Can Morphometrics Predict Sex in Varanids?

J. G. Smith, 1,2 B. W. Brook, 1 A. D. Griffiths, 1 and G. G. Thompson 3

¹School for Environmental Research, Charles Darwin University, Darwin, Northern Territory, Australia, 0909 ³Centre for Ecosystem Management, Edith Cowan University, Joondalup Drive, Joondalup, Western Australia, Australia, 6027

ABSTRACT.—Varanid lizards are difficult to sex in the field because commonly used techniques are not completely reliable and definitive techniques are not logistically or economically feasible for many field-based applications. Previous work has shown that variation in morphometric variables can be used to determine sex in some species of varanid. Here we build on these previous exploratory analyses by developing a set of a priori models (containing morphometric variables) to predict the sex of six species of Australian varanid, and then examining their relative support under the information-theoretic framework. We then use cross-validation procedures to determine the reliability of the best-supported models' predictive ability. Our analysis suggests that a large sample size is required for building models to predict sex in many species. The most important sexually diagnostic features for many species were a number of head variables and (to a lesser extent) scaling of limb proportions. This analysis provides some useful statistical tools for the field-sexing of adult and juvenile Varanus gouldii with a known level of reliability and also serves to highlight the danger of extrapolating from potentially spurious results when using exploratory methods or null hypothesis testing.

Many aspects of an animal's biology are sex related. Habitat preferences, home- and activity-range size, behavior and feeding strategies are some of the ecological parameters affected by sex differences (Calder, 1984; Shine et al., 1998b). Despite this, little is known about the influence of sex on varanid life histories, primarily because it is very difficult to determine their sex in the field (Green and King, 1978; Shine, 1986; Gaulke, 1997; Sweet, 1999).

A variety of methods have been use to determine sex in varanids (Pianka et al., 2004). Adults of some species can be sexed ex situ by the radiographic visualization of hemipenial bones if present (Shea and Reddacliff, 1986), but the absence of these bones does not always guarantee a female, or small ossifications in some females can be confused with hemipenial bones. Fiberoptic laparoscopy (Davis and Phillips, 1991) and coelioscopy (Schildger et al., 1999) can be used for the sexing of individuals of almost any age, however, logistical and financial constraints generally prohibit these techniques being readily available to researchers in the field. Adult males of many species in the Odatria subgenus can be identified by scalation differences adjacent to the vent (G. Husband pers. comm.; Gaulke, 1997), whereas other species exhibit sexual dimorphism in snout size (Bennett, 1998) and overall body size (Shine, 1986; Auffenberg et al., 1991). Manual or

auto-eversion of hemipenes (Auffenberg et al., 1991; Thompson, 1992; Weavers, 1993; Thompson et al., 1999) and probing of hemipenial pockets (Auliya and Erdelen, 1999; Gaulke et al., 1999) have also been used as sex determining techniques although females of some species are known to possess similarly eversible structures (Bohme, 1991) and conscious wild varanids actively resist probing and attempts at manual eversion (Gaulke, 1997). More recently, Mayes et al. (2005) used a combination of hemipene eversion and sex hormone ratios with considerable success. However, the cost and effort associated with the hormonal analysis excludes it as a useful tool in the field.

Although there are numerous techniques for determining varanid sex, they all have pitfalls. After reviewing these techniques, Gaulke (1997) cautioned that no field methods of sex determination in varanids is completely reliable, including behavioral observations such as combat (once presumed to be only males) and the visiting of egg-laying sites following egg deposition. Importantly, the uncertainty inherent in estimating a varanids' sex in the field is not amenable to direct quantification, and as such, an unmeasured yet implicit level of uncertainty is always carried forward into further analyses but hitherto never accounted for. This may be at least part of the reason why past attempts at determining sex with statistical methods have met with mixed success.

Thompson (2002) determined that bodylength to head-length ratios could not be used

²Corresponding Author. E-mail: james.smith@cdu.edu.au

to determine sex in many species of the *Varanus* subgenus but could be useful (when combined with other methods) in assessing sex in some members of the *Odatria*. Exploratory analyses (using stepwise discriminant analysis) of various morphological characters in Australian varanids (of known sex) using museum specimens suggested that morphological characters could be used to predict sex in 10 of the 18 Australian varanid species they studied (Thompson and Withers, 1997). However, they found no single morphological variable or suite of variables that could discriminate reliably between sexes for this genus.

The aim of this paper is to build on the exploratory analysis of Thompson and Withers (1997) by examining the morphometric variables they noted for sex prediction (among others derived from the literature and other fieldworkers) for six species of varanid from the tropical north of Australia, using the largest dataset yet assembled for these species. Because exploratory analysis lacks any basis for strong inference, we used an Information-Theoretic framework (Burnham and Anderson, 2001) with the goal of developing a suite of morphological variables that can be measured in the field and used to predict sex with a known level of reliability.

MATERIALS AND METHODS

A review of the relevant literature and conversations with many varanid field biologists and captive breeders was carried out to generate a suite of morphological variables most likely to enable the determination of sex (Fig. 1). The only variables chosen were those that were unlikely to change following preservation of specimens. These morphological variables were measured in six species of varanids from the Museum of the Northern Territory, the Queensland Museum and the Western Australian

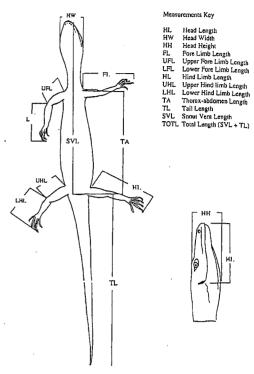


Fig. 1. Morphometric measurements used in model construction.

Museum (Table 1). Measurements were made to \pm 1 mm with the body of each specimen placed in the approximate position shown in Figure 1. For some specimens, where the end of the tail had obviously broken off, the tail measurement was not used. The actual sex of each individual was determined by visual inspection of the gonads.

Model Development.—Following the recommendations of Burnham and Anderson (2002), multiple working hypotheses were developed

TABLE 1. Number of specimens examined, mean snout—vent lengths (SVL) \pm SE and subgeneric classification for six species of variand measured.

Species	Subgenus	Sex	N	SVL
V. gouldii	Varanus	M	96	310.90 ± 0.98
•		F	5 9	267.46 ± 1.16
V. mertensi	Varanus	M	30	348.03 ± 3.56
+		F	21	347.38 ± 2.74
V. panoptes	Varanus	M	22	315.55 ± 6.92
•		F	11	324.00 ± 7.24
V. eremius	Odatria	M	40	148.43 ± 0.43
		F	23	134.04 ± 1.06
V. glebopalma	Odatria	M	24	313.79 ± 1.53
•		F	7	251.71 ± 3.86
V. mitchelli	Odatria	M	25	206.04 ± 2.31
		F	19	214.58 ± 1.59

TABLE 2. Explanation of all derived parameters used in model construction.

Parameter	Derivation	Explanation		
HeadL	HĹ/SVL	Head length divided by SVL		
HeadW	HW/SVL	Head width divided by SVL		
HeadH	HH/SVL	Head height divided by SVL		
AVL		Average length of all limbs divided by SVL		
HV	((FL·2+HL·2)/4)/SVL 648.05·exp ^(0.0093·SVL)	The relationship between head volume ((Head Width · Head Length · Head Height)/2) and SVL		
HL_FL	(HL/FL)/SVL	(Hind-limb length divided by forelimb length), all divided by SVL		
UpperFL	UFL/SVL	Upper forelimb length divided by SVL		
UpperHL	UHL/SVL	Upper hind-limb length divided by SVL		
Tail	TL/SVL	Tail length divided by SVL		
Ta	TA/SVL	Thorax-abdomen length divided by SVL		
LowerHL	LHL/SVL	Lower hind limb divided by SVL		
UpperFL	UFL/SVL	Upper forelimb divided by SVL		
LowerFL	LFL/SVL	Lower forelimb divided by SVL		

a priori in an attempt to explain which morphometric variables can best predict sex. These hypotheses were based on a review of the relevant literature, discussions with fellow varanid biologists, and the authors' experience. Many parameters were derived from relationships between morphometric variables (Table 2), and then a set of models (incorporating single derived variables, multiple variables or combinations of variables, Table 3) was developed to represent each hypothesis. In addition, a further model was generated separately for each species, incorporating the best supported parameters that Thompson and Withers (1997) found to predict sex in varanids.

Consistent with Burnham and Anderson (2001), the number of models (R) compared to sample size for each species was kept low (R = 9 for all species except Varanus mitchelli, where R = 8, see Table 3), by dismissing some hypotheses suspected to be unrealistic or uninformative for this dataset on a priori grounds. For example, many museum specimens had broken tails; therefore, the hypothesis that males have longer tails in some species (Gaulke, 1997; Shine et al., 1998a) could not be examined. Because very large adults of many species can be recognised as males (Shine, 1986), the question of whether the sex of individuals of similar size can be discerned by morphometrics is more interesting and applicable to field researchers; therefore, the hypothesis of total size was also excluded. Because the candidate set for each species had one model that differed from the other species, the resultant global models (which incorporate all parameters in every model) were correspondingly different. A null model (where no morphological variable can predict sex, with the prediction based simply on the observed proportion of male:fe-

male) was also incorporated into each candidate set, because this is another plausible hypothesis.

Model Fitting.—Each model in the candidate set was analyzed as a binomial generalized linear model with a logit link function using sex as the response variable, in the program R (vers. 1.9.0, R Development Core Team, Vienna, Austria, 2004). Generalized linear models were fit firstly to the entire dataset of each species. Then where sample size allowed, datasets were split into mature individuals (based on size at known maturity from the literature) and the same models were refit to each of the adult subset and the juvenile subset where sample sizes allowed (N > 20).

Model Selection.-Model selection was performed using Information-Theoretic model selection methods based on Akaike's Information Criterion (AIC, Burnham and Anderson, 2002). This procedure uses Kullback-Leibler information as an objective basis for selecting the model that explains the most substantial proportion of variance in the data yet excludes unnecessary parameters that cannot be justified by the data (the most "parsimonious model," sensu Burnham and Anderson, 2002). Because the ratio of sample size to parameters was always low, the second-order bias corrected form AICc was used as the basis for model selection (Burnham and Anderson, 2002). These AICC values were then rescaled as simple differences (Δ_i) allowing a quick comparison for the ranking of candidate models (Burnham and Anderson 2001). Akaike weights (w_i) were calculated for each species' candidate set of models, thus providing a measure of the relative likelihood of each model, given each dataset and each candidate set. Models were deemed to have substantial support if Δ_i fell within 1–2 of the best model (Burnham and Anderson, 2001).

TABLE 3. Candidate model sets for predicting the sex of each species, the hypothesis examined under each model and references concerning sexual dimorphism in varanids leading to each model. The first seven models were used for every species. An eighth model for each species was developed, incorporating parameters suggested by Thompson and Withers (1997). Therefore, the global models are model nine (below) with the addition of the new terms included in model eight for that species. *Varanus mitchelli* had no new parameters added; therefore, its global model is model eight.

No.	Model	Hypothesis	Reference Gaulke (1997)		
1	HL	Hind-limb length varies in relation to body size (SVL) between sexes			
2	HeadW .	Head width varies in relation to body size (SVL) between sexes	This study		
3	AVL	Average limb length varies in relation to body size (SVL) between sexes	Gaulke (1997)		
4	HeadV	Head volume varies in relation to body size (SVL) between sexes	Bennett (1998) Thompson (2002)		
5	HeadV + AVL	A combination of average limb length and head volume vary in relation to body size (SVL) between sexes	Gaulke (1997) and this study		
6	HL_FL	A ratio of hind-limb length to forelimb length, varies in relation to body size (SVL) between sexes	Gaulke (1997)		
7	~1 V. glebopalma				
8	UpperFL + UpperHL + Tail	A combination of upper forelimb length, vary in relation to body size (SVL) between sexes	Thompson and Withers (1997)		
8	V. gouldii UpperHL + HeadH	A combination of upper hind-limb length	"		
		and head height, all vary in relation to body size (SVL) between sexes			
	V. mertensi		,,		
8	Ta + LowerHL + Tail	A combination of thorax abdomen length, lower hind-limb length and tail	<i>"</i>		
		length , all vary in relation to body size (SVL) between sexes	·		
_	V. eremius	TT for all old located and a selection to	u		
8	UpperFL	Upper forelimb length varies in relation to body size (SVL) between sexes			
8 .	V. panoptes LowerHL + LowerFL +UpperFL	A combination of upper hind-limb length, lower forelimb length and upper forelimb length, all vary in relation to body size (SVL) between sexes	<i>"</i>		
9	HeadL + AVL + HeadV + HeadW + HL_FL	Global model: all parameters together predict sex. *plus additional parameters in model 8 (above) for each species			

To examine the utility of each model as a predictive tool, the K-fold cross-validation prediction error (Blum et al., 1999) was estimated for all models in each candidate set with a substantial level of support. In this procedure the data are divided randomly into K-groups. For each group the generalized linear model is fit to data omitting that group and the prediction error (interpreted as percentages) associated with predicting the observed responses (i.e., those left out of the fitting) in each group from the model fit, is generated. In this case, leave-one-out cross-validation was used (where K = the number of individuals), allowing all

possible splits of the data to be examined. These values were then expressed as levels of prediction reliability (1-prediction error).

Characteristic Body Size.—Kratochvil et al. (2003) recommend cautious inspection of body scaling parameters before analyses and interpretations of sexual dimorphism are made. Therefore, to establish which of three highly correlated variables best characterized the "body size" of a varanid (for use in model development), snout-vent length (SVL), total length (TOTL) and thorax-abdomen length (TA) were fit as generalized linear models (with sex as the response variable) separately across

Table 4. Summary of second-order Akaike's information criterion (AICc) and associated statistics for all candidate models for the analysis of sex prediction in the adult and juvenile *Varanus gouldii* subsets. All models are ranked according to support, thus $\Delta_i = 0$ for the best model. Akaike weights (w_i) and the leave-one-out cross-validation prediction reliability for all models with substantial support ($\Delta_i \leq 2$) are also shown. Only models displaying a reasonable level of support ($\Delta_i < 10$) are shown.

Model	log(L)	K	AICc	Δ_i	w_i	cv. reliability (%)
Adults	(N = 83)					
global HV AVL + HV	-20.7914 -26.7820 -26.3263	6 3 4	54.1503 59.7228 60.9192	0.0000 5.5725 6.7689	0.9093 0.0561 0.0308	84
Juveniles	(N = 69)			00,	0.0000	
global HV AVL + HV HL.FL	-33.7063 -36.9545 -36.7216 -39.5729	6 3 4 3	79.9801 80.0680 81.7098 85.3047	0.0000 0.0879 1.7297 5.3246	0.4010 0.3838 0.1689 0.0280	71 67 67

all species. All three models had substantial support, all having Δ_i within 1–2 of the best model. Therefore, they could not be discerned from one another (Burnham and Anderson, 2001). SVL is the most widely used in the literature (Wikelski et al., 1997; Shine et al., 2001; Webb et al., 2001; Perry and Garland, 2002) and was, therefore, chosen as the characteristic body size determinant.

Many physiological variables do not covary in a linear fashion with body mass, and the intercept of the regression line between them does not go through zero (Packard and Boardman, 1999). To examine this potential bias in our data, we plotted all variables used against SVL and fit each intercept through zero. All variables had r^2 -values of over 0.8, with the only exception being the variable Head Volume (HV) that was shown to vary exponentially with SVL. Therefore, each equation for this relationship was incorporated into all models containing the HV parameter.

RESULTS

Combined Adult and Juvenile Varanids.—For three of the six monitors studied (Varanus panoptes, V. mitchelli, and Varanus mertensi), the most parsimonious model selected in each candidate set was the null model, indicating that none of those models examined was able to predict varanid sex substantially better than chance. All candidate sets that ranked the null as the most likely model also ranked models containing head variable parameters with substantial support. Among the most supported models in most other species, various head variables, either solely or (less often) in combination with limb length parameters, were more prevalent in higher ranked models than models containing limb length parameters only. For Varanus eremius, the model containing the single variable HL_FL was clearly the most supported in the candidate set, explaining 61.5% of the total variance. The cross-validation prediction reliability, however, was 63%, indicating that using this parameter alone to determine sex is again not much better than chance (50:50%).

The model set for Varanus gouldii contained three models that were ranked with substantial support. None of the models could be easily distinguished from each other, as indicated by the Akaike weights (Burnham and Anderson, 2002). The resultant cross-validation prediction reliability across the three best ranked models (mean = $57\% \pm 0.05$ SD) indicated that these parameters are of little use for determining sex in this species. Varanus glebopalma was the only species for which a model or combination of other parameters (HV and AVL + HV) were the best supported models. The global model fit for this species was 58%, and the resultant crossvalidation prediction reliability estimations averaged 82%.

Adult Varanids.—For two of the three species where sample sizes of adults were large enough for analysis (V. mertensi and V. mitchelli), two closely ranked best models both contained elements of head and limb variables, suggesting that the morphological differences between males and females in these species is either very slight or is associated with a change in overall allometry, rather than one single attribute.

The global model for adult *V. gouldii* was ranked as the best model, because it was 18 times better than the next best model in the candidate set (based on their evidence ratios, Anderson and Burnham, 2002). Cross-validation prediction reliability was very high (84%), indicating that the global model for this species could prove useful for predicting sex in adults (Table 4). Standardized regression coefficients (as used by Conroy and Brook, 2003) for the

global model showed that the head volume parameter (HV) accounted for three times the variation of the other parameters.

Juveniles.-Only three species had sufficient sample size (N > 20) of juveniles for this analysis. In juvenile V. panoptes, the null model could not be discerned from the other highest ranked models model set, indicating that no model could be used to predict sex. The V. mitchelli juvenile dataset had HL_FL ranked as the best model, and its evidence ratio indicated it was 3.4 times better than the next best model. The V. mitchelli global model explained 41% of the total variation and the cross-validation prediction reliability for this model was 70%. This model is potentially a useful tool for sexing V. mitchelli. The three best ranked models for sexing juvenile V. gouldii were the same best ranked models in the adult and all individualscombined datasets. The average cross-validation prediction reliability for these models within the juvenile subset was 68.4%.

Previous Hypotheses.—Across all species, in all of the expanded data sets and adult subsets, none of the models predicted by Thompson and Withers (1997) were ranked within $\Delta_i = 1-2$ of the best model, and only 5.6% of the time, they were ranked amongst those models with a reasonable level of support ($\Delta_i \leq 10$).

sonable level of support ($\Delta_i \leq 10$). Sex Prediction in Varanus gouldii.—Because the V. gouldii dataset was the largest (N=155) and the resultant global models for the adult subset had a reasonable level of explained deviance (64%) and high cross-validation prediction reliability (84%), equations were derived from the global models to predict sex in this species. Male and female V. gouldii appear to mature at different sizes (Shine, 1986); therefore, the utility of the following equation is only practical when applied to specimens larger than the size at maturity for males. To solve for sex (male; y > 0.5 < y; female) in an adult (SVL > 320 mm), V. gouldii with 84% reliability:

$$y = \frac{1}{1 + e^{-(\text{Model})}}$$

where model = $14.9 + (1 \cdot \text{AVL}) + (0.0037 \cdot \text{HV}) + (5125.9 \cdot \text{HL_FL}) + (11.34 \cdot \text{UpperHL})$, the terms AVL, HL_FL, and UpperHL are as defined in Table 2 and HV = $648.05 \cdot \exp^{(0.0093 \cdot \text{SVL})}$. To solve for sex (y) in a juvenile (SVL < 280 mm) *V. gouldii* with 71% reliability:

$$y = \frac{1}{1 + e^{-(Model)}}$$

where, model = $-6.9 + (19.3 \cdot AVL) + (0.00557 \cdot HV) + (325 \cdot HL_FL) - (35.7 \cdot UpperHL)$, the

terms AVL, HL_FL and UpperHL are as defined in Table 2 and HV = $648.05 \cdot \exp^{(0.0093 \cdot \text{SVL})}$.

DISCUSSION

Sexual dimorphism is common in lizard species (Olsson et al., 2002), with the most consistently dimorphic traits being head size (males having larger heads) and trunk length (the distance between the front and hind legs) is greater in females. Our analysis also suggests that numerous head variables (principally head volume) and (to a lesser extent) scaling of limb proportions can also be important diagnostic features for sex prediction in some species of varanids. Bennett (1998) stated that male Varanus salvadorii and Varanus albigularis develop bulbous snouts with extreme old age. Investigation of sexually mature individuals of these and other species may show similar head volume dissimilarities.

Although sexual dimorphism has been recorded among neonate snakes (King et al., 1999), allometric sexual dimorphism may not be present in varanids until maturation. In this analysis, the candidate sets fit to adult varanids showed a higher proportion of models that could be discerned from the null models and higher levels of explained deviance. However, the degree of precision by which these parameters can be used to determine sex, based on our cross-validation assessment, was in most cases not high enough to warrant their use as a predictive tool.

The most effective sex prediction tool was developed for *V. gouldii*, where the global model for adult monitors, which combined several head and limb proportion variables, was able to predict sex with a reasonably high level of accuracy. Given that sex prediction in *V. gouldii* appears much more reliable than in other species, with higher levels of variation explained by the global model and high percentage of correct predictions, it is possible that either *V. gouldii* is more sexually dimorphic than other species or higher sample sizes may be required for effective sex prediction models to be developed for other species.

None of the models that Thompson and Withers (1997) found to be significant using null hypothesis testing were well supported for any of the species we analyzed. This striking difference between the results of the two studies highlights the limitations of the null hypothesis approach and shows, as suggested by Anderson and Burnham (2002), how exploratory analysis can sometimes produce spurious results. Clearly, although data-driven methods can be useful in the early stages of analysis, we now have the benefit of more objective techniques, such as the

Information-Theoretic paradigm (Burnham and Anderson, 2002), which allow more powerful inferences to be made.

Varanid lizards probably recognize the sex of conspecifics using behavioral cues and pheromones. Because varanids can be extremely shy animals, behavioural observation studies can be very labor- and time-intensive, and discerning sex by behavioral observation is not possible for most research projects unless definite mating/ copulatory behavior is observed (e.g., King and Green, 1979; Auffenberg, 1981; Carter, 1990; McCoid and Hensley, 1991). Long-term studies of varanids could take advantage of the olfactory sensitivity of a dog trained in recognizing different sexes of a certain species by their odor. Other predictive techniques that have been suggested by various authors, such as examination of scale rosettes cranial to the vent in males (Auffenberg, 1981) and more prominent skin flaps and scale micropores (S. Sweet, pers comm.; Gaulke, 1997), should be investigated in more detail for Australian varanids.

The most reliable (albeit expensive and time-consuming) method of sexing monitor lizards is by direct examination of the gonads (e.g., Schildger et al., 1999). However for the field biologist, sex-specific DNA probes, requiring a blood sample to be taken from each individual, would probably be less costly, both economically and logistically. There is currently such a probe available for *Varanus komodoensis* (Murphy et al., 2002) and *Varanus rosenbergii* (W. Smith, pers. comm.); but further work needs to be done before it is available for other species.

Creating larger datasets of the morphometrics of other species and analyzing them using an a priori multiple working hypothesis approach could provide more useful sex prediction models. When used in conjunction with other methods, these models will help to expand the capabilities of researchers and others to predict the sex of varanids in the field, quickly, inexpensively, and with a known level of uncertainty that can be appropriately propagated in further statistical analyses.

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LITERATURE CITED

Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using Information Theoretic methods. Journal of Wildlife Management 63:912–928.

- AUFFENBERG, W. 1981. The Behavioural Ecology of the Komodo Monitor. University Presses of Florida, Gainesville.
- Auffenberg, W., Q. Nazar, and N. Khurshid. 1991. Preferred habitat, home range and movement patterns of *Varanus bengalensis* in southern Pakistan. Mertensiella 2:7–28.
- AULIYA, M. A., AND W. ERDELEN. 1999. A field study of the water Monitor Lizard (*Varanus salvator*) in west Kalimantan, Indonesia. New Methods and Old Problems. Mertensiella 11:247–266.
- Bennett, D. 1998. Monitor Lizards: Natural History, Biology and Husbandry. Frankfurt am Main, Frankfurt, Germany.
- BLUM, A., A. KALAI, AND J. LANGFORD. 1999. Beating the hold-out: bounds for K-fold and progressive crossvalidation. In Proceedings of the 10th Annual Conference on Computational Theory, pp. 203–208.
- BOHME, W. 1991. Hemiclitoris discovered: a fully differentiated erectile structure in female Monitor Lizards (*Varanus* spp.) (Reptilia: Varanidae). Journal of Systematics and Evolution Research 33:129–132.
- BURNHAM, K. P., AND D. R. ANDERSON. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. Wildlife Research 28:111–119.
- 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd ed. Springer, New York.
- CALDER, W. A. 1984. Size, Function and Life History. Harvard University Press, Cambridge, MA.
- CARTER, D. B. 1990. Courtship and mating in wild Varanus varius (Varanidae: Australia). Memoirs of the Queensland Museum 29:333–338.
- CONROY, S. D. C., AND B. W. BROOK. 2003. Demographic sensitivity and persistence of the threatened white-and orange-bellied frogs of Western Australia. Population Ecology 45:105–114.
- DAVIS, R. B., AND L. G. PHILLIPS. 1991. A method of sexing the Dumeril's Monitor Varanus dumerilii. Herpetological Review 22:18–19.
- GAULKE, M. 1997. Sex determination of Monitor Lizards in the field- A review of methods. Hamadryad 22:28–31.
- GAULKE, M., W. ERDELEN, AND F. ABEL. 1999. A radiotelemetric study of the water Monitor Lizard (Varanus salvator) in north Sumatra, Indonesia. Mertensiella 11:63–78.
- GREEN, B., AND D. KING. 1978. Home range and activity patterns of the Sand Goanna, Varanus gouldii (Reptilia: Varanidae). Australian Journal of Wildlife Research 5:417–424.
- KING, D., AND B. GREEN. 1979. Notes on diet and reproduction of the Sand Goanna, Varanus gouldii rosenbergi. Copeia 1979:64–70.
- KING, R. B., T. D. BITTNER, A. QUERAL-REGIL, AND J. H. CLINE. 1999. Sexual dimorphism in neonate and adult snakes. Journal of the Zoological Society of London 247:19–28.
- Kratochvíl, L., M. Fokt, I. Rehák, and D. Frynta. 2003.
 Misinterpretation of character scaling: a tale of sexual dimorphism in body shape of common lizards. Canadian Journal of Zoology 81:1112–1117.
- MAYES, P. J., S. D. Bradshaw, and F. J. Bradshaw. 2005. Successfully determining the sex of adult *Varanus* mertensi (Reptilia: Varanidae) using a combination

of both hemipenile eversion and the ratio of androgens estradiol in plasma. Annals New York Academy of Science 1040:402-405.

McCoid, M., J., and R. A. Hensley. 1991. Mating and combat in Varanus indicus. Herpetological Review 22:16-17

MURPHY, J. B., C. CIOFI, C. DE LA PANOUSE, AND T. WALSH (EDS). 2002. Komodo Dragons: Biology and Conservation. Smithsonian Institution Press, Washing-

Olsson, M., R. Shine, E. Wapstra, B. Ujvari, and T. MADSEN. 2002. Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity

selection. Evolution 56:1538-1542.

PACKARD, G. C., AND T. J. BOARDMAN. 1999. The use of percentages and size-specific indices to normalize physiological data for variation in body size: wasted time, wasted effort? Comparative Biochemistry and Physiology A 122:37-44.

PERRY, G., AND T. GARLAND. 2002. Lizard home ranges revisited: effects of sex, body size, diet, habitat, and

phylogeny. Ecology 83:1870–1885. Pianka, E. R., D. King, and R. A. King (eds). 2004. Varanoid Lizards of the World. Indiana University Press, Bloomington.

SCHILDGER, B., H. TENHU, M. KRAMER, M. GERWING, G. KUCHLING, G. THOMPSON, AND R. WICKER. 1999. Comparative diagnostic imaging of the reproductive tract in monitors. Radiology-Ultrasonography-Coelioscopy. Mertensiella 11:193-211.

SHEA, G., AND G. L. REDDACLIFF. 1986. Ossifications in the hemipenes of Varanids. Journal of Herpetology

20:566-568.

SHINE, R. 1986. Food habits, habitats and reproductive biology of four sympatric species of Varanid lizards in tropical Australia. Herpetologica 42:346-360.

SHINE, R., AMBARIYANTO, P. S. HARLOW, AND MUMPUNI. 1998a. Ecological traits of commercially harvested Water Monitors, Varanus salvator, in northern Sumatra. Wildlife Research 25:437-447.

SHINE, R., P. S. HARLOW, J. S. KEOGH, AND BOEADI. 1998b. The influence of sex and body size on food habits of a giant tropical snake, Python reticulatus. Functional Ecology 12:248-258.

SHINE, R., D. O'CONNOR, M. P. LEMASTER, AND R. T. MASON. 2001. Pick on someone your own size: ontogenetic shifts in mate choice by male garter snakes result in size-assortative mating. Animal Behaviour 61:1133-1141.

Sweet, S. 1999. Spatial ecology of Varanus gauerti and V. glebopalma in northern Australia. Mertensiella

11:317-366.

- THOMPSON, G. 2002. The feasibility of using body proportions in Western Australian varanids (Varanus) as a method for determining a specimen's sex. Records of the Western Australian Museum 20:437-439.
- THOMPSON, G. G. 1992. Daily distance travelled and foraging areas of Varanus gouldii (Reptillia: Varanidae) in an urban environment. Wildlife Research 19:743-753.
- THOMPSON, G. G., AND P. C. WITHERS. 1997. Comparative morphology of Western Australian varanid lizards (Squamata: Varanidae). Journal of Morphology 233:127-152.
- THOMPSON, G. G., M. DE BOER, AND E. R. PIANKA. 1999. Activity and daily movements of an arboreal monitor lizard, Varanus tristis (Squamata: Varanidae) during the breeding season. Australian Journal of Ecology 24:117-122.

Weavers, B. W. 1993. Home range of male lace monitors Varanus varius (Reptilia: Varanidae), in south-eastern Australia. Wildlife Research 20:

303-313.

WEBB, J. K., G. P. Brown, and R. Shine. 2001. Body size, locomotor speed and antipredator behaviour in a tropical snake (Tropidonophis mairii, Colubridae): the influence of incubation environments and genetic factors. Functional Ecology 15:561-568.

WIKELSKI, M., V. CARRILLO, AND F. TRILLMICH. 1997. Energy limits to body size in a grazing reptile, the Galapagos Marine Iguana. Ecology 78:2204-2217.

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