A Comparative Assessment of Varanid Lizard Thermal Husbandry in Zoos and Private Collections: Disparate Ideologies or a Paradigm Disconnect?

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Abstract. Zoos and private herpetoculturists have both played crucial roles in advancing the keeping and breeding of varanid lizards (Genus: *Varanus*) in captivity. From a historical perspective, herpetological husbandry in zoos and private collections has often differed due to various factors including, but not limited to differences in their keeping philosophies, spatial constraints and available resources. To gain a better understanding of contemporary varanid husbandry practices and determine whether significant differences in captive management exist between these two keeping groups, this study investigated the thermal conditions currently offered to varanid lizards in captivity by surveying 31 North American zoos and 236 private keepers from 21 countries. Our results illustrate remarkable differences in thermal husbandry between zoos and private keepers, including the continued usage of outdated keeping methodologies that conflict with what is currently understood about varanid thermal biology. Private keepers offered significantly greater maximum surface basking temperatures and thermal gradients than North American zoos. Significant differences in thermal husbandry were also apparent between private keepers from different geographical regions, with North American and Australian keepers offering greater basking temperatures and thermal gradients than European and Asian keepers. In light of these findings, we discuss why such a dichotomy in thermal husbandry exists between zoos and private keepers as well as between private keepers from different geographical regions, and identify specific areas of captive management that may be affecting the range of thermal conditions being offered. Additionally, we highlight the importance of maintaining familiarity with current literature on the biology and captive management of varanids, as well as the need for improved communication and collaboration between zoos and private keepers for advancing standards of husbandry and improving keeping success.

Key words: *Monitor lizards, varanids, Varanus, captivity, thermal husbandry, zoos, private herpetoculturists.*

Introduction

On account of their unique physical attributes, intelligence and behavioral complexity, monitor lizards (Varanidae: *Varanus*) are popular in captivity and have been kept by zoological parks and private reptile keepers for nearly two centuries (Cox, 1831; Mitchell, 1852; Anonymous, 1859). Varanid husbandry progressed very slowly over most of this time, due largely in part to a poor understanding of their biology, as well as the lack of sophisticated heating, lighting, and other husbandry equipment. Beginning around the 1970s, however, varanid husbandry began to advance rapidly, with many of the world's first captive breeding events soon taking place in zoos and private collections across Europe, North America, and Australia (see Horn & Visser, 1989, 1997). As a direct result of improved husbandry techniques and various publications contributed by pioneering zoos and private keepers, varanids are now living longer in captivity and reproducing with greater frequency than in previous decades (Horn & Visser, 1989, 1997; Retes & Bennett, 2001; Brown 2012; Mendyk, 2012, 2015). Yet, even with these dramatic improvements, there are still various husbandry-related challenges and health issues that continue to affect this group in captivity (Boyer & Boyer, 1997**;** Hartdegen, 2002; Spelman, 2002; Horn, 2004; Mendyk, 2012, 2015; Mendyk *et al*., 2013). One key aspect of their husbandry that is often overlooked or misunderstood and may be affecting long-term keeping and breeding success in this group is thermal husbandry- the range of temperatures provided to captives for thermoregulation (Mendyk *et al*., 2014).

With efficient control over their thermoregulation and breathing, varanid lizards can maintain activity for extended periods over a broad range of temperatures (Earll, 1982; Auffenberg, 1994; Thompson & Withers, 1997; Thompson, 1999; Sweet & Pianka, 2007). As heliotherms, they typically thermoregulate by moving between sunlit and shaded areas or sheltered retreats depending on their thermal needs throughout the day. As a group, they have surprisingly high preferred body temperatures in the field, ranging from 35 to 39° C for most species (*e.g.*, Stebbins & Barwick, 1968; Pianka, 1970, 1994; King *et al*., 1989; Wikramanayake & Dryden, 1993; King & Green, 1999; Heger & Heger, 2007), although several taxa have been recorded with occasional field body temperatures greater than 40° C (King *et al*., 1989; Auffenberg, 1994; Pianka, 1994; King & Green, 1999; Thompson *et al.*, 1999; Ibrahim 2000). Since conductive heat transfer with heated substrates appears to be more important to their thermoregulation than direct solar radiation alone (Auffenberg, 1994), varanids often bask atop heated substrates and surfaces that are considerably hotter (often exceeding 45° C) than their preferred body temperatures (Mendyk *et al*., 2014). Reaching these temperatures quickly can be advantageous for reducing the amount of time spent basking in open and exposed areas to avoid predation, and often requires selecting elevated surface temperatures for basking activities (Mendyk *et al*., 2014). Equally as important to their thermoregulation, varanids also seek out burrows and other sheltered retreats, where temperatures can range more than 18° C cooler than the outside ambient air temperature (Warburg, 1965). Thus, varanid lizards regularly utilize a wide range of available temperatures to satisfy changing thermal needs throughout the day.

Ideally, reptiles maintained in captivity should be provided with access to a similar range of environmental conditions to what they would normally encounter in nature to enable them to satisfy their behavioral, physiological and psychological needs (Peaker, 1969; Arena & Warwick, 1995; Guillette *et al*., 1995; Lilywhite & Gatten, 1995). Meeting the thermal demands of varanids and other reptiles in captivity can be challenging, however, as spatial limitations and anthropomorphic interpretations of natural habitats and their thermal clines can interfere with keepers' abilities to recreate an accurate and appropriate range of conditions within enclosures (Arena & Warwick, 1995). These difficulties can be further exacerbated by a lack of available ecological data for many species, as well as a general unfamiliarity with, or limited access to current literature on their biology and captive husbandry (Mendyk, 2015).

Inappropriate thermal husbandry can have profound effects on the keeping and breeding success of reptiles in captivity (Arena & Warwick, 1995; Lilywhite & Gatten, 1995). A recent review of varanid thermal husbandry discussed various keeping methodologies as well as the potential effects of inappropriate thermal conditions in captive settings (Mendyk *et al*., 2014). Early discussions during the course of this research by the authors with zoo professionals and private keepers on this topic alluded to potential differences in keeping methodologies between these two groups. As a follow-up to this initial study, we investigated the thermal conditions currently offered to varanids in zoological institutions and private collections to determine whether significant differences in husbandry practices exist. Additionally, we sought to answer several other questions, specifically whether the thermal conditions offered to varanids in captivity differ taxonomically or by age class, whether zoos provide different thermal conditions depending on the type of enclosure used, and whether thermal husbandry differs between private keepers from different geographic regions. Gaining an understanding of these current keeping practices can provide valuable insight into specific areas of captive management that may be in need of modification or improvement, to help advance varanid husbandry.

Methods

Data collection

To identify the thermal conditions currently being offered to varanid lizards in captivity, an online survey was distributed to North American zoological institutions accredited by the Association of Zoos and Aquariums (AZA) and experienced private herpetoculturists from around the world. We considered experienced private keepers to be comparable to zoological institutions since both groups have contributed significantly to the advancement of varanid husbandry (*e.g*., Horn & Visser, 1989, 1997). Participation from private keepers was solicited through several online, English-language interest groups and message boards that are dedicated exclusively to the keeping and breeding of varanid lizards; the online communities selected tend to be dominated by long-term keepers and breeders of varanids rather than entry-level hobbyists. Participation from zoos and aquariums (hereafter referred to collectively as 'zoos') was solicited through several online AZA listservs and by email.

Participants were asked to answer questions about the thermal conditions provided in each varanid enclosure within their collection; zoos and private keepers maintaining multiple enclosures of the same species were asked to submit separate survey responses for each enclosure since thermal conditions could vary within the same collection. In addition to the same questions asked of private keepers, zoos were also asked to specify whether the enclosure is maintained on public display or in an off-exhibit holding area, as this could potentially identify variations in husbandry within zoo collections.

Data analysis

Species were clustered into 13 groups based on currently recognized phylogenetic relationships (Ast, 2001; Fitch *et al*., 2006; Ziegler *et al*., 2007; Table 1). On account of their divergence from other clades and ecological distinctness, *V. rudicollis*, *V. dumerilii*, *V. griseus*, and *V. olivaceus* were treated individually as their own groups. Survey responses that omitted the species were grouped together as "unspecified."

Since participants were asked to identify 5° C temperature ranges in which the maximum surface basking temperature (MSBT) and lowest surface temperature fell between, specific minima and maxima were unavailable for calculating precise thermal gradients (TGs). Therefore, although we acknowledge the likelihood of underestimation, we conservatively approximated TGs by subtracting the highest value of the minimum surface temperature range from the lowest value of the MSBT range. For comparisons of MSBTs between zoos and private keepers, we conservatively used the lowest values within the selected 5° C temperature ranges for analysis.

For statistical comparisons between zoos and private keepers, only species groups with sample sizes of 10 or more responses for each keeping class were analyzed. Data were analyzed using IBM SPSS v19 statistical software. Because the data were not normally distributed, nonparametric tests were used; both the median and mean (± standard error) were reported to identify the direction of any statistical differences. The Kruskal-Wallis Test for Independent Samples was used for assessing variation in thermal husbandry offered to different age classes. The Mann Whitney U Test for Independent Samples was used for all individual comparisons. Differences were considered significant if $p < .05$. To avoid an increase in the probability of a Type II error (Caldwell *et al*., 2005), Bonferroni corrections were not applied.

Results

A total of 463 completed surveys were received, including 114 responses from 31 North American zoological institutions and 349 responses from 236 private varanid keepers in 21 countries: Argentina (n = 1), Australia (n = 35), Austria (n = 1), Brazil (n = 1), Canada (n = 15), Cyprus (n = 2), Denmark (n = 1), Finland (n = 1), France (n = 3), Germany (n = 19), Holland (n = 20), Indonesia (n = 12), Luxembourg (n = 3), Poland (n = 2), Portugal (n = 2), South Africa (n = 7), Spain (n = 2), Sweden (n = 4), Switzerland (n = 5), United Kingdom (n = 69) and the United States (n = 140). Total responses included 47 species of *Varanus* and one hybrid (Table 1); 23 responses did not specify a species and seven did not specify an age class. The two most commonly reported species in private collections were *V. exanthematicus* (17.2%) and *V. acanthurus* (12.6%), whereas the most commonly reported species in North American zoos were *V. prasinus* (21.1%) and *V. komodoensis* (17.5%).

Table 1. Varanid taxa and species group designations used in analyses in the present study.

Subgenus	Species group	Taxon	Zoological Institutions (n)	Private Keepers (n)
Empagusia	*dumerilii*	*dumerilii*	-	5
	rudicollis	*rudicollis*	1	7
Euprepiosaurus	*indicus*	*cerambonensis*	-	1
		doreanus	-	2
		indicus	-	3
		jobiensis	-	4
		melinus	2	11
		rainerguentheri	-	1
		yuwonoi	-	1
	prasinus	*beccarii*	8	10
		boehmei	-	1
		kordensis	-	3
		macraei	4	4
		prasinus	24	14
		reisingeri	-	5
Odatria	*acanthurus*	*acanthurus*	5	44
		baritji	-	2
		brevicauda	-	1
		bushi	-	1
		caudolineatus	-	1
		gilleni	-	5
		kingorum	-	4
		storri	1	4

Table 1 (continued). Varanid taxa and species group designations used in analyses in the present study. The taxon *gouldii x* refers to a hybrid.

Subgenus	Species group	Taxon	Zoological Institutions (n)	Private Keepers (n)
	tristis	*glauerti*	-	19
		glebopalma	-	1
		mitchelli	-	2
		pilbarensis	-	4
		scalaris	-	4
		similis	-	2
		timorensis	-	7
		tristis	1	9
Philippinosaur	*olivaceus*	*olivaceus*	1	1
Polydaedelus	*albigularis*	*albigularis*	2	8
		exanthematicus	2	60
	niloticus	*niloticus*	-	7
		ornatus	1	2
Psammosaurus	*griseus*	*griseus*	1	0
Soterosaurus	*salvator*	*cumingi*	-	4
		marmoratus	-	2
		salvator	3	31
Varanus	*gouldii*	*giganteus*	1	-
		gouldii	5	1
		gouldii x panoptes	-	1
		mertensi	8	7
		panoptes	2	13
		rosenbergi	-	1
		spenceri	-	2
Varanus	*varius*	*komodoensis*	20	-
		salvadorii	10	5
		varius	-	11
Unspecified			12	11

Maximum surface basking temperature (MSBT)

Private herpetoculturists offered significantly greater MSBTs than zoos (Mann Whitney U = 32366.5, z = 10.14, p < 0.001) (Table 2; Fig. 1). Accounting for potential biases from other geographical regions, North American private keepers alone (n = 155) also offered significantly greater MSBTs than North American zoos (U = 15067.0, z = 9.96, p < 0.001). The most frequently offered range of MSBTs in private collections was 55.1-60.0° C (20.3%), followed by 60.1-65.0° C (16.9%). A total of 83.4% of private keeper responses reported the use of MSBTs exceeding 45°

C, and 59.6% reported MSBTs over 55° C. In contrast, the most frequently offered range of MSBTs in zoos was 40.1-45.0° C (24.6%), followed by 35.1-40.0° C (21.1%). A total of 39.5% of responses from zoos reported MSBTs exceeding 45° C, and 8.8% of responses over 55° C. Of the 13 species groups, three had sample sizes large enough ($n > 10$) in each keeping group for statistical comparisons (Table 3). Private keepers offered significantly greater MSBTs than zoological institutions for all three of these groups: the *V. varius* ($U = 401.5$, $z = 3.78$, $p < 0.001$), *V. prasinus* ($U = 884.5$, $z = 2.47$, $p = 0.014$), and *V. gouldii* ($U = 300.5$, $z = 2.71$, $p = 0.007$) groups (Fig. 2).

Thermal gradient (TG)

Private keepers also offered significantly greater TGs than zoos ($U = 31{,}990.0$, $z = 9.84$, $p < 0.001$) (Table 2; Fig. 3). North American private keepers alone offered significantly greater TGs than North American zoos ($U = 14{,}897.0$, $z = 9.69$, $p < 0.001$). A total of 63.3% of private keeper responses reported the use of TGs in excess of 25° C, whereas only 16.7% of responses from zoos reported TGs of more than 25° C. When assessed according to species group, private keepers offered significantly greater TGs than zoos for all three comparable groups: the *V. varius* ($U = 411.0$, $z = 4.0$, $p < 0.001$), *V. prasinus* ($U = 874.5$, $z = 2.36$, $p = 0.019$), and *V. gouldii* ($U = 313.5$, $z = 3.06$, $p = 0.002$) groups (Fig. 4).

Table 2. Breakdown of the maximum surface basking temperatures (MSBT) and thermal gradients (TG) offered to varanid lizards in zoos and private collections. Mean and median are expressed in °C. Deviation from the mean is expressed as ± SE.

Category	n	MSBT		TG	
		Median	Mean	Median	Mean
Zoos	114	40.1	41.3 ± 0.77	15.1	14.0 ± 0.81
Private keepers (all)	349	55.1	53.5 ± 0.57	25.1	25.73 ± 0.56
Private keepers (North America)	155	55.1	55.5 ± 0.82	25.1	27.8 ± 0.84
V. varius group (zoos)	30	42.5	41.7 ± 1.34	15.1	13.9 ± 1.45
V. varius group (private keepers)	16	52.5	53.4 ± 2.18	25.1	27.6 ± 2.50
V. prasinus group (zoos)	36	40.1	40.1 ± 1.12	15.1	14.5 ± 1.38
V. prasinus group (private keepers)	37	45.1	45.1 ± 1.57	15.1	19.4 ± 1.48
V. gouldii group (zoos)	16	40.1	42.8 ± 2.92	12.6	15.1 ± 3.06
V. gouldii group (private keepers)	25	55.1	54.4 ± 2.44	30.1	27.1 ± 2.18

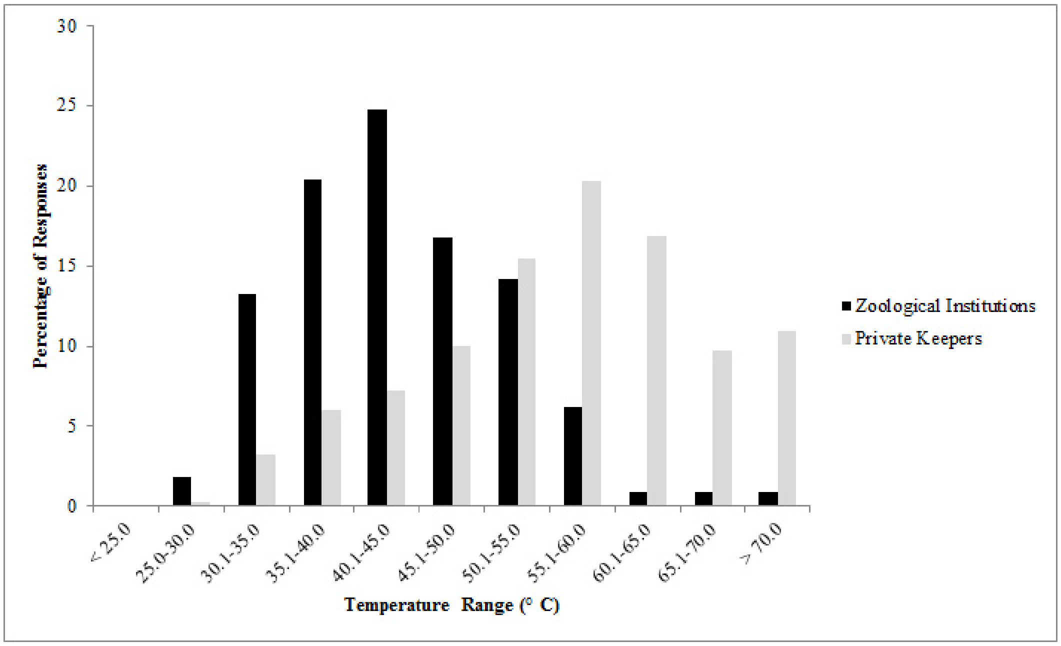

Figure 1. Histogram depicting the frequency of maximum surface basking temperature (MSBT) ranges reported by zoos and private keepers.

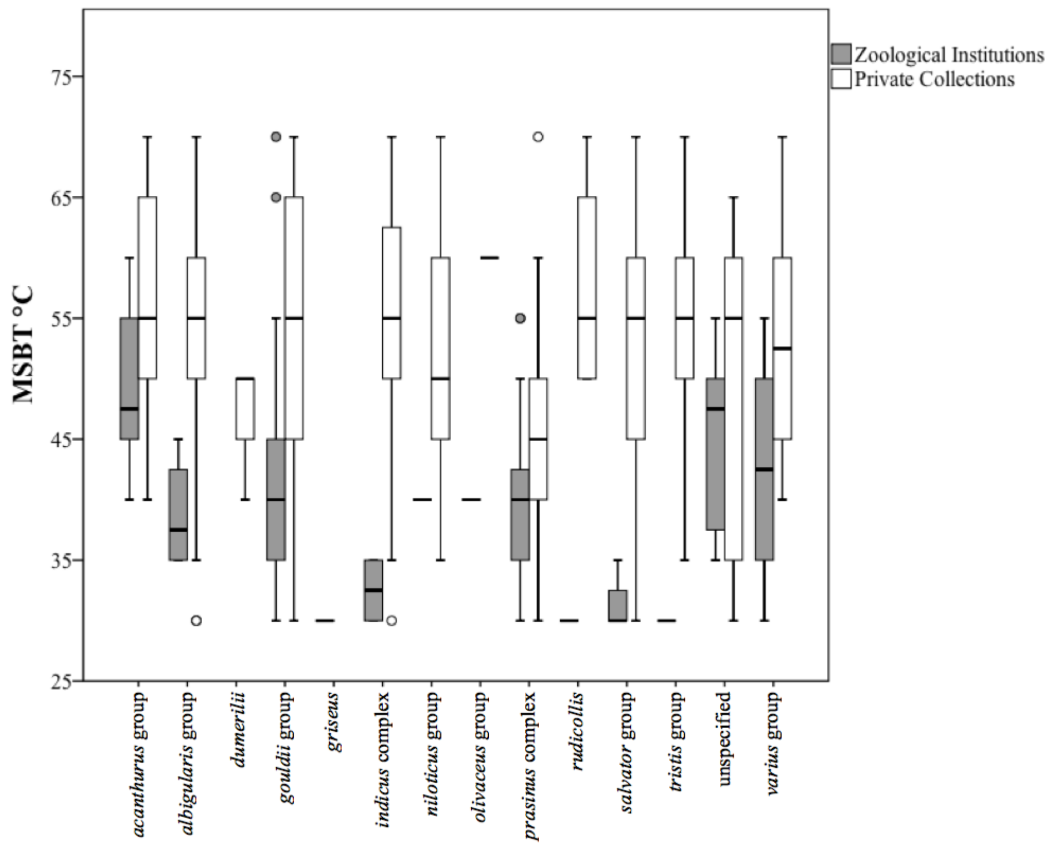

Figure 2. A comparison of the median and interquartile range of maximum surface basking temperatures (MSBT) offered by zoos and private keepers for the 13 species groups. Only three groups (*V. prasinus, V. gouldii* and *V. varius* groups) had samples sizes large enough for statistical comparisons (n > 10). Whiskers represent 5th and 95th percentiles and circles represent outliers.

Table 3. Breakdown of maximum surface basking temperatures (MSBT) and thermal gradients (TG) according to species group, with comparative maxima from the literature.

Species Group	Zoological Institutions					Private Keepers					Maximum Records from the Literature		
	n	MSBT (%)	% > 45 C	% > 55 C	TG (%)	n	MSBT (%)	% > 45 C	% > 55 C	TG (%)	MSBT	TG	References
acanthurus	6	45.1-50.0 (33.3)	83.3	33.3	25.1-30.0 (50.0)	62	55.1-60.0 (27.4)	96.8	72.6	25.1-30.0 (33.9)	78.0	63.0	van der Reijden, 2006
albigularis	4	35.1-40.0 (50.0)	25.0	0	10.1-15.0 (75.0)	68	60.1-65.0 (27.9)	82.4	63.2	30.1-35.0 (23.5)	63.0	42.0	Bennett and Thakoordyal, 2003; Sprackland, 2010
gouldii	16	35.1-40.0 (31.3)	43.8	18.8	5.1-10.0 (25.0) 15.1-20.0 (25.0)	25	60.1-65.0 (20.0)	76.0	64.0	30.1-35.0 (20.0)	62.8	38.8	Burokas, 2012
indicus	2	30.1-35.0 (50.0) 35.1-40.0 (50.0)	0	0	5.1-10.0 (100)	23	55.1-60.0 (34.8)	91.3	65.2	30.1-35.0 (34.8)	60.0	32.0	Brown, 2012
niloticus	1	40.1-45.0 (100)	0	0	20.1-25.0 (100)	9	45.1-50.0 (22.2) 50.1-55.0 (22.2) 60.1-65.0 (22.2)	88.9	44.4	25.1-30.0 (33.3)	45.0	20.0	Hennessy, 2010
prasinus	36	40.1-45.0 (44.4)	25.0	5.6	15.1-20.0 (30.6)	37	45.1-50.0 (24.3)	59.5	18.9	15.1-20.0 (35.1)	54.0	27.0	Mendyk, 2006
salvator	3	25.1-30.0 (33.3) 30.1-35.0 (33.3) 35.1-40.0 (33.3)	0	0	0.1-5.0 (66.6)	37	55.1-60.0 (32.4)	81.1	62.2	25.1-30.0 (32.4)	48.9	-	Rodriguez, 2009
tristis	1	30.1-35.0 (100)	0	0	5.1-10.0 (100)	48	50.1-55.0 (20.8) 55.1-60.0 (20.8)	87.5	60.4	25.1-30.0 (29.2)	66.0	38.0	Retes and Bennet, 2001
varius	30	45.1-50.0 (23.3) 50.1-55.0 (23.3)	50.0	3.3	15.1-20.0 (30.0)	16	45.1-50.0 (25.0)	93.8	50.0	20.1-25.0 (31.3)	65.0	> 35.0	Trout, 2007
rudicollis	1	30.1-35.0 (100)	0	0	5.1-10.0 (100)	7	50.1-55.0 (42.9)	100.0	57.1	30.1-35.0 (42.9)	-	-	-
dumerilii	0	-	-	-	-	5	50.1-55.0 (40.0)	80.0	20.0	20.1-25.0 (40.0)	-	-	-
olivaceus	1	40.1-45.0 (100)	0	0	51-10.0 (100)	1	60.1-65.0 (100)	100.0	100.0	35.1-40.0 (100)	-	-	-
griseus	1	30.1-35.0 (100)	0	0	5.1-10.0 (100)	0	-	-	-	-	-	-	-

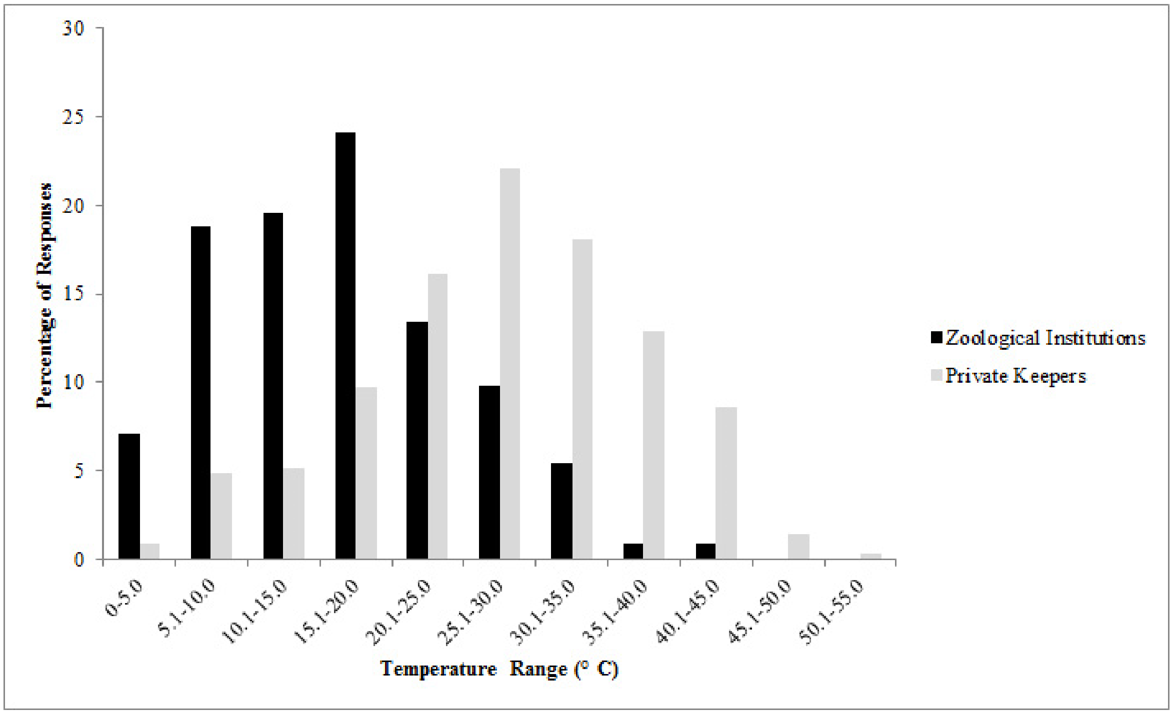

Figure 3. Histogram depicting the frequency of thermal gradient (TG) ranges reported by zoos and private keepers.

Geographical variation in private collections

Due to small sample sizes, data from private keepers in South America (n = 2) and Africa (n = 7) were excluded from statistical comparisons of thermal husbandry by geographic region (Table 4). North American keepers offered significantly greater MSBTs than European (n = 138; U = 8500.0, z = -3.07, $p = 0.002$) and Asian keepers ($U = 519.5$, $z = -2.57$, $p = 0.01$), but not Australian keepers ($U = 2919.5$, $z = 0.715$, $p = 0.475$). Australian keepers offered significantly greater MSBTs than European ($U = 1{,}709.5$, $z = -2.70$, $p = 0.007$) and Asian keepers ($U = 312.5$, $z = 2.546$, $p = 0.011$), and European keepers offered significantly greater MSBTs than Asian keepers ($U = 1{,}121.0$, $z = 2.049$, $p = 0.041$). Similarly, North American keepers offered significantly greater TGs than keepers from Europe ($U = 8155.5$, z = -3.55, $p < 0.001$) and Asia ($U = 403.0$, $z = -3.3$, $p = 0.001$), but not Australia ($U = 2958.5$, $z = 0.849$, $p = 0.396$). Australian keepers offered significantly greater TGs than European ($U = 1545.0$, $z = -3.33$, $p = 0.001$) and Asian keepers ($U = 336.0$, $z = 3.156$, $p = 0.002$), and European keepers offered greater TGs than Asian keepers ($U = 1203.0$, $z = 2.629$, $p = 0.009$).

Variation between enclosure types

In zoos, there was no significant difference in MSBTs between exhibits on public display (n = 58, median = 40.1° C, mean = 40.1 ± 0.98° C) and off-exhibit holding enclosures (n = 56, median = 40.1° C, mean = 42.6 ± 1.18° C; $U = 1904.5$, $z = 1.62$, $p = 0.11$); nor was there a difference between TGs for exhibits on public display (median = 10.1, mean = 13.03 ± 1.09° C) and off-exhibit holding enclosures (median = 15.1, mean = 15.01 ± 1.21° C; $U = 1865.0$, $z = 1.39$, $p = 0.17$).

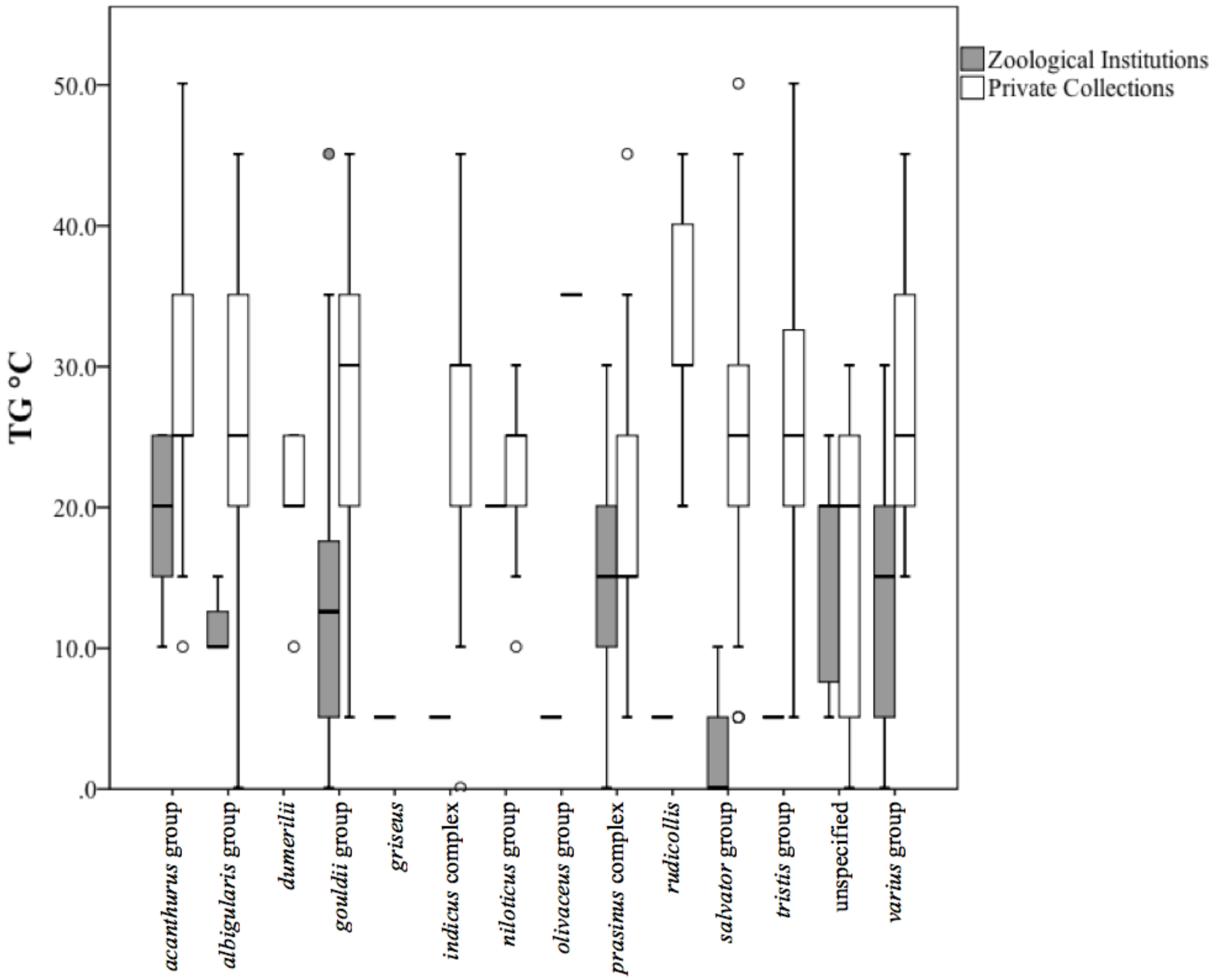

Figure 4. Comparison of the median and interquartile range of thermal gradients (TG) offered by zoos and private keepers for the 13 species groups. Only three groups (*V. prasinus*, *V. gouldii* and *V. varius* groups) had samples sizes large enough for statistical comparisons (n > 10). Whiskers represent 5th and 95th percentiles and circles represent outliers.

Table 4. Breakdown of maximum surface basking temperatures (MSBT) and thermal gradients (TG) in private collections according to geographical region. Median and mean are expressed in °C. Deviation from the mean is expressed as ± SE.

Region	n	MSBT		TG	
		Median	Mean	Median	Mean
North America	155	55.1	55.5 ± 0.82	25.1	27.8 ± 0.84
Europe	138	55.1	51.7 ± 0.86	25.1	23.6 ± 0.83
Australia	35	55.1	57.3 ± 1.4	25.1	29.8 ± 1.45
Asia	12	35.1	42.9 ± 4.75	7.6	13.4 ± 3.66

Variation by age class

No significant differences in MSBTs or TGs (Table 5) were observed between different age classes in zoos ($H[2] = 2.55$, $p = 0.279$ and $H[2] = 0.778$, $p = 0.678$, respectively) or private collections ($H[2] = 0.693$, $p = 0.707$ and $H[2] = 2.601$, $p = 0.272$, respectively).

Table 5. Breakdown of maximum surface basking temperatures (MSBT) and thermal gradients (TG) according to age class in zoos and private collections. Deviation from the mean is expressed as ± SE.

Age class	n	MSBT		TG	
		Median	Mean	Median	Mean
Hatchling/juvenile (zoos)	12	45.1	45.4 ± 3.04	17.6	15.9 ± 2.88
Hatchling/juvenile (private keepers)	51	51.1	52.5 ± 1.50	25.1	24.2 ± 1.53
Subadult (zoos)	27	40.1	41.9 ± 1.77	10.1	13.6 ± 1.85
Subadult (private keepers)	115	55.1	53.3 ± 1.00	25.1	25.0 ± 0.94
Adult (zoos)	68	40.1	40.5 ± 0.93	15.1	13.8 ± 1.05
Adult (private keepers)	183	55.1	54.0 ± 0.78	25.1	26.6 ± 0.79

Discussion

Mendyk *et al*. (2014) provided an extensive historical overview of the thermal husbandry of varanid lizards which focused on a major paradigm shift from the mid-1990s which incorporates elevated surface basking temperatures in excess of 45° C and broad thermal gradients of more than 25° C (Anonymous, 1997, 1998a,b; Good, 1999; Retes & Bennett, 2001). Multiple independent lines of evidence supporting the provision of these thermal conditions in captivity were presented by Mendyk *et al*. (2014), including data and photographs of wild varanids utilizing similar elevated surface basking temperatures (*e.g*., *V. varius* basking at 56° C), photographs of captive representatives of most varanid subgenera utilizing elevated surface temperatures in excess of 45° C for basking (some as high as 66° C), and documentation of more than 35 publications on the keeping and breeding of varanids since the late 1990s which utilize and promote surface basking temperatures in excess of 45° C (some as high as 78° C). Using this information as a guideline for what can be considered current and biologically-appropriate husbandry, we can evaluate the thermal conditions described in the present study that are currently being offered by North American zoos and private herpetoculturists worldwide.

Zoos vs. private keepers

The results of this study illustrate a remarkable dichotomy in thermal husbandry between North American zoos and private herpetoculturists (Figs. 1 & 3). Even when compensating for potential biases caused by the inclusion of private keeper data from other geographical regions, North American zoos still provide significantly lower MSBTs and TGs than private keepers. Although this study represents participants from only 31 zoological institutions and some of these facilities did report offering appropriate temperature ranges, these findings demonstrate that many North American zoos are providing outdated thermal husbandry to varanid lizards. Most surprising is the fact that some zoos are offering MSBTs that may be cooler than the preferred active body temperatures of most varanids in nature (Licht *et al*., 1966; Stebbins & Barwick, 1968; Christian & Weavers, 1996; King & Green, 1999; Heger & Heger, 2007). With MSBTs that are lower than these preferred values, captives are physically incapable of reaching the appropriate body temperatures necessary for maintaining a normal physiology. Even MSBTs of up to 40° C conflict with the surface temperatures typically utilized by varanids for basking in nature as well as in captivity (when given the ability to do so), and can prevent captives from reaching their preferred body temperatures within an acceptable timeframe, leading to prolonged basking activity, lethargy, and obesity (Mendyk *et al*., 2014). As highlighted in earlier studies on mortality in captive varanid lizards, inappropriate thermal conditions can affect various biological processes including, but not limited to reproduction, and have been implicated in several diseases and disorders commonly seen with this group in captivity (Mendyk *et al*., 2013; Mendyk, 2015). The outdated thermal husbandry documented in this study may also play an important contributing role in the surprisingly low life expectancies reported for varanids in North American zoos (Mendyk, 2015).

Perplexing questions arise from these results. First, why are many North American zoos providing thermal conditions that are inconsistent with varanid thermal biology, and why is there such a clear dichotomy in husbandry between zoos and private keepers? Second, do these differences reflect opposing keeping philosophies, available resources, or unfamiliarity with what is currently known and accepted about these animals' thermal biology and husbandry? Answers to these questions can be explained at least in part by some of the husbandry challenges faced by each group which stem from differences in their available resources, management and oversight, and spatial constraints.

In zoos and aquariums, reptiles are frequently housed in non-specialized, generic exhibits that have previously been used to house a variety of taxa. Although some exceptions exist, particularly with large crocodilians and Komodo dragons, most herpetological exhibits in zoos are not designed and constructed with a single taxon in mind. Therefore, to properly house a species, some modifications and alterations to an enclosure are usually necessary to meet the specific behavioral, physiological and psychological needs of the species. Permanently retrofitting a zoo exhibit for a particular taxon where installing new heating and lighting fixtures or relocating existing basking areas to more optimal locations are needed may not be possible in cases where exhibits must remain usable for other taxa in the future. Difficulties with repositioning heating and lighting fixtures can have a direct effect on the ability to offer surface basking temperatures hot enough for varanid lizards. In contrast to zoos, private keepers usually construct custom enclosures for varanids since commercially available caging is largely inadequate for all but the smallest species (*i.e.*, *Odatria*). Without the need to modify enclosures or maintain their functionality for a variety of taxa, private keepers may have greater flexibility in incorporating the necessary heating elements and structures and positioning them in optimal locations to meet the thermal demands of a species.

Along similar lines, maintaining the aesthetics of exhibits by keeping unsightly heating, lighting and plumbing fixtures out of public view is an important design challenge for zoos that can also affect thermal conditions within enclosures. For example, positioning key lighting and heating elements up and out of view from visitors, often at considerable heights above the closest basking surfaces can be prohibitive to establishing surface basking temperatures hot enough for varanids, especially for more terrestrial species that are less inclined to climb to reach elevated perching for basking. Private keepers may not face such a challenge since the aesthetics of enclosures, particularly the placement of heating and lighting fixtures and whether they are visible, are of a lesser concern.

Spatial limitations can affect the ability to provide appropriate environmental conditions in captivity. Private herpetoculturists typically maintain their captives at home in their houses and apartments; therefore, a major husbandry constraint affecting this group is the limited amount of space available for housing reptiles. Assuming that zoos typically have more available space to dedicate to housing varanids than private keepers (although this was not tested in the present study), one might then expect private keepers to experience greater difficulties maintaining broad TGs inside their smaller enclosures. To the contrary, this study showed that private keepers offer greater TGs than zoos (Fig. 2). Although the lower TGs in zoos appear to be directly related to the lower MSBTs being offered, providing access to temperatures that are substantially cooler than the ambient air within an enclosure can also be challenging in a zoological setting. Deep natural substrates (> 45 cm), which are now widely used by private varanid keepers for a variety of terrestrial species (*e.g.*, Markland & Brown, 2009; Rodriguez, 2009; Burokas, 2012), facilitate the construction of deep burrows that varanids can access for cooler temperatures than the ambient air. Some zoos may be unable or reluctant to provide deep substrates since captives could potentially spend considerable time inside burrows and out of view from visitors. In other cases, older zoo enclosures may not feature the depths needed to support deep substrate for burrowing. Without access to deep burrows or other refugia where temperatures would be cooler, the lowest temperatures available in an enclosure would be the ambient air temperature or standing water in a pool or basin (which may eventually equalize with the ambient air temperature).

Enacting changes to captive husbandry, even when based on sound science, can be challenging in some zoos. Unlike private keepers, who can make immediate changes and adjustments to their husbandry situationally, proposed husbandry changes in some zoos must pass through a hierarchical chain of approval (*e.g.*, keeper → supervisor → curator [and sometimes → veterinarian]). These added steps and the involvement of multiple parties could lead to delays and ultimately affect the adoption of such changes. Thus, it is possible that more modern keeping practices have been proposed or suggested in some of the zoos surveyed in this study, but have not yet been adopted because of safety concerns (see below) or disagreement in the methods somewhere along the approval process.

Arbuckle (2014) coined the term "folklore husbandry" to describe herpetological husbandry practices that lack a biological basis but still continue to be practiced, often out of tradition. The continued usage of low basking temperatures and narrow thermal gradients with varanids can be considered an example of folklore husbandry, as these parameters reflect older keeping methodologies that conflict with what is currently understood about their thermal biology as well as widely-established keeping practices that have been in use since the 1990s (Anonymous, 1997, 1998a,b; Good, 1999; Retes & Bennett, 2001, Mendyk *et al*., 2014). Without testing the thermal tolerances and preferences of captive specimens under one's care, it is understandable why some zoos and private keepers may be reluctant to offer the ranges of temperatures promoted in this, and other reports (*e.g.*, Good, 1999; Retes & Bennett, 2001; Mendyk *et al*., 2014), for fear of captives overheating or sustaining thermal burns (Good, 1999). Anthropomorphic interpretations of what may be too hot for a species or taxonomic group may be affecting keepers' abilities to provide appropriate temperature ranges to captives. Surface basking temperatures once perceived to be too hot, fatal or injurious to captive reptiles (*i.e*., > 45° C) have since been proven to be safe and highly effective with varanids when suitable thermal gradients are provided (Retes & Bennett, 2001; Mendyk *et al*., 2014). By offering access to a broad thermal gradient ranging well above and below their preferred active body temperatures, the animals themselves can select from a wide range of temperatures to satisfy their needs at any given time. If a particular basking spot is too hot for an individual, it will simply choose not to use it, or will bask at cooler temperatures along its periphery (R. Mendyk, pers. obs.).

The apparent paradigm disconnect observed with North American zoos may also indicate a general unfamiliarity with current information on the biology and captive management of varanids. For instance, Mendyk (2015) noted that taxon management accounts for *V. beccarii*, *V. olivaceus*, *V. prasinus* and *V. rudicollis* included in the most recent Asian forest monitor North American regional studbook (Peavy, 2010) were compiled nearly 20 years ago and therefore do not include current information on the biology and husbandry of these species from literature that has come to light more recently. Some zoo professionals may not be familiar with reptile hobbyist publications (Murphy *et al*., 1997), and could potentially be missing out on important information that may include alternative keeping methodologies and perspectives. Indeed, the paradigm shift in varanid thermal husbandry highlighted here and discussed by Mendyk *et al*. (2014) was originally developed by private North American herpetoculturists and first promoted in several popular reptile hobbyist publications (Anonymous, 1997, 1998a,b; Good, 1999; Kuhn & Julander, 1999). Expanding, diversifying and updating zoo libraries to include more herpetological and herpetocultural publications and promoting literature research as an important component of captive husbandry can help improve keeping standards for varanid lizards, and other reptiles in zoos.

Interspecific variation in thermal husbandry

It is not surprising that some differences in thermal husbandry appear to exist between species groups in both zoos and private collections (Figs. 2 & 4). For example, both zoos and private keepers tend to offer members of the *V. prasinus* group lower MSBTs and TGs than some other groups such as the *V. acanthurus*, *V. gouldii* and *V. varius* groups (Table 3). In captivity, some species appear more inclined to select higher temperatures for basking than others. For instance, diminutively sized members of the subgenus *Odatria* appear to seek out greater MSBTs than larger representatives of the genus, particularly those belonging to the *V. indicus* or *V. salvator* complexes (see Mendyk *et al*., 2014 and references therein; Table 3). Considering the variation in body size and coloration between species and the wide range of habitats they occupy, interspecific variation in their thermal tolerances and preferences in captivity can be expected. Further investigations are needed to test and determine the individual thermal preferences and tolerances of the 50+ species of varanid currently maintained in captivity in order to better shape and refine their husbandry.

Zoo exhibits vs. off-exhibit holding enclosures

The fact that there were no significant differences in MSBTs or TGs between zoo exhibits and off-exhibit housing is surprising, considering that we would expect zoos to have better control over temperatures in off-exhibit holding enclosures which tend to be smaller in size than exhibits on public display and are not subjected to the same aesthetics-related challenges of hiding heating and lighting fixtures from view, as previously discussed. While average MSBTs and TGs were slightly higher in off-exhibit housing, these values are still lower than the temperatures typically sought out by varanids. This further suggests that the primary reason why many zoos are not offering elevated MSBTs and broader TGs is not because of a physical inability to do so, but rather unfamiliarity with this paradigm shift, or a reluctance to adopt these husbandry practices.

Age-based variation in thermal husbandry

This study did not find any major differences in thermal husbandry across varanid age groups in zoos or private collections; however, ontogenetic shifts in thermal husbandry may represent a hitherto unexplored frontier of varanid husbandry, as changes in thermoregulatory habits have been recorded in at least some wild populations. For example, Harlow *et al*. (2010) noted thermoregulatory differences between different age classes of *V. komodoensis*, with smaller individuals relying more on sun-shuttling for thermoregulation than adults. Since habitat usage and dietary composition for some species can also change dramatically as individuals grow and mature (*e.g*., Bennett, 2002; Imansyah *et al*., 2007; D'Amore, 2015), the way in which environmental parameters such as basking sites and thermal gradients are sought out and utilized may also change over time. Further research into this area is needed to determine how varanids of varying age groups respond to different thermal conditions in captivity.

Geographic variation in thermal husbandry

Surveys for this study were solicited in such a way that the data obtained from private keepers may be heavily biased against non-English speaking countries (Table 1), reflecting only the keeping methodologies of keepers that are English-proficient. English-proficient keepers are more likely to have been introduced to literature and other private keepers promoting these modern thermal husbandry practices which originated in North America (Anonymous, 1997, 1998a,b; Good, 1999; Retes & Bennett, 2001). It appears that varanid keepers from German-speaking countries (Germany, Austria, Switzerland) have less-frequently adopted the elevated surface temperatures and broad thermal gradients hitherto discussed, with many utilizing instead more traditional thermal conditions outlined in several important German-language publications on varanid husbandry and breeding from the 1980s and 90s (Stirnberg & Horn, 1981; Eidenmüller & Horn, 1985; Eidenmüller, 1990; Eidenmüller & Wicker, 1991,1993; Horn, 1991; Kirschner, 1999). Mendyk *et al*. (2014) did note that this general trend appears to be changing, with more European keepers shifting their husbandry towards broader thermal gradients and higher basking temperatures.

Private keepers in Australia appear to have widely adopted elevated surface basking temperatures and broad thermal gradients, mirroring North American keepers in terms of the thermal conditions offered to captives. In addition to having familiarity with, and access to English-language literature, many Australian keepers also have the ability to observe varanid lizards in nature. Instead of developing potentially misguided anthropomorphic assumptions about their habits and habitats, many Australian keepers can gain firsthand knowledge of the environmental conditions and variation that varanids have access to and utilize in nature. Private keepers from Asia (Indonesia) on the other hand consistently reported the lowest MSBTs and TGs among private keepers in this study. These captive conditions may reflect a general level of inexperience among keepers related to the relatively young age of the reptile hobby in Indonesia. Standards of care in Indonesian private collections may change as private keepers gain further access to online literature, interest groups and social networking sites where experienced reptile hobbyists exchange information, ideas and more progressive husbandry practices.

Outlook

In sum, this study has shown that private herpetoculturists are currently offering more appropriate thermal conditions for varanid lizards in captivity than North American zoos and aquariums. This apparent dichotomy is suggestive of various husbandry-related challenges faced by zoos and a level of unfamiliarity with current husbandry practices, but also implies that there has been very limited communication or collaboration between these two keeping groups. Although several authors have emphasized the importance and success of zoo-academic herpetological collaborations (Murphy & Chiszar, 1989; Chiszar *et al*., 1993; Kreger, 1993; Pough, 1993; Card *et al*., 1998), little has been written on the potential benefits of collaborative relationships between zoos and private herpetoculturists (Murphy *et al*., 1997). Historically, differences in keeping motivation and ethics between zoos and private keepers have often prevented the two groups from working together; in some cases, zoos have been hesitant to collaborate with private keepers because of selfish or money-making interests of some individuals (Murphy *et al*., 1997). Despite these differences and occasional philosophical clashes, there have been many examples of successful collaborative partnerships between zoos and private reptile keepers. In Europe in particular, collaborations between zoos and private keepers have led to many important published works which have helped advance varanid biology, taxonomy, husbandry and breeding (*e.g*., Bredl & Horn, 1987; Horn & Visser, 1989, 1991, 1997; Eidenmüller & Wicker, 1991, 1993, 1995, 1997, 1998, 2005; Kok, 1995; Wicker *et al*., 1999; Engelmann & Horn, 2003; Visser, 2003). Given the disparity in keeping methodologies highlighted in this study, it would be in both parties' best interests to reach out and communicate with each other regularly as a way to gain and maintain familiarity with current approaches to captive husbandry and breeding. To ignore the knowledge, experiences and important achievements of either group would be a major hindrance to the progression of varanid husbandry.

Finally, beyond raising specific concerns about varanid husbandry in zoos and private collections, this study raises broader questions about the state of herpetological husbandry as a whole. If such dramatic differences in keeping methodologies exist between zoos and private keepers for one particular taxonomic group, how does the husbandry offered to other taxa compare? Do the results of this study point to a much larger issue of poor communication and collaboration between zoos and private herpetoculturists? If so, identifying these husbandry differences, finding common ground, and working together to share experiences and explore new ideas can help solve and overcome many of the health- and husbandry-related challenges currently affecting reptiles and amphibians in captivity, and help improve keeping and breeding success.

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