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COMMERCIAL HARVESTING OF GIANT LIZARDS: THE BIOLOGY OF WATER MONITORS *Varanus salvator* IN SOUTHERN SUMATRA

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Abstract

The Asian water monitor Varanus salvator *is the second-largest lizard species in the world (to > 1 m SVL, 2·5 m total, 20 kg), and is heavily exploited (> 1 million skins per annum). In the course of three trips between August 1993 and April 1995, we gathered information on 166 water monitors captured in southern Sumatra for the commercial skin trade. Relatively equal numbers of males and females were captured, but the males were almost all adults whereas half of the females were juveniles. Sex ratios and body sizes did not vary significantly among the three trips. Males grow larger than females, but the largest animals are not used in the leather trade. Males mature at around 40 cm SVL (= 1 m total, 1 kg), and females at around 50 cm. Maturation thus occurs at a small proportion of maximum size, as is typical for large species of reptiles. Adult males are more heavy-bodied than females, and have longer tails, but fat stores did not differ between the sexes. Prey items included crustaceans, rats and other varanids, but most lizards were kept for so long prior to slaughter that the stomach was empty of food. All adult-size males had active gonads, but testes were larger in April than in October. All adult females in the August and April samples were reproductively active, but less activity was evident in October. The egg-laying season extends from April to October (at least), and most female water monitors in southern Sumatra produce multiple clutches each year. Larger females begin to breed earlier in the year than do smaller animals. Clutch sizes ranged from five to 22, and were positively correlated with maternal body size. We measured stretched and dried skins from processed lizards to establish a predictive equation linking lizard SVL to skin width. The persistence of water monitors in southern Sumatra, despite intense harvesting, reflects the*

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large area of suitable habitat with low human densities, combined with the monitors' ecological flexibility (in habitat and diets), their high reproductive rate (early maturation and frequent reproduction), and (perhaps) the concentration of commercial harvesting on adult males. At current levels, the commercial trade may extirpate varanids from local areas but will not drive the species to extinction. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

Throughout much of the tropics worldwide, giant lizards are a conspicuous component of the fauna and are heavily utilised by indigenous people. These lizards provide an important source of dietary protein and traditional medicine, and their skins are used for domestic and ceremonial purposes (e.g. Auffenberg, 1988, 1994). Such patterns of use have occurred for thousands of years (e.g Das, 1989; Green & King, 1993), and may well be sustainable indefinitely as long as human population densities remain low and there is no degradation of habitat quality. More recently, however, a major international trade in the skins of giant lizards has developed. The lizards are collected, killed and skinned in their country of origin, and the processed skins are then exported to other parts of the world to be fashioned into high-quality leathergoods (e.g. Luxmoore & Groombridge, 1990; Fitzgerald *et al.*, 1993). The sheer volume of this international trade is extraordinary. For example, Jenkins and Broad (1994) estimated that every year approximately 2·3 million varanid lizards are killed worldwide for the leather industry. The long-term sustainability of these high off-take levels has often been questioned, and local reductions in lizard numbers have been attributed to

over-collecting for this trade (Gaulke, 1992; Green & King, 1993). Nonetheless, the only thorough examination of such a system (*Tupinambis* lizards in South America) concluded that the trade is unlikely to exterminate the harvested species over most of its range (Fitzgerald *et al.*, 1993).

The potential impact of the international leather trade is particularly important in the case of the Asian water monitor *Varanus salvator* because this species is both the largest lizard in the leather trade, and the most heavily exploited species. Among the world's lizards, the only species that clearly attains a larger size than the water monitor is the Komodo dragon *V. komodoensis* (Taylor, 1963). Water monitors are widely distributed through Asia, from Sri Lanka in the west to the Philippines and Sulawesi in the east (Gaulke, 1991*b*), and are heavily exploited by humans over most of this range. A recent review identified Indonesia (especially Sumatra and Kalimantan) as the primary source for harvested specimens, and estimated that between 600,000 and 1·5 million lizards of this species are taken from the wild for the leather industry each year in Indonesia alone (Luxmoore & Groombridge, 1990). Research to document the basic biology of this species, as a first step in evaluating sustainable levels of harvesting, is thus an urgent priority (Luxmoore & Groombridge, 1990). Perhaps because of its massive size and its wide geographic distribution, there have been several studies on *V. salvator*. However, most have been based on small numbers of captive animals, or have been carried out in areas of the range (e.g. India, Philippines) with very different ecological characteristics (especially climates) than those in the area of most intensive commercial harvesting of this species. Considerable variation has already been documented among populations of *V. salvator* from different areas, in traits such as body sizes, morphology, colour, breeding seasonality and clutch sizes (e.g. Auffenberg, 1981; Gaulke, 1989). Thus, we need information on the biology of water monitors from the areas in which they are most heavily exploited. A pioneering study by Erdelen (1991) provided information on population densities, trapping methods of skin-collectors and general biology of *V. salvator* in southern Sumatra. Our study is based on the same area, and provides additional information on morphology, reproductive biology and commercial harvesting of Sumatran water monitors, with the aim of identifying and addressing issues relevant to long-term ecologically sustainable use of these lizards.

MATERIALS AND METHODS

We gathered data during three trips to the city of Palembang in southern Sumatra: 29 July–6 August 1993, 6–20 October 1994 and 3–19 April 1995. We spent most of each day at the commercial premises of P.D. Budiman Co., where live varanids (as well as

pythonid and acrochordid snakes) are brought to be killed and skinned (Fig. 1). The lizards are collected over a wide area and the area of origin of individual lizards could not be determined. As well as examining specimens at the Budiman skinning factory, we visited other skinners in Palembang and arranged for a small number of skinned carcasses from other premises to be brought to the Budiman factory so that we could examine those animals also. Additionally, we travelled to one of the areas (Sembilan River) from which varanids were harvested, to observe the techniques used in collection and processing of animals in the field.

At the skinning factory, we weighed and measured lizards as soon as they were killed, and then examined their bodies after skinning. We did not weigh lizards that had already been skinned, or that had their alimentary tracts pumped full of water prior to skinning. We measured snout-vent length (SVL), tail length (only for complete tails) and head length (along the lower jaw, from the tip of the snout to the posterior edge of the quadrate-articular projection). We recorded any prey items in the stomach, and removed such items for later analysis if we could not identify them at the time. We gave each lizard a 'fat body score' (an integer from 0 to 3) to represent the size of the inguinal fat bodies. The gonads were examined to determine sex and reproductive condition. Males were scored as mature if they had enlarged turgid testes and/or thickened opaque efferent ducts (indicating the presence of sperm). Lengths and widths of testes were measured on the 1994 and 1995 trips, and used to calculate testis volumes (from the equation for volume of an ellipsoid: James & Shine, 1985). Females were scored as mature if they had enlarged vitellogenic follicles (arbitrarily defined as > 8 mm diameter), oviductal eggs, or thickened muscular oviducts. We also examined the ovaries for ovulation scars (corpora lutea) from previous clutches. In order to facilitate comparisons between dried, stretched skins and the animals from which they were obtained, we remeasured tagged skins after drying to quantify the relationship between skin width (the variable most often reported for skins in the commercial trade) and lizard SVL.

RESULTS

We obtained data from 166 specimens of *V. salvator* (32 in 1993, 41 in 1994, 93 in 1995). Of these animals, 122 (75%) were adults, but the proportion of adult specimens was much higher in males (80 of 86, = 93%) than in females (42 of 77, = 55%). A contingency-table test confirmed that the relative numbers of juvenile versus mature specimens differed between the sexes ($\chi^2 = 29\cdot94$, 1 d.f., $p < 0\cdot0001$). These relative proportions of juvenile and mature specimens did not vary significantly among the three trips (for males, $\chi^2 = 5\cdot34$, 2 d.f., $p = 0\cdot069$; for females, $\chi^2 = 1\cdot46$, 2 d.f., $p = 0\cdot48$). Sex ratios also did not vary among the three
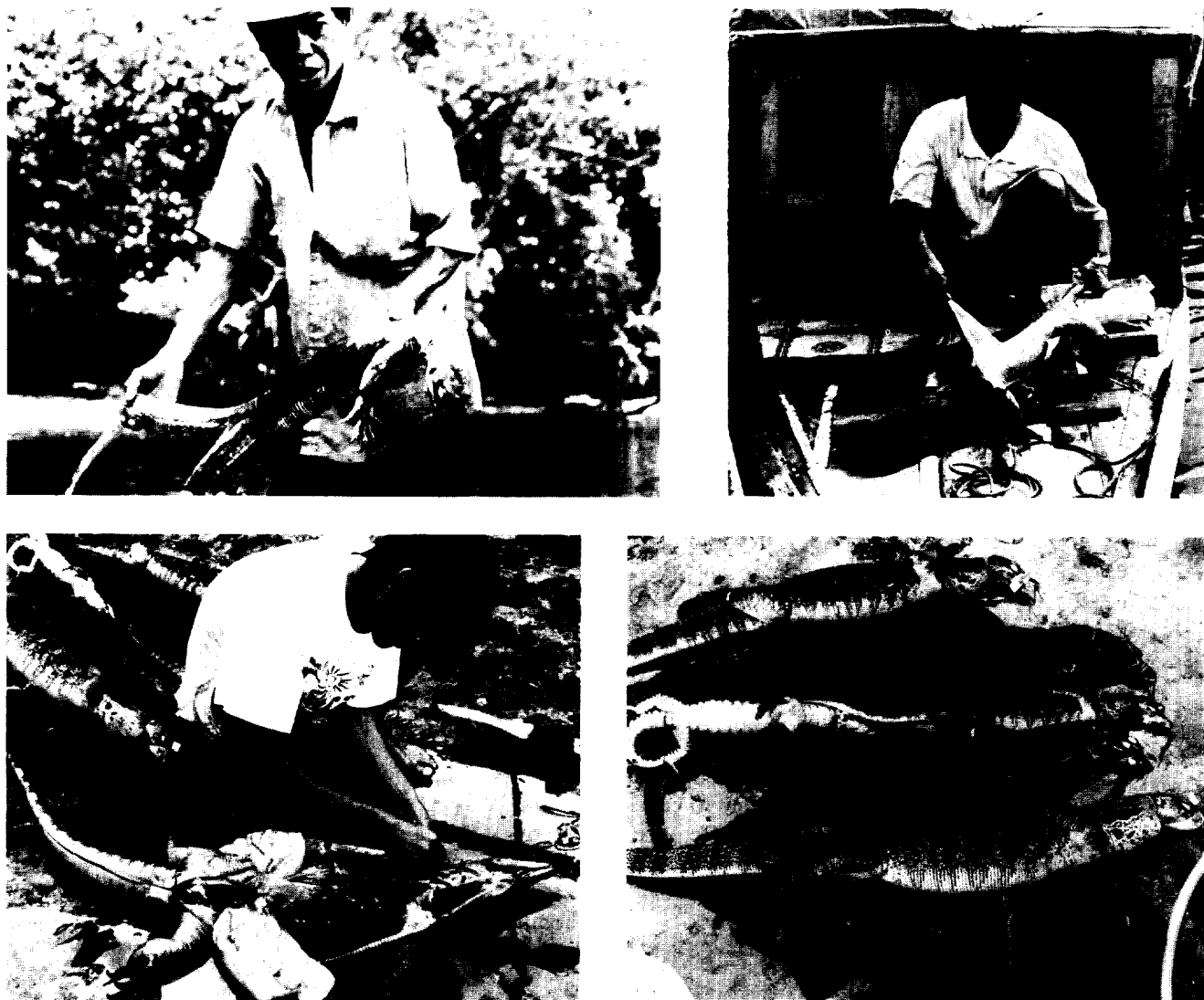
Fig. 1. Processing of water monitors in southern Sumatra for the commercial skin trade. Many of the lizards are captured in baited snares set in mangrove swamps (upper left; note snare on midbody of lizard). Some are killed immediately and skinned by the collectors on their boats (upper right) whereas others are brought to central slaughterhouses in Palembang to be killed and skinned (lower left). A wide size range of varanids is used (lower right).

trips (for adults, $\chi^2 = 2.73$, 2 d.f., $p = 0.26$; for juveniles, $\chi^2 = 2.09$, 2 d.f., $p = 0.35$).

Morphology

The largest male we examined measured 91 cm SVL (= 2.03 m total length, 11.3 kg), and the largest female was 77 cm SVL (= 1.87 m total length, 8.2 kg). However, three other larger lizards (16 – >20 kg) were brought in but not killed and skinned. We were told that their skins were too scarred and thick to be of any commercial value, and that the animals would later be released. Tail length relative to SVL was greatest in small specimens, with the ratio of tail length to SVL declining significantly in larger animals (ratio of tail to SVL versus SVL: $r = -0.34$, $n = 93$, $p < 0.001$). Males matured at around 40 cm SVL (= 100 cm total length), but females considerably larger (47 cm SVL, 120 m total length). However, occasional larger specimens

(especially females) were judged to be juveniles. The largest immature male was 44 cm SVL, and the largest immature female was 57 cm SVL. Our analyses detected no significant differences between the sexes in mean adult body length, tail length, head length or body mass (Table 1). Similarly, the frequency distributions of body lengths did not differ appreciably between the sexes (Fig. 2).

However, more detailed analysis of allometric relationships revealed significant sex differences in relative proportions. The slope of the linear regression between tail length and SVL was higher in males than in females, with adult males having longer tails than do conspecific females at the same SVL (heterogeneity of slopes test, $F_{1,123} = 4.30$, $p < 0.04$). Also, males were more heavy-bodied than females (ln mass relative to SVL: slopes $F_{1,107} = 15.55$, $p < 0.001$). The sexes did not differ significantly in head length relative to SVL

Table 1. Sample sizes, body sizes and sexual dimorphism in adult water monitors, *Varanus salvator*, killed for the leather industry in southern Sumatra

The table shows mean values for each sex (with standard deviation in brackets), and tests of the null hypothesis of no sexual dimorphism using an unpaired two-tailed *t*-test with 120 d.f.

	Males	Females	t	p
Sample size	80	42		
Mean snout-vent length (cm)	56·6 (10·11)	59·0 (6·07)	1·39	0·17
Range of SVLs	39·0 – 91·0	47·0 – 77·0		
Mean tail length (cm)	86·1 (13·60)	90·6 (9·76)	1·68	0·10
Range of tail lengths	60·0 – 130·0	68·0 – 108·0		
Mean head length (cm)	10·67 (1·64)	10·89 (0·94)	0·77	0·44
Range of head lengths	8·00 – 15·60	9·00 – 13·70		
Mean body mass (kg)	3·24 (2·11)	3·52 (1·38)	0·67	0·51
Range of body masses	1·05 – 11·30	1·80 – 8·20		

(slopes $F_{1,114}$ = 2·58, p = 0·11; intercepts $F_{1,115}$ = 2·96, p = 0·09) or in 'fat body scores' (unpaired t_{151} = 0·73, p = 0·47).

We found no significant differences in mean body sizes of adult lizards among the three trips (using a one-way ANOVA with trip number as the factor: for males, $F_{2,73}$ = 0·95, p = 0·39; for females, $F_{2,43}$ = 0·57, p = 0·57), but condition showed a significant temporal shift (one-way ANCOVA, with trip number as the factor, SVL as the covariate, and ln mass as the dependent variable: slopes $F_{2,105}$ = 1·83, p = 0·17; intecepts $F_{2,107}$ = 5·66, p < 0·005). This significant result was due to condition factors being lower for lizards in trip 2 (October

1994) than in the other two trips, particularly trip 3 (April 1995). Both sexes exhibited the same ranking of condition factors among trips, and Tukey–Kramer *post-hoc* testing showed that the difference in condition factors between trips 2 and 3 was significant (p <0·05) for male lizards. Our 'fat body scores' also varied significantly among trips (Kruskal–Wallis nonparametric test: H = 10·83, 2 d.f., p < 0·005).

Food habits

Most varanids did not contain identifiable prey in the stomach, suggesting that they may have been held in captivity for a significant time period before being killed. We obtained records of prey in only nine lizards. Most of the prey records were vertebrates, perhaps because these animals remain longer in the alimentary tracts than do smaller invertebrate prey items. Two lizards contained fiddler crabs, and one contained a large beetle. Three varanids contained rats, and microscopic analysis of the fur (in comparison with a reference collection from the Bogor Museum) revealed that two were ricefield rats *R. argiventer*. The third was a long-tailed giant rat *Leopoldamys sabarus*. A large (65 cm SVL) female lizard contained a 14-cm mammalian ulna, and a medium-sized (53 cm SVL) male varanid had eaten a conspecific lizard not much smaller than itself (approx. 40 cm SVL). Lastly, one monitor's stomach contained feathers of a domestic chicken, and a large fish-hook. The skinners told us that villagers sometimes catch pythons using hooks baited with rats or chickens, and it seems likely that the lizard was captured in this way.

Reproduction

Male cycle

All mature males that we examined had large turgid testes, with thick opaque efferent ducts containing sperm. Testis volume increased with male body size (regression of testis volume versus body mass: r = 0·70, n = 47, p < 0·0001), such that the ratio of testis volume to male body mass was not significantly correlated with SVL (r = 0·27, n = 48, p = 0·07). Testes were signifi-
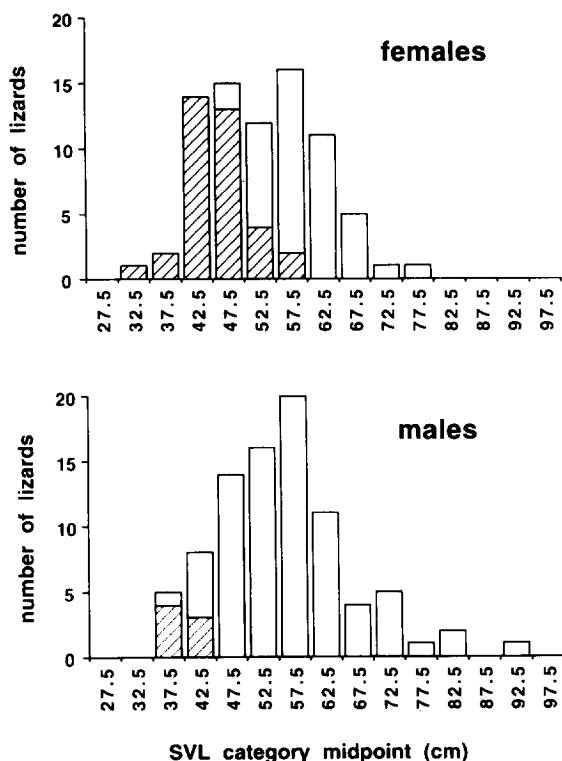

Fig. 2. Frequency distributions of the body sizes (SVL) of the male and female water monitors examined at Palembang. Upper graph shows female lizards, and lower graph shows males. Hatched histograms represent juvenile lizards, whereas open histograms show adults.

cantly larger relative to male body size during the 1995 trip than the 1994 trip (one-way ANOVA, with trip number as the factor, and the ratio of testis volume to body mass as the dependent variable: $F_{1,45} = 16\cdot75$, $p < 0\cdot0003$); the difference was approximately two-fold.

Female cycle

All of the adult female varanids examined in August 1993 and April 1995 were reproductively active (with oviductal eggs, or vitellogenic follicles) when killed, but very little reproductive activity was seen in October 1994 (no oviductal eggs; one female with ovarian follicles 22 mm, two with 10 mm follicles, and all others with follicles ≤ 8 mm). The incidence of ovarian scars (corpora lutea) from previous clutches also varied among the trips. Such scars were recorded on only 10 of 24 females from the April 1995 trip (suggesting that reproduction was just beginning), but were prevalent later in the year (9 of 11 females in August 1993, and 10 of 11 in October 1994). These data indicate a significant temporal difference in the proportion of females breeding prior to each trip ($\chi^2 = 10\cdot04$, 2 d.f., $p < 0\cdot007$), and suggest a long breeding season each year, with females producing eggs from March through to September. The reproductive season may begin earlier and end later, but we have no information to assess this possibility. Also, the October trip on which we found few reproductive female *V. salvator* took place at the end of one of the most prolonged and severe droughts recorded in Sumatra, so may have been atypical in its effects on reproductive output. The lizards were in poor physical condition at this time (as judged by mass/length relationships), so the decline in reproductive output may have been a response to the drought rather than a seasonal phenomenon. Analysis of body sizes of females that had already reproduced prior to the April trip, compared to those that had not yet reproduced (i.e. with vs without corpora lutea) showed that reproduction had commenced earlier in larger females (means $= 61\cdot2$ cm vs $54\cdot4$ cm SVL; $t_{23} = 2\cdot47$, $p < 0\cdot021$).

The prolonged reproductive season resulted from each female producing multiple clutches, rather than asynchrony among females in the timing of production of a single clutch per year. Except during April (which we infer to be close to the beginning of reproductive activity each year), almost all females with vitellogenic ovarian follicles also contained corpora lutea from recent clutches (see above), indicating that multiple-clutching is the norm in this population.

Reproductive output

Clutch sizes determined for 15 clutches ranged from five to 22 eggs (mean $= 13\cdot00$, SD $= 4\cdot46$), and fecundity was significantly correlated with maternal SVL ($r = 0\cdot86$, $n = 15$, $p < 0\cdot001$: Fig. 3). Oviductal eggs in five clutches averaged $45\cdot3$, $46\cdot3$, $55\cdot0$, $60\cdot0$ and $60\cdot9$ g

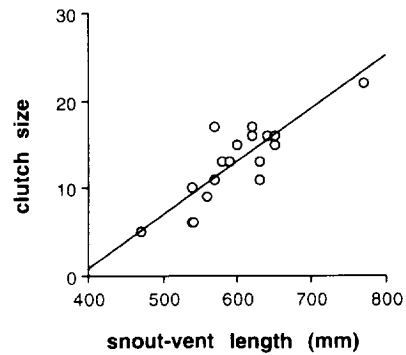**Fig. 3.** Clutch size relative to maternal SVL in Sumatran water monitors. See text for statistical analysis of these data.

(overall mean $= 53\cdot5$ g), and measured $70\text{–}80 \times 35\text{–}40$ mm. Relative Clutch Masses (total egg mass divided by maternal mass, not including the clutch mass in the denominator) in three females were $0\cdot156$, $0\cdot164$ and $0\cdot210$.

Harvesting

Based on our field excursion to Sembilan River, and on conversations with people involved in the leather industry, we reached the following conclusions about harvesting techniques. The lizards come from a large area of southern Sumatra, probably most of the southern one-third of the island. The habitats from which the lizards are captured include extensive tidal mangrove swamps along the east coast. The hunters generally do not specialise only on varanids, but catch these lizards in the course of other foraging activities (primarily for fishes). Many lizards are captured in noose snares, to which they are attracted by large piles of rotting fish (as described by Gaulke, 1989, and Erdelen, 1991). Some lizards die in the snares and are skinned when the snares are checked. Others are bagged and brought to Palembang (often, the limbs are tethered in some way inside the bag) where they may be kept alive for a few days prior to being killed and skinned (see Fig. 1).

The lizards are killed by a variety of methods in different establishments; these methods include blows to the head, direct pithing with a knife blade or wire, and suffocation by tight elastic bands around the head and neck. The skin is removed by means of an incision made along the ventral midline and anterior third of the tail, and sometimes (especially with larger specimens), the gall bladder is removed to be dried and sold for medicinal purposes. The skin is then scraped free of adherent tissue and pegged out on a board to dry in the shade. Skins are traded by width (measured just posterior to the axilla) and stretch slightly when pegged out. Based on 10 specimens that we followed throughout processing, the SVL of a lizard can be predicted from the width of its dried skin using the following linear regression: SVL $= 1\cdot9306 \times$ skin width $-6\cdot5417$ ($r^2 = 0\cdot877$: see Fig. 4). Dried skins also shrink slightly during tanning.

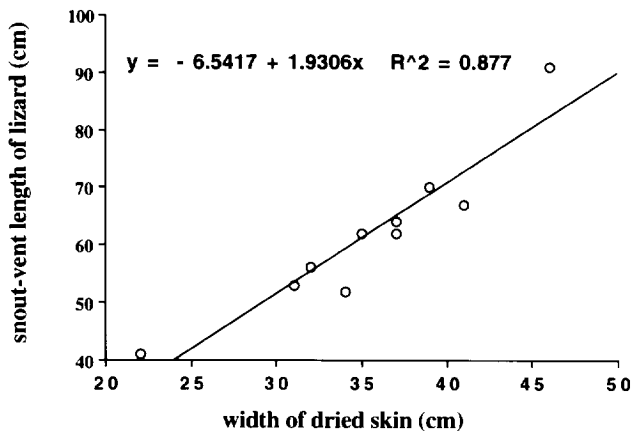y = - 6.5417 + 1.9306x   R^2 = 0.877

Fig. 4. The relationship between SVL (measured at the time the monitor was killed) and the width of the pegged, dried skin removed from that lizard. Skin width was measured immediately posterior to the axilla, and is the measurement most frequently used to describe lizard sizes in reports of commercial trade. Skin width is used as the independent variable (rather than vice versa) in this regression, because the purpose of this analysis is to allow the prediction of body length from a measurement of the dried skin.

DISCUSSION

We first compare our results with previously-published information on *Varanus salvator*, and on other monitors, before considering questions related to the sustainability of harvesting this species in Sumatra. In general, our results are consistent with previous studies on water monitors. For example, our *V. salvator* displayed an allometric change in relative tail length (smaller lizards had relatively longer tails) as described previously for other varanid species (e.g. Horn & Visser, 1991; Auffenberg, 1994). Previous reports on sex differences in body shape appear contradictory. For example, Auffenberg (1994) noted that male *V. bengalensis* were 9·2% heavier than females of the same SVL, but also reported that there was no significant difference in the ratio of mass to body length between adult males and females of the same body size. Khan (1969) suggested that males were more heavy-bodied than non-reproductive females in Malaysian specimens of *V. salvator*. Our data confirmed this sex difference in general body shape (mass relative to length), and showed that adult males have longer tails than do conspecific females at the same SVL. Similar sex differences are widespread among other squamate reptiles (King, 1989; Shine, 1993; de Buffrénil *et al.*, 1994).

One surprising result from our morphological analyses was the lack of significant sexual dimorphism in body sizes in our sample of *V. salvator*. Males typically exceed females in body size in varanids (Auffenberg, 1994), although there are several exceptions to this rule (e.g. Shine, 1986). Previous work on other populations of *V. salvator* has indicated that dimorphism is slight, but that males are indeed larger (Khan, 1969; Gaulke, 1989). The same situation is probably true of our

southern Sumatran animals; the largest lizards that we examined were males (Fig. 2), and the really large animals (probably, entirely males) are not harvested for the leather industry because of the poor quality of their skins. Hence, our data underestimate the degree of size dimorphism in this population. Males mature at smaller sizes than do females, as suggested by Vogel (1979) but not Andrews (1995). The captive lizards described by Andrews matured at around 50 cm SVL in both sexes, at the end of their second year. Males in our sample matured at SVLs less than 50 cm, whereas females matured at about this size (Table 1). The delayed maturation of female *V. salvator* offers a plausible explanation for the significant sex difference that we observed in the numbers of juvenile versus mature animals of each sex. The body-size distributions of the two sexes taken for skinning are similar, so the disparity in proportions of juvenile animals between the two sexes is due almost entirely to the difference in size at maturation (Fig. 2).

The proportion of maximum SVL at which maturation is attained varies widely among varanid species: Auffenberg (1994) cites values of 30% for females of *V. komodoensis*, 47% for *V. bengalensis*, and 71% for *V. olivaceus*. Based on our data, the equivalent figure for *V. salvator* would be 43% for males, and 61% for females. What causes this interspecific variation? Previous analyses on squamate reptiles have identified a significant allometry in the relative size at maturation, with larger species tending to mature at a smaller proportion of maximum size (Andrews, 1982; Shine & Charnov, 1992). Analysis of Auffenberg's (1994) data, together with analogous information on four Australian varanid species (Shine, 1986) suggests that the same phenomenon occurs within the Varanidae: females mature at a relatively smaller size in larger species (linear regression of % maximum SVL at female maturation versus mean adult female SVL: $r = -0·80$, $n = 7$, $p < 0·033$). Thus, the low relative size at female maturation in *V. salvator* is related to the very large body size of this species.

Previous work on varanids has generated contradictory results with respect to clutch sizes, and the relationship (or lack thereof) between clutch size and maternal body size. Clutch sizes for *V. salvator* have been reported as 1–14 (from captive lizards: Vogel, 1979), 7–17 (from captive lizards: Andrews & Gaulke, 1990), 15–30 (Smith, 1935), 20–35 (Jasmi *et al.*, 1986), and 16–40 (Erdelen, 1991). Erdelen (1991) speculated that records of very low clutch sizes (as in van der Meer-Mohr's (1931) record of a seven-egg clutch in a Sumatran water monitor) might result from the females laying a few eggs at a time, rather than depositing the entire complement of eggs in a single nest. Our data show that this explanation is unnecessary: small clutches are common in the Sumatran population (Fig. 3). A limited sample of captive lizards led Andrews (1995) to suggest that clutch size does not

increase with maternal body size in *V. salvator*, although Auffenberg (1988) cited unpublished field notes to infer that clutches tended to be larger in areas where adult females had larger average body sizes. Our data (Fig. 3) show that clutch size does indeed increase significantly with maternal body size, as is widespread in other reptiles.

Egg sizes in Asian water monitors appear to be relatively invariant across the species' wide geographic range. The mean mass of oviductal eggs we recorded for Sumatran lizards (*c.* 54 g) is slightly lower than most figures for freshly-laid eggs reported by previous authors (65 g — Horn & Visser, 1991; 60 g — Andrews, 1995; 39–61 g — Acharjyo & Mohapatra, 1980; 58·2 g — Biswas & Kar, 1981; 55–78 g — Andrews & Gaulke, 1990), as would be expected since eggs may gain water (and thus, mass) rapidly after deposition (Biswas & Kar, 1981). The dimensions of our eggs (*c.* 75 × 40 mm) were also similar to figures in most published reports for this species (e.g. 73 × 38 mm — Horn & Visser, 1991; 70 × 40 mm — Smith, 1935; 79 mm long — Andrews, 1995; 76 × 34 mm — Acharjyo & Mohapatra, 1980; 72 × 39 mm — Biswas & Kar, 1981; 73 × 40 mm — Andrews & Gaulke, 1980), although much larger eggs (92–100 × 35–38 mm) were reported by Deraniyagala (1953).

Relative Clutch Mass (total clutch mass divided by post-oviposition maternal mass) has been reported as averaging 0·23 in Philippine *V. salvator* (Auffenberg, 1994) and 0·29 in captive Indian specimens (Andrews, 1995). The three RCM estimates from our own study are slightly lower (mean = 0·18), perhaps because they are based on oviductal eggs that had not yet attained their full mass at oviposition. The limited available data suggest that varanid species are relatively conservative in RCMs (*bengalensis* 0·21, *olivaceus* 0·18, *komodoensis* 0·19: Auffenberg, 1994).

In contrast to the overall consistency in egg sizes and RCMs, breeding seasonality appears to show strong geographic variation within *V. salvator*. Such diversity is not surprising, because the geographic range of *V. salvator* encompasses a considerable diversity of climates on both sides of the equator. In India and Thailand, breeding seems to occur primarily from April to July (Smith, 1935; Biswas & Acharyjo, 1977; Acharjyo & Mohapatra, 1980; Whitaker & Khan, 1982; Andrews, 1995). Less consistency is apparent in the eastern part of the species' range: for example, Gaulke (1992) inferred that lizards on one Philippine island bred in May whereas conspecifics on another island bred in November. Based on a large sample of dissected animals, Khan (1969) found that Malaysian *V. salvator* reproduced year-round, but with a very pronounced peak in September–October. Our data support Erdelen's (1991) suggestion that water monitors in southern Sumatra can breed for most or all of the year. Although we documented significant differences among trips in both male and female reproductive activity

(testis sizes in males, proportions of reproductive females), reproduction occurred during all three trips (i.e. in April, August and October). All adult males had active gonads when examined, and the same was true for females from two of the three trips. Thus, the broad spread of reproductive activity cannot be attributed to a combination of data from specimens captured in different areas, with each area having a brief reproductive season that is asynchronous with reproductive activity in other areas. Different regions in southern Sumatra may well vary in terms of the timing and duration of reproductive activity in water monitors, but the overall pattern seems to be the production of multiple clutches by each female, over a large part of the year. Such extended reproductive activity is not surprising in an area so close to the equator, with monthly mean temperatures varying only between 25 and 27°C throughout the year in the lowlands, and with > 200 mm rainfall in at least 7 months each year (Erdelen, 1991).

The high incidence of fresh corpora lutea in females with vitellogenic follicles examined during two of those trips (August and October) indicate that females typically produce more than one clutch per year. Captive female water monitors have been recorded to produce successive clutches at intervals of three months (Andrews & Gaulke, 1990), so that Sumatran female monitors would have time to produce at least three clutches per year. This high reproductive frequency seems to be atypical of large varanid species, with *V. salvator* appearing to be the only large species regularly to produce more than one or two clutches a year, in captivity (Andrews & Gaulke, 1990; Horn & Visser, 1991; Hairston & Burchfield, 1992) as well as in the wild (Erdelen, 1991; Auffenberg, 1994; present study). This conclusion stands in strong contrast to some previous inferences: for example, Bowers (1981) suggested that these lizards might be biennial breeders. Our comparison of body sizes of females relative to the seasonal onset of reproduction (i.e. those showing corpora lutea in April) suggests that larger females commence reproduction earlier than small females. The same pattern has been documented in a variety of lizard taxa (e.g. Jones *et al.*, 1987) and may be a widespread phenomenon.

We turn now to the relevance of this information to sustainable levels of harvesting of water monitors. The immediate challenge is to understand how this species has managed to persist (and indeed, remain common) over much of its range despite several decades of intensive hunting for the leather industry (Luxmoore & Groombridge, 1990; Erdelen, 1991). Our data suggest that the monitors' ability to withstand these high levels of offtake is a consequence of the following factors.

(1) Water monitors display extraordinary ecological flexibility, and occur in a very wide variety of habitats ranging from mangrove swamps to the vicinity of large towns and cities (Erdelen, 1991). Tidal swamps

may be particularly important, because they cover vast areas in the two regions (Sumatra and Kalimantan) from which most monitors are harvested (Luxmoore & Groombridge, 1990), and may contain unusually high population densities of water monitors (Gaulke, 1989).

(2) Water monitors are relatively abundant in many parts of their range, so that the numbers taken for the leather industry each year, although huge, may represent a small proportion of the standing crop. The total annual offtake of water monitors in southern Sumatra (provinces of Lampung, Sumatera Selatan and Bengkulu) is around 230,000 (Luxmoore & Groombridge, 1990), from a total area of approximately 160,000 km^2 (Erdelen, 1991). Thus, about 1·5 lizards per km^2 are removed by commercial harvesting. Information on population densities of *V. salvator* are very difficult to obtain; estimates include 4·5 per km^2 in Java (Vogel, 1979), 5 per km^2 inside forests, but much higher along rivers (from skin suppliers in Sumatra: Erdelen, 1991), 6·6 per km^2 in Bangladesh (Khan, 1988, in Luxmoore & Groombridge, 1990), 24·3 per km^2 on a Philippine island (Gaulke, 1989), and > 250 per km^2 in mangrove habitats on the same island (Luxmoore & Groombridge, 1990, based on Gaulke's data). The wide range in these estimates makes it difficult to compare natural densities with rates of removal of lizards for the leather industry. Presumably, the impact of harvesting is negligible in many regions, but very significant in others.

(3) Water monitors have an extremely broad diet (Losos & Greene, 1988; Gaulke, 1991a), and are able to take advantage of food resources resulting from human activities. Thus, an increase in human populations may not necessarily disadvantage these lizards. For example, several authors have reported that water monitors will feed on human food wastes, faecal material and even human corpses if given the opportunity (e.g. Taylor, 1963; Auffenberg, 1981). The monitors' liking for carrion, and their ability to locate it, have been documented several times (e.g. Auffenberg, 1988) and are the basis for the usual trapping technique used in the Philippines (Gaulke, 1989) and Sumatra (Erdelen, 1991 and personal observations).

(4) Removal of larger older animals may enhance survival of younger monitors, if density-dependent mortality is important in the population. We have no information on the determinants of population density in these lizards, but our record of cannibalism in *V. salvator* (and note a similar record for Philippine water monitors: Gaulke, 1991a) suggests that smaller individuals might benefit from removal of the larger animals.

(5) Water monitors have a high reproductive rate. Our data support Erdelen's (1991) inference that this species breeds for most of the year in southern Sumatra, and it seems clear that most females produce more than one clutch per year. Production of three or four clutches per female per year may not be unusual, so

that annual reproductive output per female is considerably higher than in other varanid species studied to date. Clutch sizes are relatively large (mean = 13 eggs), and data from captives suggest that maturation is attained fairly quickly (at the end of the second year of life) in both sexes (Andrews, 1995). Our observation that reproduction continued (albeit at a lower rate) even after prolonged and severe drought, suggests that year-to-year climatic variation may not induce major curtailments of reproductive output.

(6) The technique used by commercial lizard-hunters (trapping in carrion-baited snares) may capture mainly adult male lizards, due to the higher activity levels and lesser caution of male varanids than of conspecific females (e.g. Auffenberg, 1994). Nonetheless, the sex bias is less extreme in our sample (66% male among adults, but only 53% of all lizards taken) than has been reported by previous studies (Erdelen, 1991 = 78%; Khan, 1969 = 70%; Vogel, 1979 = 71%). The body-size distribution of our captured varanids (Fig. 2) was similar to that in the smaller sample measured by Erdelen (1991). However, Erdelen's belief that hunting for these lizards occurred in only 6 months of the year is not consistent with our experience, unless we have considerably underestimated the duration of time for which the lizards are held in captivity prior to slaughter. A previous inference that hunting for the leather trade was concentrated on juvenile rather than adult animals (Luxmoore & Groombridge, 1990) is also in error, primarily because the size at maturation (especially in males) is considerably lower than these authors inferred from observations of captive specimens. This example shows the danger of extrapolation from captivity to the wild, particularly with a wide-ranging species that displays significant geographic variation in life-history traits. The allometry of relative size at maturation in varanids (as in other squamates) has interesting implications for the degree to which commercial hunting focuses on juvenile versus mature lizards. One might expect that harvesting of larger species would focus more heavily on immature specimens, because the larger size at maturation in such taxa would increase the relative proportions of juvenile animals in the population, and also mean that many juveniles exceed the minimum size at which their skins become valuable for the leather industry. However, this trend will be counterbalanced by the shift in relative size at maturity in larger species, so that sizes and ages at maturation will be more similar to those of smaller taxa than might have been predicted from simple isometric relationships.

(7) A disproportionately high proportion of offspring may come from a small number of very large females, that are less vulnerable to hunting than are younger smaller animals. Sexual size dimorphism seems to be relatively slight in *V. salvator* (compared to the situation in many other large varanid species), so that the population contains some very large females with high

reproductive output (large clutches, and a long reproductive period). According to the skin-traders, the largest water monitors are of little commercial value because their skins are too thick and scarred. In keeping with this statement, the three largest monitors we saw brought in were not killed (although it remains possible that they were killed at a later date, or slaughtered for another purpose). If indeed the larger specimens are not used for the skin trade, then some of the largest females may escape hunting. These larger (and presumably, older) animals may also be more wary, and hence less likely to fall prey to snares. The increase in reproductive output with maternal body size suggests that measures to preserve these occasional large females may be worth considering. If indeed there is less financial return from the largest lizards, there may be little resistance from the leather industry to introduce a management scheme imposing maximum sizes that are low enough to include at least some of the largest females. Such a system (protection for the largest animals) was developed for crocodile conservation in New Guinea, to protect breeding adults (Hollands, 1987).

Although *V. salvator* possess several characteristics that enable them to withstand intense harvesting (see above), nonetheless there is anecdotal evidence of population declines in some areas (e.g. Gaulke, 1992). Although habitat destruction is likely to pose a more important long-term threat to varanids than is the current commercial trade, extirpation of local populations may occur through overcollecting. The survival of the species as a whole is not under immediate threat, but there is an urgent need for more research to determine sustainable levels of offtake in specific habitats. Detailed field research is essential if we are to ensure the continued viability of varanid populations across the tropics.

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