 1800 reticulated pythons collected for the skin trade in Sumatra. Many broad similarities between the two samples of pythons are evident, but many differences are apparent also. In the following discussion, we first compare and contrast the pythons from northern versus southern Sumatra, before using the combined data set to speculate on the sustainability of the current commercial harvest of wild pythons.

One of the strongest patterns to emerge from both data sets is the importance of seasonal effects, despite the year-round high temperatures and relatively aseasonal rainfall regimes in Sumatra. For example, reproductive cycles in both males and females are strongly seasonal in both areas, although with a very different timing. Oviposition occurs around April–May in the Medan area, versus September–October at Palembang (Shine et al., 1998a). This discrepancy plausibly reflects climatic differences between the two areas, due in turn to their positions on either side of the equator (2°N versus 2°S).

The pythons examined on the four different trips in northern Sumatra (and the three trips to Palembang) also displayed strong among-trip variation in traits such as feeding frequency (judged by the proportions of animals containing identifiable prey), and the size and sex composition of the harvested specimens. Changes in sex ratios and feeding rates may reflect reproductive activity, with the differing reproductive roles of males and females affecting both their feeding rates and their vulnerability to predation at different times of the annual cycle (e.g. Brown, 1991; Shine, 1993). Changes among trips in the relative numbers of adult and juvenile specimens may similarly be due to reproductively mediated shifts in adult activity levels, but also (because so many of the harvested animals are close to the age of maturation) reflect relatively synchronous maturation in cohorts of these seasonally-breeding animals (Shine et al., 1998a).

The pythons from northern versus southern Sumatra are similar in a series of traits such as sexual dimorphism (males mature at smaller sizes than females, and do not grow as large), reproductive output (less-than-annual production of large clutches of large eggs) and diets (mostly rats in smaller animals, shifting to larger mammals in larger pythons: Shine et al., 1998a,b). In some cases, the degree of similarity is very high (Table 3); for example, the relationship between maternal body size and clutch size is virtually identical in the two populations (Fig. 3; one-factor ANCOVA with location as the factor, maternal SVL as the covariate and clutch size as the dependent variable: slopes are

Table 2
Prey species recorded from alimentary tracts of harvested reticulated pythons in northern Sumatra

Family	Species	Total number of prey	*Number in male*		*Number in female*	
			Juvenile	Adult	Juvenile	Adult
Muridae	Rat (*Rattus* sp.)	139	24	49	29	37
Viverridae	Palm civet (*Arctogalidia trivirgata*)	2	–	–	1	1
Manidae	Pangolin (*Manis javanica*)	4	–	1	2	1
Tupaiidae	Palm shrew (*Tupaia javanica*)	2	–	–	1	1
Suidae	Wild pig (*Sus scrofa*)	1	–	–	–	1
Cercopitheidae	Leaf monkey (*Presbytis melalophos*)	1	–	–	1	
Phasianidae	Domestic chicken (*Gallus gallus*)	14	1	3	5	5

Table 3
A comparison between ecological traits of reticulated pythons in two regions of Sumatra: the southern area near Palembang (data from Shine et al. 1998a) and the northern area near Medan (this study)

Trait	*Palembang*	*Medan*	*Statistical test for geographic difference*
Sample size	1046	784	–
Adult sex ratio (% male)	83%	64%	$\chi^2 = 42.52$, 1 df, $p < 0.0001$
% Juveniles among:			
Males	11%	18%	$\chi^2 = 8.75$, 1 df, $p < 0.004$
Females	79%	49%	$\chi^2 = 84.16$, 1 df, $p < 0.0001$
Snout-vent length (cm) at maturity in:			
Males	137	190	–
Females	210	240	–
Mean adult snout-vent length (cm) for:			
Males	252.5	262.8	$t_{815} = 3.51$, $p < 0.01$
Females	359.7	315.3	$t_{296} = 5.90$, $p < 0.001$
Maximum snout-vent length (cm) for:			
Males	425.0	64	–
Females	608.0	583	–
Mean clutch size	23.8	24.2	$t_{33} = 0.09$, $p = 0.93$
Mean egg mass (g)	23.8	252	$t_7 = 4.14$, $p < 0.005$
Proportion of adult females reproductive per year	38%	30%	$\chi^2 = 0.37$, 1 df, $p = 0.54$
Proportion with prey	48.2%	58.2%	$\chi^2 = 8.59$, 1 df, $p < 0.004$
Proportion of commensal prey (rats and chickens) in diet	78%	94%	$\chi^2 = 19.11$, 1 df, $p < 0.0001$
Mean number of gut parasites	5.43	0.86	$t_{1076} = 4.17$, $p < 0.0001$
Mean fat-body score	1.16	0.65	$t_{1805} = 12.55$, $p < 0.0001$

Statistical tests comprise contingency-table analyses or unpaired two-tailed *t*-tests.

homogeneous—interaction $F_{1,31} = 0.14$, $p = 0.71$; intercepts are similar—$F_{1,32} = 0.29$, $p = 0.59$; main effect of SVL, $F_{1,32} = 79.64$, $p < 0.0001$). However, when one looks in more detail, many substantial differences are apparent between snakes from the two areas, in terms of basic biology (dietary composition, egg size) as well as the kinds (sizes, sexes, reproductive status) of the animals that are harvested (Table 3).

Compared to their southern conspecifics, the snakes from northern Sumatra are characterised by larger body sizes at maturation (in both sexes), larger eggs, a higher frequency of feeding, a lower parasite load, and lower fat stores (Table 3). Male reticulated pythons grow larger in the north than in the south, but females are smaller; the end result is that the degree of sexual dimorphism in mean adult body size (snout-vent length) varies significantly between the two areas (two-factor ANOVA with gender and location as factors, adult SVL as the dependent variable: interaction $F_{1,1111} = 58.89$, $p < 0.0001$).

The differences between the two locations (approximately 780 km apart) undoubtedly results from a series of factors. Climatic phenomena are probably responsible for the seasonal shifts in reproductive cyclicity, but the two areas differ in other ways as well. Most notably, the habitats from which the pythons are collected in northern Sumatra are highly disturbed by agricultural activities (especially, oil-palm and rubber plantations), whereas the area around Palembang contains massive tidal swamps that bear little evidence of anthropogenic degradation. The lower parasite numbers in northern Sumatran snakes (Table 3) might reflect the drier conditions and more restricted diets of the snakes in this region. The combination of lower parasite burdens and higher feeding frequencies in the Medan snakes (Table 3) might be expected to result in higher growth rates, and thus in larger body sizes and lower fat stores (because energy is allocated to growth rather than storage). These predictions are fulfilled for fatbody scores, for sizes at maturation in both sexes, and for mean adult body size in males (Table 3). However, very large female pythons are notably absent from the Medan sample (Fig. 2).

The scarcity of very large female pythons from northern Sumatra is one of the most intriguing results from our study. The less disturbed southern region presumably contains a greater diversity and abundance of large mammals (the main prey for very large reticulated pythons in this area: Shine et al., 1998b) whereas the Medan area has very high abundances of commensal rodents. This geographic difference in habitat types and prey availability fits well with the observation that the Medan snakes feed primarily on commensal prey items, whereas the Palembang snakes take a wider range of non-commensal mammals (Table 3). The scarcity of very large female pythons in the Medan samples also fits with this interpretation. Such snakes might either be genuinely rare in northern Sumatra (because of the scarcity of suitable habitat and prey), or else occur but (because they are restricted to less disturbed areas) be less likely to be encountered and captured by humans. Very large specimens may be relatively scarce in other natural python populations also (Bhupathy, 1990).

We speculate that the high levels of anthropogenic habitat disturbance in northern Sumatra have disadvantaged very large pythons, but considerably advantaged any python small enough to live in disturbed areas and feed on rats. Even large reticulated pythons in the Medan area feed almost entirely on rats, whereas same-sized conspecifics in southern Sumatra shift to larger mammals (Shine et al., 1998b). Also, two smaller congeneric python species that feed almost entirely on commensal rats (*P. curtus* and *P. brongersmai*) are more abundant in northern than southern Sumatra (e.g. Groombridge and Luxmoore, 1991; David and Vogel, 1996). We thus infer that the harvest of reticulated pythons in northern Sumatra is focussed on relatively young snakes (mostly close to the size and age at maturity) from anthropogenically modified habitats, whereas the harvest in southern Sumatra is based on pythons of a wider range of sizes and ages, coming from natural swamps as well as disturbed habitats.

Our study also provides a cautionary tale about the dangers of extrapolating from limited data on captive animals, when attempting to infer the impacts of harvesting on wild populations. By far the most comprehensive and authoritative analysis of the Asian python harvest is that by Groombridge and Luxmoore (1991). These authors assembled an enormous data set on the attributes of the harvest, but found it difficult to translate this information into ecological terms because of the very sparse data on critical traits such as sizes at maturation and average clutch sizes. Our study shows that their caution was well warranted. Available estimates of sizes at maturity from captive animals (3 to 3.5 m) suggested that the commercial harvest was focussed on juvenile snakes, whereas this is clearly not true (e.g. from Table 3, $<20\%$ of the slaughtered male pythons were juveniles). Similarly, their putative "average clutch size" of 48 eggs was based on large wellfed captives, and is about twice as high as the real average (Table 3). The same problems arose in inferring these traits in varanid lizards (Groombridge and Luxmoore, 1991; Shine et al., 1996). The problems are exacerbated by considerable variation in both traits; for example, sizes at maturation differ considerably between pythons from northern versus southern Sumatra (Table 3) and vary strongly among individual snakes (Fig. 2). The frequency of reproduction of adult females may be one of the most crucial variables determining the ability of the python population to withstand high offtake levels, but again the story is complex. Reproductive frequencies shift with maternal body size in reticulated pythons (Shine et al., 1998a), so that changes in female size distributions (as between Palembang and Medan) are likely to influence reproductive frequencies as well.

What, then, can we conclude about the sustainability of the commercial harvest of reticulated pythons in Sumatra? We cannot make any quantitative recommendations on harvest quotas, but our results support Groombridge and Luxmoore's (1991) conclusion that the commercial skin trade is unlikely to result in the extirpation of reticulated pythons from their Indonesian range. Undoubtedly, the large numbers of animals taken for the skin trade depress local abundances of pythons, and might eliminate these animals from small sections of highly fragmented habitats. The central issue in terms of sustainability of the trade, however, does not involve the possibility of extinction. Instead, it concerns the role of pythons as predators of commensal rodents (e.g. Lim, 1974). If pythons do indeed help to reduce rodent numbers, then the economic benefits of the snake harvest need to be offset against the costs of increased rodent damage to crops and food stores.

The conclusion that reticulated python populations are able to resist intensive commercial exploitation will be strongly counter-intuitive to many professional herpetologists, especially those whose primary expertise lies with the biology of temperate-zone species. Large snakes in temperate-zone habitats are characterised by slow growth rates, late maturation, high adult survival rates and low reproductive output (e.g. Parker and Plummer, 1987), and hence may be vulnerable to additional mortality due to human activities (e.g. Campbell et al., 1989; Brown, 1991). In contrast, reticulated pythons display a very different suite of life-history traits involving rapid growth, early maturation, and relatively high reproductive output (i.e. infrequent production of large clutches of large eggs). These animals also tolerate severe habitat degradation, and thrive even in highly disturbed landscapes in the suburbs of large cities (e.g. Wall, 1926; Smith, 1943; Pope, 1975; David and Vogel, 1996; Cox, 1997).

How can such large snakes survive in close proximity to urban centres? Some local people leave the pythons unmolested because of their value as controllers of rodents (e.g. Groombridge and Luxmoore, 1991), but it is likely that many pythons simply escape detection. This ability reflects both the climate of Sumatra, and the foraging biology of the snakes. Unlike many temperate-zone snakes, tropical pythons rarely need to move about (and thus, expose themselves to collectors) because of thermoregulatory concerns (e.g. Shine and Madsen, 1996). This fact probably contributes to the low frequency of large female pythons in our samples. Reproductive females of many cool-climate snake species bask frequently, and hence may be disproportionately vulnerable to human predators (e.g. Peterson et al., 1993). Similarly, one of the other primary reasons for overt activity (foraging) is inapplicable to these well-camouflaged ambush predators (Mushinsky, 1987).

The harvested population of reticulated pythons (especially in disturbed areas such as those near Medan) may consist primarily of relatively young animals. Their ability to thrive in highly modified habitats, feeding on commensal rodents and domestic chickens, means that the abundance of this species may well have increased rather than decreased due to human activities. The same situation has been documented in large pythons inhabiting agricultural and suburban landscapes in subtropical eastern Australia (Slip and Shine, 1988; Shine and Fitzgerald, 1996). Far more information will be needed before we can confidently assess sustainable levels of offtake of Indonesian pythons; detailed monitoring of the numbers and sizes of snakes taken for the commercial trade would be the first step towards developing quantitiative estimates. One certainty, however, is that we will need to shed our temperate-zone preconceptions before we can truly grasp the dynamics of this situation.

Acknowledgements

We thank the Asia-Pacific Science Foundation and the Australian Research Council for financial support. The work would not have been possible without the cooperation of the Indonesian Reptile and Amphibian Traders Association (IRATA), especially Mr. George Saputra, and of the skin-traders at whose premises we worked (Mr. Alian Ruswan, Mr. Sukoso, Mr. Sudirman, Mr. Acai and Mr. Supri).

References

Arakawa, H., 1969. Climates of Northern and Eastern Asia. Elsevier Publishing, Amsterdam.

Brown, W.S., 1991. Female reproductive ecology in a northern population of the timber rattlesnake, *Crotalus horridus*. Herpetologica 47, 101–115.

Bhupathy, S., 1990. Blotch structure in individual identification of the Indian python *Python molurus molurus* Linn. and its possible usage in population estimation. J. Bombay. Nat. Hist. Soc. 91, 399–404.

Campbell, J.A., Formanowicz, D.R., Brodie, E.D.J., 1989. Potential impact of rattlesnake roundups on natural populations. Texas J. Sci. 41, 301–317.

Choquenot, D., 1996. The ecological basis of wildlife harvesting. In: Bomford, M., Caughley, J. (Eds.), Sustainable use of wildlife by Aboriginal peoples and Torres Strait Islanders. Australian Government Printing Service, Canberra, pp. 48–59.

Cox, M.J., 1997. Reticulate pythons (*Python reticulatus*) in Bangkok. Reptile and Amph. Mag. 46, 20–24.

David, P., Vogel, G., 1996. The Snakes of Sumatra. Edition Chimaira, Frankfurt.

Grigg, G.C., 1995. Sustainable use of wildlife: a new direction in conservation In: Grigg, G., Hale, P., Lunney, D. (Eds.), Conservation through Sustainable Use of wildlife. Centre for Conservation Biology, University of Queensland, Brisbane, pp. 3–5.

Groombridge, B., Luxmoore, R., 1991. Pythons in south-east Asia. A review of distribution, status and trade in three selected species. Report to CITES Secretariat, Laussane, Switzerland.

James, C., Shine, R., 1985. The seasonal timing of reproduction: a tropical–temperate comparison in Australian lizards. Oecologia 67, 464–474.

Jenkins, M., Broad, S., 1994. International Trade in Reptile Skins: a Review and Analysis of the Main Consumer Markets, 1983–91. TRAFFIC International, Cambridge, UK.

King, M., 1995. Fisheries Biology, Assessment and Management. Fishing News Books, Oxford.

Lim, B.L., 1974. Snakes as natural predators of rats in an oil palm estate. Malay Nat. J. 27, 114–117.

Lim, F.L.K., 1976. The reticulated python. Nature Malaysiana 6, 14–17.

Mushinsky, H.R., 1987. Foraging ecology. In: Seigel, R.A., Ford, N.B., Novak, S.S. (Eds.), Snakes: ecology and evolutionary biology. Macmillan, New York, pp. 302–304.

Parker, W.S., Plummer, M.V., 1987. Population ecology. In: Seigel, R.A., Ford, N.B., Novak, S.S. (Eds.), Snakes: ecology and evolutionary biology. Macmillan, New York, pp. 253–301.

Peterson, C.R., Gibson, A.R., Dorcas, M.E., 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. In: Seigel, R.A., Collins, J.T. (Eds.), Snakes: ecology and behavior. McGraw-Hill, New York, pp. 241–314.

Pope, C.H., 1975. The Giant Snakes. Alfred A. Knopf, New York.

Roberts, C., 1997. Ecological advice for the global fisheries crisis. Trends Ecol. and Evol. 12, 35–38.

Roth, H.H., Mertz, G., 1997. Wildlife Resources. A Global Account of Economic Use. Springer, Berlin.

Rothschild, B.J., 1983. Achievement of fisheries management goals in the 1980's. In: Rothschild, B.J. (Ed.), Global Fisheries. Perspectives for the 1980's. Springer-Verlag, New York, pp. 151–77.

Shine, R., 1993. Ecological studies on Australian pythons. In: Uricheck, M. (Ed.), Proceedings of the Fifteenth International Herpetological Symposium. International Herpetological Symposium Inc., Seattle, Washington, pp. 29–40.

Shine, R., Fitzgerald, M., 1996. Large snakes in a mosaic rural landscape: the ecology of carpet pythons, *Morelia spilota* (Serpentes:

Pythonidae) in coastal eastern Australia. Biological Conservation 76, 113–122.

Shine, R., Madsen, T., 1996. Is thermoregulation unimportant for most reptiles? An example using water pythons (*Liasis fuscus*) in tropical Australia. Physiol. Zool. 69, 252–269.

Shine, R., Harlow, P.S., Keogh, J.S., Boeadi, 1996. Commercial harvesting of giant lizards: the biology of water monitors, *Varanus salvator*, in southern Sumatra. Biological Conservation, **77**, 125–34.

Shine, R., Harlow, P.S., Keogh, J.S., Boeadi, 1998a. The allometry of life-history traits: insights from a study of giant snakes (*Python reticulatus*). J. Zool. (London), 244, 405–414.

Shine, R., Harlow, P.S., Keogh, J.S., Boeadi, 1998b. The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*. Funct. Ecol., 12, 248–258.

Slip, D.J., Shine, R., 1988. Habitat use, movements and activity patterns of free-ranging diamond pythons, *Morelia s. spilota* (Serpentes: Boidae): a radiotelemetric study. Aust. Wildl. Res. 15, 515–531.

Smith, M.A., 1943. The Fauna of British India, Ceylon and Burma including the Whole of the Indo-Chinese Sub-region. Reptilia and Amphibia. Volume III—Serpentes. Taylor and Francis, London.

Wall, F., 1926. The reticulate python *Python reticulatus* (Schneider). J. Bombay Nat. Hist. Soc. 31, 84–90.