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Zoo Indonesia
Bidang Zoologi, Puslit Biologi LIPI
Gd. Widyasatwaloka
Jl. Raya Bogor-Jakarta KM. 46
Cibinong 16911

Telp. (021) 8765056

Fax. (021) 8765068

zooindonesia@yahoo.com (www.biologi.lipi.go.id)

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- Flannery, T. 1990. Mammals of New Guinea. Robert Brown & Associates. New York.
- Nelson, M.E & L.D Mech. 1987. Demes with a Northeastern Minesota Deer Population. In: B.D Chepko-Sade & Z Tanghapin (edits.) Mammalian Dispersal Pattern-The Effect of Social Structure on Population Genetics. University of Chicago Press. 230-243.
- Youngson, R.W. 1970. Rearing red deer calves. Journal of Wildlife Management 34:467-470.

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Redaksi Zoo Indonesia
d/a Bidang Zoologi - Puslit Biologi LIPI
Jl. Raya Bogor-Jakarta Km. 46
Cibinong 16911
zooindonesia@yahoo.com

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AN OVERVIEW ON THE ECOLOGY OF VARANID LIZARDS

Evy Arida

*Herpetology Laboratory, Museum Zoologicum Bogoriense-LIPI
Jln. Raya Bogor-Jakarta Km 46, Cibinong 16911
e-mail: evyarida@lycos.com*

ABSTRACT

Arida, E. 2008. An overview on the ecology of Varanid lizards. Zoo Indonesia 17(2): 67-82. *Body size is a morphological character that can be useful to estimate the size of home range in varanids. It may also be used to cue for habitat type and mode of life of varanid lizards. Nevertheless, although body size may be a good predictor of home range size, it may not be useful to infer population density, because non-territoriality nature of varanid lizards generates home range overlaps. Although non-territoriality nature may hinder inference of population density, it can signal for high density through the signature of aggression. However, the magnitude of density itself would not be well quantified. An approach to population density estimation is the use of reproductive biology data. Reproductive biology data of wild varanids can be used to base a projection on population trends. Despite the notion, data on reproduction from wild populations seems to be scarce, especially from some regions in Asia. Regular population monitoring for general census and reproductive status is definitely still needed to allow for sound estimates of population density and its dynamics.*

Keywords: *body size, home range, varanids, density, reproduction.*

ABSTRAK

Arida, E. 2008. Tinjauan ekologi kelompok biawak. Zoo Indonesia 17(2): 67-82. *Daerah jelajah biawak dapat diperkirakan melalui ukuran tubuhnya. Ukuran tubuh biawak dapat pula digunakan untuk mencirikan tipe habitat dan cara hidupnya. Meskipun demikian, ukuran tubuh tidak dapat digunakan untuk memperkirakan kepadatan populasi, yang disebabkan oleh daerah jelajah yang tumpang tindih. Daerah jelajah yang tumpang tindih ini terjadi karena biawak tidak mempunyai teritori, yaitu daerah yang dipertahankan dari kedatangan hewan lain. Dengan keadaan ini, masih ada kemungkinan terjadinya agresi, yang merupakan suatu penanda tingginya kepadatan populasi tersebut, walaupun kepadatan populasi ini tidak dapat diperkirakan dengan pasti. Perkiraan kepadatan populasi dapat dilakukan dengan pendekatan yang berdasarkan pada data perkembangbiakan, yang pada prinsipnya digunakan untuk memproyeksikan dinamika populasi. Namun demikian, data perkembangbiakan dari populasi liar belum banyak tersedia, terutama data dari beberapa wilayah di Asia. Pemantauan populasi yang teratur dalam rangka cacah jiwa dan pemantauan status perkembangbiakan, masih diperlukan untuk memperkirakan kepadatan populasi dan dinamikanya dengan benar.*

Kata kunci: *ukuran tubuh, daerah jelajah, biawak, kepadatan, perkembangbiakan.*

INTRODUCTION

An attempt to characterise varanid lizards' population can possibly be made by taking ecological properties such as home range size and reproductive biology information into account. Morphological characteristics, for example body size, can be used to predict ecological repertoire. Here, a possible relationship between body size, home range, and reproductive biology of varanid lizards will be elaborated to characterise the general trend on the population, based on available published literatures.

Population

Population ecology is the study of interaction among organisms in relation to environmental aspects with emphasize on demography (*Begon et al.* 1996). It has a tight connection with conservation biology, because assessment of population viability for conservation is based on population size estimates together with the dynamics of this population. Despite commercial exploitation of many species and endemism of several varanid species, there are probably only a handful population studies on these lizards. This is probably due to logistical difficulties in applying mark-recapture technique especially when involving large individuals. On the other hand, the complexity of integrated population study involving demographic parameters including those requiring long-term continuous observation e.g., reproductive biology, is another factor that hinders data collection.

From a taxonomic perspective, continuous new species discoveries and species complex (*Böhme* 2003) may confound long-term population monitoring and census. In addition, the broad ecological repertoire and agility of monitor lizards may render difficulties and biases in census.

In spite of the scarce full-length data on monitor lizard populations, a number of data from related studies e.g., spatial ecology and reproductive biology might be useful to predict trends in varanid populations. A range of factors affecting the magnitude and dynamics of monitor lizard populations has been postulated and includes basic demographic parameters such as size, age, and sex. These parameters affect population size indirectly through a mechanism that regulates patterns of individual movement and/or home range (*Perry & Garland* 2002).

Population density and species distribution can also be affected by environmental parameters such as seasons (*Phillips* 1995; *Guarino* 2002) and behavioural parameters such as habitat preference (*Bondarenko* 1989; *Thompson et al.* 1999) and social system (*Stanner & Mendelssohn* 1987). In addition, intraspecific competition may directly regulate population size and dynamics of these large lizards (*Luiselli et al.* 1999). Furthermore, energetic-related factors such as dietary shift and mode of life i.e., arboreality, terrestriality, aquatic) may also influence the magnitude and dynamics of varanid populations.

Ecological & behavioural repertoire

Monitor lizards are generally good runners, climbers, and/or swimmers. This repertoire in movement suggests an ability to move through variable habitats. *V. bengalensis* and *V. salvator* in Asia and *V. gouldii* and *V. tristis* in Australia utilised many different habitats and are among varanid species that are widely distributed (*King & Green* 1999). The broad diet of some monitor lizard generally suggests an opportunistic foraging nature (*Shine* 1986). Thus, some species are plastic and may adapt to a wide range of habitat types. However, some species are specialised to live in a particular

habitat type. Species within the *Varanus prasinus* group are specialised to live on trees, which indicates habitat restriction to forested areas and dietary restriction to preys available in this habitat.

The broad ecological repertoire of some varanid lizards may enhance their successful dispersal. Following multiple successful dispersal, broad ecological repertoire may give rise to phenotypic plasticity suggesting invasiveness (Agrawal 2001). Evidence of plastic behaviour in varanid lizards was shown by the Nile monitor (*Varanus niloticus*), a species of African origin, that warrants population monitoring and eradication in south western Florida, USA (Enge *et al.* 2004). Similarly, the Pacific monitor (*Varanus indicus*) is considered as invasive in Guam, on the island of Hawaii, USA (Bergman *et al.* 2000).

Persistence in disturbed area, where habitat are changed and human continuously present, also suggests a signature of plastic adaptation. This is shown by the Asian Water monitor (*V. salvator*), which has a wide distribution in Asia (Gaulke *et al.* 1999). Nevertheless, there is no evidence that *V. salvator* is an invasive species.

Body size & home range

Differential body size, in terms of Snout-Vent Length (SVL), within the extant varanid lizards could have been a signature of evolutionary forces that is reflected on morphological characteristics. The relatively rapid evolution of body size among varanid lizards seems to be a fine-tuning on habitat variation, given three different lineages of dwarf, large, and gigantic species occurring within the boundary of Australian continent (Pianka 1995). Thus, morphological character i.e., variation in species body size (SVL) of varanid lizards may have an association with the type of habitat a species living

in. Further on, species with broad ecological repertoire seem to be associated with a few habitat types or even changed habitats. Such species are presumably of medium SVL, because medium SVL is likely to enable effective distant movement beyond the habitat boundary. An eventual consequence of adaptability to new area (habitat) may give rise to wider foraging area or larger home range size. Nevertheless, in large species that is relatively adaptable to changed habitats such as *V. salvator* (Gaulke *et al.* 1999), probably only medium size individuals that make the cross beyond habitat boundaries. This is true since juveniles tend to live on trees, whereas giant adults are very rarely caught during harvest or captures for study purposes (E. Arida, pers. obs.).

Home range is defined as the area traversed by animals during routine activities. It accounts for the behavioural and physiological demands of the individuals (Perry & Garland 2002). A fraction of an animal's home range that is patrolled and defended from intruders for access to resources is commonly defined as territory (Simon 1975; Kaufmann 1983). Varanids are generally non-territorial and many species within the family have a large home range that overlaps (Stanner & Mendelssohn 1987; Thompson 1994; Lenz 1995; Gaulke *et al.* 1999; King & Green 1999; Sweet 1999; King *et al.* 2002) within and between the sexes (Stanner & Mendelssohn 1987; Thompson 1994; Sweet 1999).

Despite some published ecological data on home range of varanid lizards, there has not been any published trend on home range size plotted with variation in SVL as a measure of body size. This is probably due to the relatively few published data on home range (King & Green 1999) as well as inadequate uniformity in published SVL measurements. However, correlation

between home range size and body mass has been formulated as:

$$H = 0.0307 \times W - 0.5068$$

where H= home range (ha) and W= body weight (g) (Guarino 2002).

Table 1 shows some data on home range size and maximum SVL of 53 *Varanus* from three continents. It is always the case that males of a species have larger home range than conspecific females, presumably because adult males are generally larger than females. Accordingly, larger species are likely to have larger size of home range relative to smaller species. Home range size may have a direct relationship with SVL at adult stage. Within species, this direct relationship may be more obvious in large monitors than in small or medium size monitors. The adult males of large species e.g. *V. komodoensis* and *V. giganteus* are larger than conspecific females (Table 1), whereas SVL of adult males and females of some small to medium size monitors are likely to be similar (monomorphic) e.g. *V. mitchelli* and *V. mertensi*, both of which are semi-aquatic (Shine 1986), and may show no significant distinction in home range size between the sexes.

Direct relationship between SVL and home range size between species can be exemplified in the Pygmy Goanna (*V. breviceauda*), the smallest species among all *Varanus*. *Varanus breviceauda* is relatively sedentary compared to its larger sympatric congeneric i.e., *V. gilleni*, *V. eremius*, and *V. caudolineatus* occurring on the central and western deserts of Australia (James 1996). This suggests that small species travel shorter distance and therefore cover relatively smaller area, making their home range also smaller. Size of activity area in monitor lizards is also associated with mode of life (Thompson 1994; King *et al.* 2002). Many arboreal species are smaller in size compared to some terrestrial

species, which tend to have larger home range. Nonetheless, data on home range size of arboreal monitors are relatively rare and many species have non-strict mode of life.

There are some other factors that directly or indirectly affect the size of home range. For example, variation in home range size of monitor lizards can be related to climatic factors such as rainfall (Auffenberg 1988; Auffenberg 1994) and temperature (King 1980). During wet season that is associated with abundance of prey insect, *V. bengalensis* moved a greater distance (Auffenberg 1994), suggesting larger home range during this period. Thus, rainfall is the indirect factor that indicates prey availability, whereas insect abundance is the direct factor that drives animals to forage. The Sand goanna, *V. gouldii*, were found remain in their burrow during extreme temperatures (King 1980), suggesting no movement during this period. Therefore, one can expect smaller home range for this species during harsh climate than during the period of mild temperature.

Intra and interspecific interaction between individuals may also set boundary to home range size. Since monitor lizards are non-territorial, one can expect that these interactions between individuals within a species or individuals between species would not be easily observed. The degree of interspecific competition among varanid species seems to be minimised by niche segregation (Wikramanayake & Dryden 1993) and this may be corroborated by their broad dietary range (Shine 1986). Niche segregation seems to be also the strategy to minimise intraspecific competition, for example in adult avoidance by juveniles and age-class segregated niche e.g. in *V. komodoensis* (Auffenberg 1981; Imansyah *et al.* 2007). In this regard, niche segregation within and between

species may be used to locate home range or points of species distribution. However, segregated niche might be inadequate to index home range size, if there is no accompanying data on the animals' movement.

Geographic barrier in terms of island may also limit body size, including SVL, and the consequent size of home range. Varanid lizards living on islands are expected to be smaller than those living on mainland, particularly due to depletion of resources and/or increased aggression. This can probably be explained by the absence of predator on island and the non-territorial nature of monitor lizards, which may allow rapid increase of density (Buckley & Jetz 2007) promoting resource overexploitation leading to aggression resulting from severe competition (Case & Schwaner 1993; Pianka 1995). Thus, one can expect overlapping home ranges as a consequence of non-territoriality despite the reduced space on island. Further, home range size is expected to be smaller on island as a function of reduced body size, despite the reduced total area. This means that size of home range in varanids is not directly dependent upon population density, but it depends more directly on individual body size that can be influenced by competition as a consequence of population density.

The smallness of island varanids can be related to differential physiological requirements (Nagy 2005) of individuals surviving on island community relative to their mainland conspecific. During high density on islands, lizards may compensate growth energy for aggression, allowing slow growth that possibly results in reduced body size. Therefore, varanid lizards living on islands might have been selected for their physiology and body size. The Komodo dragon (*V. komodoensis*) is the largest living varanid species

inhabiting islands of several different sizes. The top largest individuals from the larger island of Rinca are relatively larger than the top largest individuals from the much smaller island of Gili Motang (Jessop *et al.* 2007). Although there is no direct evidence of severe competition, dragons on this small island may have been selected for their relatively smaller body size and the related physiological requirement.

Home range & population density

The size of home range in varanid lizards might be useful to estimate population density as in mammals (McNab 1963). However, non-territorial spacing of monitor lizards that is plotted as overlapping convex polygons (Weavers 1993) may bias density estimate. This is because overlapping home ranges represent more than one individual on a given space, allowing bias in the extrapolation to the total distribution area. Nonetheless, non-territoriality in varanids may be useful to cue for change in population density. The absence of territorial maintenance in varanids allows for aggression that is promoted by competition during a rapid increase of density. Unfortunately, little is known about the intraspecific competition among varanid lizards, although cannibalism is known to occur in some species e.g. *V. griseus*, *V. niloticus*, *V. salvator* and *V. komodoensis* (Auffenberg 1981; Lenz 2004).

Cannibalism can be regarded as aggression by which severe intraspecific competition is possibly manifested. Nevertheless, the possible relationship between cannibalism and population density still remains to be tested, since there has not been any direct evidence to justify this hypothesis. Population density of Varanid lizards seems to be also affected by geographical boundary, since most island varanids are likely restricted to

dispersal (Buckley & Jetz 2007). There is probably no significant difference in home range size between island and mainland populations, due to the non-territorial spacing of these lizards. This means, island population density can be limited by the presence of geographical barrier (sea water), without the size of individual home range itself being changed accordingly. Population density estimate based on home range data alone seems to be unreliable, given the possible bias generated from overlapping home ranges. Further, reliable population density estimate is almost impossible to obtain without direct census. Meanwhile, population dynamics data are the series of census data obtained from long-term periodic population monitoring. Differential mode of life in varanid lizards is another factor that hinders generalisation of home range size among all members. In addition, the elusive and secretive nature of a species can also reduce the accuracy of an estimate (Stanner 2004).

Body size & reproductive biology

All species of *Varanus* are egg-layers (Shine 1986). Body size has an influence on clutch sizes, with females of larger species having larger and more variable clutch sizes than those of smaller species (Thompson & Pianka 2001). This implies that larger species have higher reproductive output, although low offspring survival seems to counterbalance. In Komodo monitor, *V. komodoensis*, only about ¼ of clutch size is estimated to reach reproductive age, partly caused by predation of eggs and cannibalism of large adult conspecific (Auffenberg 1981). In Bengal monitor, *V. bengalensis*, about half of neonates dies by the end of their second year (Auffenberg 1994). There is only a few long-term studies on reproduction of free-ranging monitor lizards but captive animals have provided a relatively large amount of data (Bennett *et al.* 1998). Meanwhile,

dissected museum specimens can be used to infer reproductive cycle. Monitor lizards appear to be conservative in the length of gestation but highly variable in length of incubation, which may be related to period of prey abundance in the wild and can help maximising offspring survival (Phillips & Millar 1998). Table 2 shows data on reproductive characteristics, some of which are from captive specimens. Small varanids seem to lay multiple clutches over a year (e.g. *V. melinus*, *V. rudicollis*, *V. prasinus*), each with a few to just over a dozen eggs. Large species tend to lay one clutch per year within total deposition time of a few weeks e.g. *V. komodoensis* (Auffenberg 1981).

Reproductive biology & population density

A projection of population density on varanids is very difficult without reproductive success data from free-ranging animals. However, long-term monitoring for reproduction in the wild is logistically expensive, especially for tropical Asian species, since mating or egg deposition may extend to monsoon season (Auffenberg 1994; Shine *et al.* 1996). However, there are already details on reproduction from species inhabiting tropical Australia. Reproductive status and population density of traded species, for instance from Indonesia, however, can be monitored through the catch rate, although indirect data may not be as reliable as direct observation. Shine *et al.* (1996, 1998) were able to gather data on reproductive status, size, and food habits of commercially harvested *V. salvator* based on stretched skins in a holding facility in South and North Sumatra, Indonesia. Zoo captives are also useful to estimate reproductive cycle, although proof of reproductive synchrony with wild animals may not always be found (Table 2).

Conservative estimate of surviving individuals of about a quarter of original

clutch size may infer yearly recruitment close to reality, given many negative factors affecting hatching rate and survival of young animals such as predation and cannibalism. Nevertheless, direct census data is still needed repeatedly for a projection on population trend to base on.

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Table 1. Body sizes, home range sizes and habitat of genus *Varanus* by continental groups.

No	Species	Home range (ha)	Density (per ha)	Max. adult SVL (cm)	Mode of life	Reference
	Africa					
1	<i>V. albigularis</i>	18.3 ± 2.4 (♂) 6.1 ± 0.6 (♀)	--	?	Terrestrial, arboreal	Philipps (1995) Branch (1988)
2	<i>V. exanthematicus</i>	--	0.87/ hour 3.57 (juv)	75.0	Terrestrial, arboreal, aquatic	Bennett (2000) Bennett (2004)
3	<i>V. griseus</i>	7.5-1950	0.2	58.3*	Terrestrial	Stanner (2004)
4	<i>V. niloticus</i>	5 (♂) 1.5 (♀)	1.14	96.0*	Terrestrial, arboreal, aquatic	Lenz (1995) Lenz (2004)
5	<i>V. ornatus</i>	--	--	92.25*	Terrestrial, arboreal, aquatic	Böhme & Ziegler (2004)
6	<i>V. yemenensis</i>	--	--	59.0	Terrestrial, arboreal,	Gasperetti in Böhme (1989) Böhme (1989)
	Asia					
7	<i>V. bengalensis</i>	HR♂ > HR♀	--	99.17	Terrestrial, arboreal, aquatic	Pianka (2004)
8	<i>V. caerulivirens</i>	--	--	40	arboreal, semi-aquatic	Ziegler et al. (2004)
9	<i>V. cerambonensis</i>	--	--	40.9	Semi-aquatic?	Phillip et al (2004)
10	<i>V. doreanus</i>	--	13/600 ? sqm	46.0	Terrestrial	Ziegler et al. (1999)
11	<i>V. dumerilii</i>	--	--	50.0	Terrestrial, arboreal, aquatic	Bennett (2004)
12	<i>V. finschi</i>	--	--	30.5	Terrestrial, arboreal, aquatic	Phillip et al. (2004)
13	<i>V. flavescens</i>	--	--	40.0*	Terrestrial, arboreal, aquatic	Visser (2004)
14	<i>V. indicus</i>	--	--	58.0	Terrestrial, arboreal, aquatic	Wikramanayake & Dryden (1988) Dryden & Ziegler (2004)
15	<i>V. jobiensis</i>	--	--	45.0	Terrestrial, arboreal	Horn (1977) Phillip et al. (2004)

No	Species	Home range (ha)	Density (per ha)	Max. adult SVL (cm)	Mode of life	Reference
16	<i>V. juxtindicus</i>	--	--	50.4	Terrestrial, arboreal, aquatic	Böhme <i>et al.</i> (2004)
17	<i>V. komodoensis</i>	258-529 HR♂>HR♀	--	154.0	Terrestrial, arboreal, aquatic	Ciofi (2004)
18	<i>V. kordensis</i>	--	--	27.0	Arboreal	Jacobs (2004)
19	<i>V. mabitang</i>	--	--	64.0	Arboreal	Gaulke (2004)
20	<i>V. macraei</i>	--	--	36.0	Arboreal	Böhme & Jacobs (2004)
21	<i>V. melinus</i>	--	--	42.0	Arboreal, aquatic	Ziegler & Böhme (2004)
22	<i>V. olivaceus</i>	Small	--	65.0	Arboreal	Pianka (2004)
23	<i>V. prasinus</i>	--	--	29.5	Arboreal	Greene (2004)
24	<i>V. rudicolis</i>	--	--	59.0	Arboreal, terrestrial	Bennett (2004)
25	<i>V. salvadorii</i>	--	--	85.0	Arboreal	Horn (2004)
26	<i>V. salvator</i>	1.4-31.7	--	92.0	Terrestrial, arboreal, aquatic	Traeholt (1997) a,b Gaulke & Horn (2004)
27	<i>V. spinulosus</i>	--	--	31.2	Arboreal	Philipp <i>et al.</i> (2004)
28	<i>V. timorensis</i>	--	--	21.7*	Terrestrial & arboreal	King & Smith (2004)
29	<i>V. yuwonoi</i>	--	--	57.7*	Terrestrial, arboreal, aquatic	Philipp <i>et al.</i> (2004)
	Australia					
30	<i>V. acanthurus</i>	--	--	25.0	Terrestrial & arboreal,	Dryden (2004)
31	<i>V. bariitji</i>	--	--	25.2	Terrestrial/saxicolous	King (2004)
32	<i>V. breviceuda</i>	--	20	11.8	Terrestrial	James (1994) Pianka (2004)
33	<i>V. caudolineatus</i>	--	--	12.3♂ 11.8♀	Terrestrial/saxicolous & semi-arboreal	Thompson (2004)
34	<i>V. eremius</i>	large	--	16.0	Terrestrial	Pianka (2004)
35	<i>V. giganteus</i>	325.6± 127.0 (♂) 47.5 ± 9.1 (♀)	--	73.6♂ 59.1♀	Terrestrial	Heger (2000) Horn & King (2004)
36	<i>V. gilleni</i>	-	--	18.6	Terrestrial, arboreal	Horn (2004)
37	<i>V. glauerti</i>	1.25-7.36 HR♂>HR♀	--	^a 21.5♂ ^a 18.0♀	Terrestrial/saxicolous, arboreal	Sweet (1999) Sweet (2004)

No	Species	Home range (ha)	Density (per ha)	Max. adult SVL (cm)	Mode of life	Reference
38	<i>V. glebopalma</i>	3.5-7.7 HR large>HR small	--	^a 29.0♂ ^a 24.5♀	Terrestrial/saxicolous	Sweet (2004)
39	<i>V. gouldii</i>	8.91 HRlarge>HRsmall	--	^a 59.0♂ ^a 36.1♀	Terrestrial	Thompson (2004)
40	<i>V. keithhornei</i>	--	--	26.0	Arboreal	Irwin (2004)
41	<i>V. kingorum</i>	--	--	11.4	Terrestrial/saxicolous	King (2004)
42	<i>V. mertensi</i>	--	--	48.0	Semi-aquatic, arboreal	Christian (2004)
43	<i>V. mitchelli</i>	limited	--	32.0	Arboreal, semi-aquatic, terrestrial/ saxicolous	Schultz & Doody (2004)
44	<i>V. panoptes</i>	--	--	74.0	Terrestrial, arboreal	Christian (2004)
45	<i>V. pilbarensis</i>	--	--	16.9	Terrestrial/saxicolous	King (2004)
46	<i>V. primordius</i>	--	--	12.0	Terrestrial	Husband & Christian (2004)
47	<i>V. rosenbergi</i>	19.44±4.58	--	47.0	Terrestrial, arboreal	King & Green (1999) King (unpubl.)
48	<i>V. scalaris</i>	<1.5 (♂) <1.0 (♀)	--	25.3	Arboreal	Smith <i>et al.</i> (2004)
49	<i>V. semiremex</i>	--	--	27.0	Arboreal, semi-aquatic	Pianka (2004)
50	<i>V. spenceri</i>	--	--	55.0	Terrestrial	Vincent & Wilson (1989)
51	<i>V. storri</i>	Fairly small	--	13.2	Terrestrial	Eidenmüller (2004) Peters (1973)
52	<i>V. tristis</i>	40.3 (♂) 3.7 (♀)	--	30.5	Arboreal, Terrestrial/saxicolous	Pianka (2004) Thompson <i>et al.</i> (1999)
53	<i>V. varius</i>	65 ± 34(♂) 25 (♀) 184.5	--	76.5♂ 57.5♀	Arboreal, Terrestrial	Weavers (1993) Weavers (2004) Guarino (2002)

^a average*calculated using ratio of tail: SVL and total body length from Pianka *et al.* (2004)

Table 2. Body sizes, clutch sizes, and breeding periods of genus *Varanus* by continental groups.

No	Species	Clutch size	Mating period	Max. adult SVL (cm)	Sexual maturity	Reference
Africa						
1	<i>V. albigularis</i>	Max. 50 (larger, larger clutch)	July/August- September (rain season)		4-5 years	Phillips (2004)
2	<i>V. exanthematicus</i>	6-29 (Max. 41)	November	75.0	27.4 cm SVL (♀)	Bennett (2004)
3	<i>V. griseus</i>	10-20	June	58.3*	4-5 years	Stanner (2004)
4	<i>V. niloticus</i>	5-60	End of rainy season (Sept-Nov, West Africa; march-May, South Africa)	96.0*	3-4 years; 90-120 cm TL	Lenz (2004)
5	<i>V. ornatus</i>	--	bimodal	92.25*		Böhme & Ziegler (2004)
6	<i>V. yemenensis</i>	--	--	59		Gasperetti in Böhme (1989)
Asia						
7	<i>V. bengalensis</i>	8-29 ^{capt.}	June-July (Monsoon)	99.17	3-4 years ^{capt.} ≥5 years	Horn & Visser (1989)
		20.2 ^a				Pianka (2004) Auffenberg (1994)
8	<i>V. caerulivirens</i>	--	--	40	--	Ziegler <i>et al.</i> (2004)
9	<i>V. cerambonensis</i>	--	--	40.9	--	Philipp <i>et al.</i> (2004)
10	<i>V. doreanus</i>	--	--	46.0	--	Böhme <i>et al.</i> (2004)
11	<i>V. dumerilii</i>	Max. 23 ^{capt.}	--	50.0	--	Bennett (2004)
12	<i>V. finschi</i>	--	--	30.5	--	Philipp <i>et al.</i> (2004)
13	<i>V. flavescens</i>	4-30 (mean: 16)	June-July (wet season)	40.0*	26.0 cm SVL (♂) >25.0 cm SVL (♀) 3-4 yrs. (♂,♀)	Visser (2004)
14	<i>V. indicus</i>	10	Dry season	58.0	32.0 cm SVL (♂) 27.5 cm SVL (♀)	McCoid (1993) McCoid & Hensley (1991) Wikramanayake & Dryden (1988)
15	<i>V. jobiensis</i>	20-30	Simulated wet season (capt.)	45.0	--	Bayless & Dwyer (1997) Horn (1977)
16	<i>V. juxtindicus</i>	--	--	50.4	-	Böhme <i>et. al.</i> (2004)

No	Species	Clutch size	Mating period	Max. adult SVL (cm)	Sexual maturity	Reference
17	<i>V. komodoensis</i>	Max.33, mean 18	July-September (dry season) ^{capt.}	154.0	8-9 years (♂ & ♀) ^{capt.}	Ciofi (2004)
		1-30, mean 19	May-August			Auffenberg (1981)
18	<i>V. kordensis</i>	--	--	27.0	--	Jacobs (2004)
19	<i>V. mabitang</i>	6-12	May	64.0	--	Gaulke <i>et.al.</i> (2002) Gaulke (2004)
20	<i>V. macraei</i>	Multiple 3	--	36.0	--	Jacobs (2002) Böhme & Jacobs (2004)
21	<i>V. melinus</i>	1.5-3.4x (Max.12)	--	42.0	--	Ziegler & Böhme (2004)
		4x (2-7) ^{capt.}				Dedlmar & Böhme (2000)
22	<i>V. olivaceus</i>	4-11, mean 7.1	June-September	65.0	45.0 cm SVL (3 years)	Auffenberg (1988, 1994) Pianka (2004)
23	<i>V. prasinus</i>	3x (2-4)	--	29.5	2 years ^{capt.}	Greene (2004)
24	<i>V. rudicolis</i>	2-3x (Max.14, mean 8) ^{capt.}	--	59.0	--	Bennett (2004)
25	<i>V. salvadorii</i>	4-12 ^{capt.}	July & October ^{capt.}	85.0	-	Horn (2004)
26	<i>V. salvator</i>	Multiple, 5-22, mean 13 (correlated with ♀ size)	All year, peak in August	92.0	40 cm SVL (♂) 50 cm SVL (♀)	Shine <i>et. al.</i> (1998) Gaulke & Horn (2004)
27	<i>V. spinulosus</i>	--	--	31.2	--	Philipp <i>et al.</i> (2004)
28	<i>V. timorensis</i>	--	May-July	21.7*	--	King & Smith (2004)
29	<i>V. yuwonoi</i>	--	--	57.7*	--	Philipp <i>et al.</i> (2004)
	Australia					
30	<i>V. acanthurus</i>	2-18, mean 7.9	August & November (end dry season)	25.0	8.9 cm SVL (♂) 10.2 cm SVL (♀)	Dryden (2004) King & Rhodes (1982)
31	<i>V. baritji</i>	3-9	July	25.2	-	King (2004)

No	Species	Clutch size	Mating period	Max. adult SVL (cm)	Sexual maturity	Reference
32	<i>V. brevicauda</i>	2-3	September-October (Spring)	11.8	8.2 cm SVL (♂)	Pianka (1994)
					9.4 cm SVL (♀)	James (1996)
33	<i>V. caudolineatus</i>	Mean 4.3	--	12.3♂ 11.8♀	--	Pianka (1994)
						Thompson (2004)
34	<i>V. eremius</i>	2-6, mean 3.6	October - November (Spring)	16.0	11.6 cm SVL (♂) 11.0 cm SVL (♀)	Pianka (2004)
35	<i>V. giganteus</i>	13	Spring & early Summer	73.6♂ 59.1♀	45.0 cm SVL (♂) 49.0 cm SVL (♀)	King (1989) ^{mus} Horn & King (2004)
36	<i>V. gilleni</i>	Mean 4	Max. October (♀reproductive at longer period than♂)	18.6	10.0 cm SVL (♂) 9.5 cm SVL (♀)	James <i>et.al.</i> (1992) ^{mus} Horn & Visser (2004)
37	<i>V. glauerti</i>	3	mid-May to mid-July	^a 21.5♂ ^a 18.0♀	15.0 cm SVL (♂,♀)	Sweet (2004) James <i>et.al.</i> (1992)
38	<i>V. glebopalma</i>	5-7	August-October	^a 29.0♂ ^a 24.5♀	17.0 cm SVL (♂,♀)	Sweet (2004) James <i>et.al.</i> (1992) Barnett 1977)
39	<i>V. gouldii</i>	Mean 6.2	September-November	^a 59.0♂ ^a 36.1♀	25.0 cm SVL	Pianka (1994) Pianka (1970) Thompson (2004)
40	<i>V. keithhornei</i>	2x (2-4) ^{capt.}	September-May ^{capt.}	26.0	--	Irwin (2004)
41	<i>V. kingorum</i>	5x (3-6) mean 4.5 ^{capt.}	February (end of wet season) ^{mus.}	11.4	--	James <i>et.al.</i> (1992) Eidenmüller (2001) King (2004)
42	<i>V. mertensi</i>	3-14	February-July	48.0	--	Vincent & Wilson (1999) Shine (1986) Christian (2004)

No	Species	Clutch size	Mating period	Max. adult SVL (cm)	Sexual maturity	Reference
43	<i>V. mitchelli</i>	7-12	April (Late wet season) & June (mid-dry season)	32.0	22 cm SVL	Shine (1986)
		16-20 ^{capt.}	April			Schultz & Doody (2004)
44	<i>V. panoptes</i>	6-14	April	74.0	--	Christian (2004)
45	<i>V. pilbarensis</i>	Max.24 in 6x	February-March	16.9	--	King (2004)
46	<i>V. primordius</i>	2-5, mean 3.3 ^{capt.}	--	12.0	9-12 months ^{capt.}	Husband (2001)
47	<i>V. rosenbergi</i>	10-17	January-February (mid-summer)	47.0	--	Green <i>et.al.</i> (1971) King & Green (1979) King (unpbl.)
48	<i>V. scalaris</i>	3-12, mean 7.7	May-mid-June	25.3	12.5 cm SVL (♂)	Smith <i>et al.</i> (2004)
49	<i>V. semiremex</i>	2-14, mean 5.9	February-April (late wet season)	27.0	15.0 cm SVL	King (2004)
50	<i>V. spenceri</i>	1x (11-35)	August	55.0	28.0 cm SVL (♂)	Lemm & Bedford (2004) Greer (1989) Vincent & Wilson (1989) Fyfe (unpbl.)
51	<i>V. storri</i>	1-6, mean 3.9	February-March & July-November	13.2	9.0 cm SVL (♂,♀)	Eidenmüller (2004) Peters (1973) James <i>et.al.</i> (1992)
52	<i>V. tristis</i>	5-17, mean 10.1	October-November (Spring)	30.5	20.0 cm SVL (♂,♀)	Pianka (1994) Pianka (2004)
53	<i>V. varius</i>	5 ^{capt.}	mid-November to early January	76.5♂ 57.5♀	3 years ^{capt.}	Carter (1990) Weavers (2004)
			March ^{capt.}			Boylan (1995)

^{capt.} = in captivity

^{mus.} = museum specimens