

Ecological Attributes of Two Commercially-harvested Python Species in Northern Sumatra

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ABSTRACT.—Examination of specimens collected for the international leather trade provided data on two species of large, heavy-bodied snakes: blood pythons (*Python brongersmai*) from northeastern Sumatra and short-tailed pythons (*P. curtus*) from northwestern Sumatra. Measurement and dissection of 2063 *P. brongersmai* and 181 *P. curtus* revealed broad interspecific similarities in morphology (size, shape, sexual dimorphism), food habits (feeding frequencies, dietary composition) and reproductive output (reproductive frequencies, egg sizes, and clutch sizes). Females of both species attain larger sizes than males, mature at larger sizes, and contain larger abdominal fatbodies. *Python curtus* is more heavy-bodied and longer-tailed than *P. brongersmai*, and more heavily infested with gut parasites. Both species feed almost exclusively on commensal rodents. Feeding rates increase with body size, and vary seasonally. Reproduction is highly seasonal. Adult females reproduce biennially, producing an average clutch of 12 to 16 large (mean = 83 to 90 g) eggs. The data also enable us to comment on the sustainability of the existing commercial trade, which is based mainly on adult males, and adult plus juvenile females. Anthropogenic habitat modification (especially, the establishment of oil-palm plantations) has increased the abundance of these taxa. Although neither species is likely to be extirpated by current levels of offtake, we need additional information to evaluate long-term sustainability of the commercial industry based on these snakes.

The slaughter of wild-caught animals to provide skins, meat, and medicinal products supports a vast commercial trade (e.g., Fitzgerald et al., 1991; Klemens and Thorbjarnarson, 1995; Roth and Mertz, 1997). Although traditional harvesting of such resources has been going on for a long time, recent years have seen a rapid expansion of the trade in some products. At the same time, many people have questioned the ecological sustainability of high levels of commercial utilisation of wildlife (e.g., Groombridge and Luxmoore, 1991; Green and King, 1993). Unfortunately, we know so little about the underlying biology of most of the harvested systems that it is difficult to evaluate the degree to which current offtake levels will threaten population viability. Optimal sustained yield has proven difficult to determine even in systems that facilitate accurate counts, such as large mammalian herbivores in semiarid rangelands (e.g., Grigg, 1995). The problem is exacerbated in the case of poorly-known taxa (such as most reptiles) living in poorly-known regions (such as tropical forests). Until recently, the ecology of tropical reptiles has attracted very little study, despite the fact that several of these taxa are heavily exploited for their skins and meat (Groombridge and Luxmoore, 1991; Jenkins and

Broad, 1994; Klemens and Thorbjarnarson, 1995).

The dearth of information on the ecology of tropical reptiles has meant that speculations on the sustainability of the commercial trade in these animals have been based upon extrapolation from better-studied temperate-zone taxa. The potential errors involved in this approach are obvious. Climatic conditions profoundly modify many life-history characteristics of reptiles, including traits that influence a population's capacity to withstand intense harvesting (e.g., age at maturity, reproductive frequency; Fitch, 1982; James and Shine, 1985, 1988). Also, the tropics contain many reptilian lineages not represented in the temperate-zone, so that ecological inferences about the tropical fauna must be based on extrapolation from distantly-related taxa.

The urgent need for information on the harvested reptilian taxa has stimulated a rapid increase in studies on some of these species. The main focus has involved crocodylians (e.g., Webb et al., 1982, 1983, 1987; Webb and Smith, 1984) and marine turtles (e.g., Frazer and Ehrhart, 1985), but squamate reptiles have increasingly been considered also (e.g., Fitch et al., 1982; Norman, 1987). Examining specimens harvested for the commercial trade is a rapid, cost-effective way to clarify biological attributes of harvested squamates (e.g., Fitzgerald et al., 1993; Sloan et al., 1996). Most studies on commercially-har-

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vested snakes have focussed on "rattlesnake round-ups" in North America (e.g., Campbell et al., 1989; Warwick et al., 1991; Brown, 1993), but in recent years the much larger trade in Asian snakes and lizards has also attracted study. Examination of freshly-slaughtered specimens has provided biological data on most of the major taxa involved in the Asian reptile-skin trade: water monitors (Shine et al., 1996), filesnakes (Shine et al., 1995), reticulated pythons (Shine et al., 1998b, c), spitting cobras and ratsnakes (Boeadi et al., 1998). Recent reviews identify one other taxon as being the subject of major trade: approximately 200,000 *Python curtus* are taken from the wild every year to be killed for their skins (Groombridge and Luxmoore, 1991; Jenkins and Broad, 1994).

In the course of our studies on "*Python curtus*" harvested in northern Sumatra, we discovered that there are actually two distinct taxa involved in the commercial trade. DNA sequence divergence suggests that the two Sumatran "subspecies" (*P. curtus curtus* and *P. curtus brongersmai*) warrant recognition as separate species (Keogh et al., in prep.). This discovery may have important implications for the sustainability of the commercial harvest, because two distinct genetic entities are involved. In the present paper, we describe the biological attributes of harvested specimens. The information is of interest in its own right (because so little is known about the ecology of tropical snakes), and also provides the first empirical basis upon which to speculate on sustainability of the commercial trade.

MATERIALS AND METHODS

Study Species.—Both *P. brongersmai* and *P. curtus* are large (to 2.5 m) and extremely heavy-bodied (to 15 kg) nonvenomous snakes. They differ in geographic distribution, body sizes, scale characters, and coloration (Keogh et al., in prep.). The blood python (*P. brongersmai*) of eastern Sumatra and Malaysia is highly variable in dorsal colour, with red, yellow, brown, and orange morphs (Barker and Barker, 1996; Shine et al., 1998d). In contrast, the short-tailed python (*P. curtus*) has a disjunct distribution in western Sumatra and Kalimantan, and is dark brown or black in dorsal colour throughout its Sumatran range (David and Vogel, 1996; Erdelen, 1998).

Study Area and Methods.—We visited four locations in northern Sumatra (Medan, 3°35'N 98°39'E; Seisuka, 3°25'N 99°27'E; Rantauprapat, 2°05'N 99°46'E; Cikampak, 1°43'N 100°15'E) on each of four trips. The trips were evenly-spaced throughout the year (March, June, August, December), to provide information on the seasonality of ecological processes in these tropical snakes. The climate in this area is characterised

by consistently high mean temperatures (all months have mean temperatures >26°C: Arakawa, 1969) and high rainfall (mean annual precipitation >2000 mm: Arakawa, 1969). We also examined a small sample of *P. brongersmai* in southern Sumatra, at slaughterhouses in the city of Palembang.

We weighed and measured the snakes immediately after they were killed, and then dissected the freshly-skinned bodies to quantify aspects such as food habits and reproductive biology. Sex was determined by visual inspection of the gonads, and we recorded testis sizes in males, and the number and diameters of oviductal eggs, vitellogenic ovarian follicles, and corpora lutea in adult females. Males were scored as adult if they had large turgid testes and/or opaque, thickened efferent ducts. Females were classed as mature if they had thickened muscular oviducts, vitellogenic follicles (>10 mm diameter), corpora lutea, or oviductal eggs. Testicular volumes were calculated from linear dimensions, using the equation for volume of an ellipsoid (James and Shine, 1985).

Prey items in the alimentary tract (usually, faecal material from the rectum) were removed. Some of these samples were later examined microscopically to identify prey species using fur characteristics, in conjunction with a reference collection of fur from all of the common Sumatran mammal species (see Shine et al., 1998c, for further details). Abdominal fat bodies were scored on a four-point scale to provide an index of energy stores. Ascarid nematodes in the stomach were counted to provide an index of parasite burdens.

RESULTS

Collection and Processing of Snakes.—Pythons are collected in various parts of northern Sumatra, and are transported alive to the slaughterhouses. We could not pinpoint the origin of most specimens, but the two species clearly came from different areas. Short-tailed pythons (*P. curtus*) came from western Sumatra, with many from near the town of Sibolga. Shipments of this species arrived by truck, often in substantial numbers. In contrast, most of the blood pythons (*P. brongersmai*) came from oil-palm plantations near the slaughterhouses, and were often brought in (as single snakes or in small numbers) by the people who had caught them. These snakes had been captured serendipitously, usually in the oil-palm plantations. We saw no evidence of people actually setting out to capture these taxa, in the way that they sometimes do for reticulated pythons (Shine et al., 1998a). The two species were treated in the same way after arrival, and were eventually killed and processed in the same ways as we

have described for other harvested reptiles (Shine et al., 1995, 1996, 1998a).

Relative Abundances.—In the course of three trips to slaughterhouses in Palembang, southern Sumatra, we obtained data on only 35 *P. brongersmai* and no *P. curtus* (versus 1070 *P. reticulatus*, 101 *Acrochordus javanicus*, and 166 *Varanus salvator*). In contrast, these two python species constituted a high proportion of all the reptiles that we examined in slaughterhouses in northern Sumatra (2063 *P. brongersmai*, 181 *P. curtus*, versus 784 *P. reticulatus*, two *Acrochordus javanicus*, and 399 *Varanus salvator*).

Python brongersmai thus constituted a much larger proportion of the harvest than did *P. curtus* (92% versus 8%), and the latter species was not recorded at all in two of the four slaughterhouses that we visited (at Cikampak and Seisuka; versus 12.4% of the sample at Rantauprapat, and 21.7% at Medan). These differences among slaughterhouses in relative numbers of the two taxa are greater than would be expected by chance ($\chi^2 = 155.4$, 3 df, $P < 0.0001$). Additionally, the relative numbers of short-tailed pythons versus blood pythons varied among our four trips, even within the same slaughterhouse (for snakes from Rantauprapat, variation among trips $\chi^2 = 21.54$, 3 df, $P < 0.0001$; for Medan, $\chi^2 = 18.62$, 3 df, $P < 0.001$).

Age Structure and Sex Ratio of the Sample.—The two species were very similar in most respects. For example, most of the harvested snakes were adults rather than juveniles, and males slightly outnumbered females (see Table 1; pooled sample of all snakes examined, against a null hypothesis of 50% male: $\chi^2 = 4.82$, 1 df, $P < 0.05$). In both species, most of the males were adults (58% in *P. brongersmai*, 65% in *P. curtus*) whereas a high proportion of females were juvenile animals (9% in *P. brongersmai*, 21% in *P. curtus*; see Fig. 1, comparing proportions of adult animals between the two sexes in *P. brongersmai*, $\chi^2 = 252.1$, 1 df, $P < 0.0001$; in *P. curtus*, $\chi^2 = 16.5$, 1 df, $P < 0.0001$).

Body Sizes and Morphology.—Table 1 summarizes data on mean body sizes of the snakes. Females attain larger maximum sizes than males in both taxa and mature at larger sizes (Fig. 1). Blood pythons grow larger than short-tailed pythons, but the degree of sex divergence in body sizes is similar in the two taxa (a two-factor ANOVA with species and sex as the factors, and adult body size as the dependent variable, yielded a non-significant interaction term for both mass and snout-vent length). Body shapes differ between the two taxa also, with *P. curtus* being more heavy-bodied and (ironically, given its common name) longer-tailed than *P. brongersmai* of the same SVL (see Keogh et al.,

in prep. for further morphological comparisons between these taxa).

Fat Stores, Parasite Numbers, and Food Habits.—Female snakes contained larger fat-bodies than conspecific males, and blood pythons contained larger fat bodies than short-tailed pythons. A two-factor ANOVA (with species and sex as factors, and fat-body scores as the dependent variable) confirmed that these differences were greater than would be expected by chance, under the null hypothesis of equal fat stores regardless of sex or species (main effect of sex— $F_{1,1914} = 86.75$, $P < 0.0001$; main effect of species— $F_{1,1914} = 7.13$, $P < 0.01$; interaction $F_{1,1914} = 2.34$, $P = 0.13$). Parasite numbers were much higher in *P. curtus* than in *P. brongersmai* (Table 1), but did not differ between the sexes (sex effect $F_{1,1916} = 2.92$, $P = 0.09$ in a two-factor ANOVA).

Feeding habits were similar in the two species, with almost 95% of prey items consisting of rodents (Table 2). Microscopic analysis of a subsample of fur from python guts suggested that most of the rats taken by pythons were commensal species, especially ricefield rats (*Rattus argentiventer*) and wood rats (*R. tiomanicus*; see Table 2). The small sample of prey items from *P. brongersmai* in southern Sumatra (Palembang) provided a very similar picture; 20 of the 23 prey items we recorded were rodents (6 *Rattus argentiventer*, 3 *Leopoldamys sabanus*, 11 unidentified rats, 1 non-murid mammal, and 2 birds). The other species taken as prey constituted a diverse array of small native mammals, plus domestic chickens (Table 2).

Analysis detected no significant biases with respect to prey types as a function of either sex or body size (e.g., for *P. brongersmai*, non-rat prey constituted 7.2% of all prey items for females, and 7.0% of all items for males— $\chi^2 = 2.56$, 1 df, $P = 0.11$; for *P. curtus*, 7.3 versus 6.0%— $\chi^2 = 0.01$, 1 df, $P = 0.94$). Similarly, non-rodent prey were taken by small as well as large snakes.

The frequency of feeding, as judged by the proportion of snakes containing prey when killed, shows a complex pattern. This proportion increased with body size within both species (using Spearman rank correlation to test for an association between body length [in 5-cm SVL classes] and percent of snakes with prey: for *P. brongersmai*, $N = 17$ categories, $\rho = 0.51$, $P < 0.05$; for *P. curtus*, $N = 10$, $\rho = 0.95$, $P < 0.005$). The proportion of snakes containing food was higher in female than in male specimens of *P. brongersmai* ($\chi^2 = 9.55$, 1 df, $P < 0.002$), but not in *P. curtus* ($\chi^2 = 2.08$, 1 df, $P = 0.15$). Given the highly seasonal reproductive cycle of these snakes (see below), it seems likely that the sex difference in feeding frequency of *P. brongersmai* might be related to the seasonal timing of re-

TABLE 1. Morphological and ecological traits of adult blood pythons (*Python brongersmai*) and short-tailed pythons (*R. curtus*) from northern Sumatra. Table shows mean values (SD in parentheses), and the results of statistical tests of the null hypothesis of no significant differences between species in the trait of interest. F ratios are derived from one-factor ANOVAs (with species as the factor), and χ^2 values from contingency tables. N = sample size; note that sample sizes differ among traits (e.g., because alimentary tracts of some snakes had been flushed with water and so we could not determine whether or not they had contained prey). The proportions of adult females that were reproductive are based only on trips in August and December, when reproductive condition could be established most reliably.

Trait	<i>Python brongersmai</i>	<i>Python curtus</i>	Statistical test
Adult males			
N	1037	99	
Snout-vent length (cm)	132.4 (11.95)	120.7 (10.09)	$F_{1,1134} = 88.87, P < 0.0001$
Body mass (kg)	3.59 (1.01)	2.99 (0.78)	$F_{1,1110} = 31.77, P < 0.0001$
Fatbody scores	0.69 (0.90)	0.36 (0.56)	$F_{1,1134} = 12.63, P < 0.001$
Parasite numbers	0.007 (0.13)	0.62 (3.33)	$F_{1,1131} = 34.77, P < 0.0001$
Adult females			
N	732	54	
Snout-vent length (cm)	143.9 (11.82)	130.06 (7.35)	$F_{1,784} = 71.97, P < 0.0001$
Body mass (kg)	4.66 (1.50)	3.85 (0.92)	$F_{1,766} = 15.20, P < 0.0001$
Fatbody scores	1.30 (0.89)	1.21 (0.89)	$F_{1,780} = 0.49, P = 0.48$
Parasite numbers	0.06 (1.05)	0.93 (3.89)	$F_{1,784} = 18.65, P < 0.0001$
Characteristics of harvested pythons			
Proportion of juvenile snakes:	0.143	0.155	$\chi^2 = 0.11, 1 \text{ df}, P = 0.74$
Sex ratio (% male)	51.5%	58.1%	$\chi^2 = 2.55, 1 \text{ df}, P = 0.11$
Proportion of snakes containing prey			
Proportion with prey	78.2%	84.6%	$\chi^2 = 1.67, 1 \text{ df}, P = 0.20$
Number of records of each major prey type			
Rats	1296	127	
Other prey	114	8	$\chi^2 = 0.52, 1 \text{ df}, P = 0.46$
Reproductive output			
Clutch size:			
N of clutches	143	15	
Mean (SD)	15.58 (4.26)	12.47 (2.50)	$F_{1,156} = 7.70, P < 0.007$
Egg mass (g)			
N of clutches	30	4	
Mean (SD)	83.28 (20.35)	89.70 (13.66)	$F_{1,32} = 0.37, P = 0.55$
Proportion of adult females reproductive in August and December samples			
N	334	25	
Proportion reproducing	51.2%	48.0%	$\chi^2 = 0.01, 1 \text{ df}, P = 0.92$

productive activities (e.g., cessation of feeding by courting males: Shine and Madsen, 1997). In keeping with this hypothesis, the data reveal strong seasonal differences in feeding rates (proportion with prey) in both sexes of *P. brongersmai* (males—samples in the four trips range from 39 to 88% with prey, $\chi^2 = 231.7, 3 \text{ df}, P < 0.0001$; females, range from 45 to 87%, $\chi^2 = 148.3, 3 \text{ df}, P < 0.0001$). Less seasonal variation in feeding rates was evident within *P. curtus* (males—range from 67 to 75% with prey, $\chi^2 = 0.25, 3 \text{ df}, P = 0.97$; females, range from 75 to 100%, $\chi^2 = 33.95, 3 \text{ df}, P = 0.27$). Thus, the pro-

portions of snakes containing prey items suggest that feeding frequencies were consistently high in *P. curtus*, but varied between the sexes, and among seasons, in *P. brongersmai*.

Reproductive Biology.—Reproduction is highly seasonal in both species, with oviposition around April–May. Testicular volumes increased with male body mass within each species, and showed significant variation among trips ($F_{3,1139} = 4.20, P < 0.006$). Testes of both species were larger during December than during the other trips. The relationship between testis size and body mass differed between the

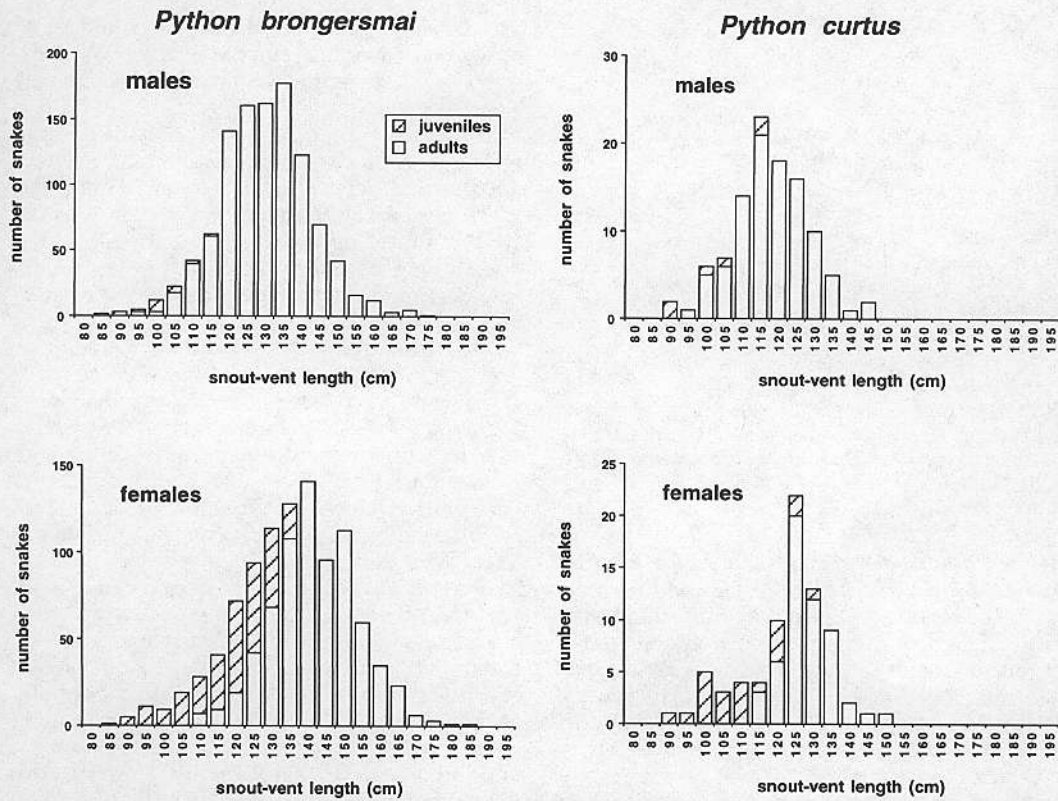


FIG. 1. Frequency distributions of body sizes (snout-vent lengths) in the two python species, as a function of sex and reproductive status. *Python brongersmai* grow larger than *P. curtus*, but general patterns (sexual size dimorphism, and relative numbers of juveniles and adults within each sex) were similar in the two species.

two species of pythons, with the testes of *P. brongersmai* significantly larger (relative to body mass) than those of *P. curtus* on two of the four trips (from one-factor ANCOVAs with species as the factor, body mass as the covariate, and tes-

ticular volume as the dependent variable, $P < 0.002$ in both August and December). The same trend was evident, but did not attain statistical significance, on the two other trips.

Mean egg sizes were similar in the two spe-

TABLE 2. Prey items identified from the alimentary tracts of blood pythons (*Python brongersmai*) and short-tailed pythons (*P. curtus*) from northern Sumatra. These items represent the subsample of items which we identified by microscopic analysis; other samples were simply classified to Family level.

Common name	Scientific name	Number in <i>P. curtus</i>	Number in <i>P. brongersmai</i>
Wood rat	<i>Rattus tiomanicus</i>	24	126
Rice-field rat	<i>R. argentiventer</i>	18	152
Norway rat	<i>R. norvegicus</i>	3	9
Polynesian rat	<i>R. exulans</i>	1	2
Long-tailed rat	<i>Leopoldamys sabanus</i>	1	12
Spiny rat	<i>Maxomys rajah</i>	1	9
Slow loris	<i>Nycticebus coucang</i>	0	1
Banded civet	<i>Hemigalus debryanus</i>	0	3
Striped civet	<i>Arctogalidia trivirgata</i>	1	2
Tree shrew	<i>Tupaia javanica</i>	0	6
Yellow-throated marten	<i>Martes flavigula</i>	0	3
Domestic chicken	<i>Gallus gallus</i>	0	18
Total		49	343

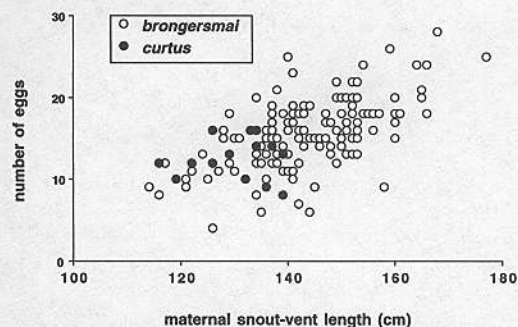


FIG. 2. Clutch sizes relative to maternal body size in the blood python (*Python brongersmai*) and the short-tailed python (*P. curtus*). Mean body sizes and mean clutch sizes differed between the species, but the relationship between these two variables was similar in both species.

cies, but clutch sizes were smaller in *P. curtus* than in *P. brongersmai* (Table 1). Given the smaller body sizes of the former species, this fecundity difference might well be a simple consequence of the body-size difference, rather than reflecting any divergence in reproductive output relative to body size. Analysis of covariance confirmed this interpretation (with species as the factor, maternal snout-vent length as the covariate, and clutch size as the dependent variable: slopes $F_{1,153} = 2.88$, $P = 0.09$; intercepts $F_{1,154} = 0.01$, $P = 0.91$; see Fig. 2). The frequency of reproduction in females is best evaluated from the samples taken in August and December, prior to oviposition. Approximately half of the adult-sized females were reproductive at this time of year, suggesting a biennial cycle in females of both species (Table 1).

DISCUSSION

Our study provides the first quantitative data on ecological attributes of these two python species. Previous information has been based on relatively small numbers of captive animals, plus anecdotal reports from faunal guides and taxonomic treatments (e.g., Barker and Barker, 1996; David and Vogel, 1996). In a companion paper to this one, we have used data from the same study to investigate ecological divergence between four different colour morphs within *Python brongersmai* (Shine et al., 1998d). *Python curtus* is substantially smaller than any of the morphs of *P. brongersmai* (mean adult SVL for the smallest morph [yellow] = 126.8 cm for males, 138.3 cm for females: Shine et al., submitted). Thus, the overall situation is that this lineage comprises several morphologically distinctive groups, differing in ecological traits as well as in geographic distribution and body sizes. However, the differences are relatively mi-

nor: for example, all of these snakes are large, heavy-bodied ambush predators that feed mostly on rats and reproduce on an approximately biennial cycle.

In the absence of field data, it is difficult to interpret most of the differences that we have documented between *P. brongersmai* and *P. curtus*. For example, the temporal variation in relative numbers of each taxon at the slaughterhouses might reflect either attributes of the snakes (e.g., different activity patterns) or attributes of the collectors (e.g., schedule of trips by trucks from the west coast to the slaughterhouses). Similarly, even for characteristics that clearly reflect underlying biological divergence (e.g., body sizes and shapes, seasonal differences in feeding rates, levels of parasite infestation), we do not know which of these differences reflect underlying genetic divergence, and which are induced by local conditions (e.g., habitat differences). Additionally, because collecting effort is also likely to be focussed more on certain habitats than on others, our sample may provide a biased view of traits such as age and size distributions, food habits, and the like. Nonetheless, such problems will occur with almost any sampling regime, especially when one is dealing with cryptic sedentary animals that are virtually impossible to find when they are inactive (e.g., Reinert, 1984; Weatherhead and Charland, 1985). The compensating advantage from the technique we have used is that much larger sample sizes can be obtained than is usually the case with ecological studies on snakes. These large samples provide a much stronger basis for any conclusions.

How does the biology of these two taxa compare with that of other giant tropical snakes? The only other snake for which comparable data are available is the reticulated python, a much larger species that is broadly sympatric with both *P. brongersmai* and *P. curtus* over much of Sumatra (e.g., David and Vogel, 1996). Nonetheless, syntopy is rare: *P. reticulatus* appears to be uncommon in the oil-palm plantations that contain most of the smaller pythons (Abel, 1998). The trophic biology of juvenile reticulated pythons is similar to that of the other two taxa, specialising on commensal rodents living in disturbed habitats (Shine et al., 1998c). Feeding frequencies increase with body size in all three python species, but are lower overall in reticulated pythons (<50% of snakes contain prey: Shine, 1998c), and the dietary habits of reticulated pythons shift substantially at larger body sizes (Shine et al., 1998c). Thus, very large reticulated pythons feed mostly on large mammals (such as pangolins, mouse deer, wild pigs, monkeys, etc.), presumably in primary forest rather in anthropogenically disturbed habitats (Shine et al.,

1998c). The smaller python species never attain a size large enough to ingest these kinds of prey, and are rarely collected in more pristine habitats where these prey are available. The massive body sizes of reticulated pythons also result in larger clutch sizes, larger eggs, and a lower reproductive frequency than in the smaller species (Shine et al., 1998b).

The association of blood pythons with oil-palm plantations is a particularly interesting aspect of the biology of this species. The skin-traders told us that *P. brongersmai* was a relatively uncommon animal in the Medan region before a rapid increase in the area planted for oil-palm plantations occurred 10 to 20 yr ago. With the profits from palm-oil plantations continuing to increase since that time, both forests and rubber plantations continue to be cleared and converted to palm-oil. Today, a huge area in Sumatra is under palm-oil cultivation. The net effect of this habitat modification, in terms of the commercial reptile trade, has been a steady increase in the abundance of blood pythons and a simultaneous decrease in the numbers of reticulated pythons (Sudirman, pers. comm.). In many ways, these plantations offer ideal habitat for predator like *P. brongersmai*. Rat densities are extraordinarily high (to >400/ha—Wood and Liau, 1978; Stuebing and Gasis, 1989), and suitable cover is abundant (piles of dead palm fronds are stacked in rows between the standing trees; pers. obs.). Although ambush predation is often associated with relatively low rates of food intake (e.g., Shine, 1980; Secor and Nagy, 1994), the high proportion of snakes containing prey remains (>75%; see Table 1) suggests that the snakes have frequent opportunities to feed (and see Lim, 1974).

The ability of these heavy-bodied ambush predators to exploit commensal rodents in highly disturbed agricultural habitats, has a strong parallel in an Australian python species. Carpet pythons (*Morelia spilota*) are large (to 4 m, 10 kg) ambush predators that are abundant in macadamia plantations, utilizing corridors of dense vegetation and feeding primarily on commensal rodents (Shine and Fitzgerald, 1996). Well-camouflaged sedentary predators are able to exploit the artificially increased rodent availability in such areas, because they can escape the attention of farm-workers. This is likely to be especially true in the tropics, because the snakes do not need to leave cover for thermoregulatory reasons (e.g., Shine and Madsen, 1996). Although the population densities of rodents in oil-palm plantations may be higher and more stable than in most natural habitats, the situation is not necessarily "artificial": some natural habitats contain very high rodent abundances, and pythons can sustain remarkably high pop-

ulation densities in such areas (e.g., Shine and Madsen, 1997).

The success of *P. brongersmai* in anthropogenically disturbed areas—habitats that are becoming a more and more common component of the landscape—has obvious implications for the sustainability of the commercial harvest. Although we have no reliable information on the habitat types from which *P. curtus* is collected, the similarity between the two python species in dietary composition (Table 2) suggests a strong similarity in habitats as well. More generally, the strong ecological similarity between the two taxa suggests that they are likely to respond to anthropogenic offtake in similar ways.

Clearly, future management plans for the skin industry should incorporate the fact that the exploitation is based on two genetically distinct entities rather than just one, but the impact on management practices is likely to be small. Many commercially exploited "species" are actually composites of several closely-related taxa, and fisheries biologists have developed several methods to deal with this complication (e.g., King, 1995). Given the disjunct distributions of the two taxa, and the fact that skins can be identified to species levels by the difference in ventral scale counts even after tanning (e.g., Barker and Barker, 1996), it may be useful for managers to keep a track of relative numbers of each taxon that are being taken from the wild. This monitoring would provide information on the relative harvesting intensity in eastern versus western Sumatra, as well as enabling regular checks of the size-frequency distributions of the harvested populations (e.g., Fitzgerald et al., 1991; Fitzgerald, 1994).

How sustainable, then, is the current commercial trade? The question cannot be answered with confidence from our data; we would need to have far more comprehensive information on the rates of exploitation, and also on rates of habitat change (because the shift to palm-oil plantations appears to advantage these taxa). Nonetheless, a partial answer is possible. The clear implication from our results is that populations of *P. curtus* and *P. brongersmai* are able to tolerate high levels of offtake. This is a surprising conclusion, given the massive volume of trade in skins and (to a much smaller degree) in live animals for the pet trade. Because these taxa are able to utilize the abundant food resources available in anthropogenically modified habitats, their populations continue to persist despite intense harvesting. Presumably, removal of some snakes simply increases food resources (and thus, rates of survival, growth and reproduction) of the remaining animals. Although the long-term maintenance of viable populations is unlikely to be threatened by the existing com-

mercial trade, several caveats attach to this conclusion. For example, it may no longer hold true if changes to agricultural practices modify the plantation habitats in ways that reduce food availability or shelter for the snakes. Shifts to "broad-acre" farming practices in some temperate-zone systems have profoundly affected wildlife populations, by removing shelter sites and reducing habitat heterogeneity (e.g., Shine and Fitzgerald, 1996). More effective rodent control could have the same impact. More generally, the predator-prey interactions between the pythons and rodents warrant additional study. We do not know if python predation significantly affects rodent numbers; if it does (even if only in certain places, at certain times), then the economic and ecological impact of python removal on the oil-palm industry may be greater than it appears. We also need much more information on the biological attributes of the harvested taxa, such as age to maturity and responses to stochastic environmental fluctuations (Fitzgerald, 1994). Unfortunately, the dearth of research on tropical reptiles means that such topics are likely to remain unstudied for many years to come.

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