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On the Thermal Husbandry of Monitor Lizards

Thermal husbandry, the range of temperatures offered to reptiles in captivity, is one of the most basic, yet critical aspects of herpetological husbandry. As poikilothermic ectotherms, reptiles are unable to physiologically maintain constant body temperatures and must instead thermoregulate behaviorally by utilizing the range of temperatures available to them within their environment (Cowles and Bogert 1944; Bogert 1949, 1959). Because reptiles vary considerably in their thermal tolerances, preferences and thermoregulatory strategies, providing taxon-specific husbandry consistent with a species' ecology and thermal biology should be a primary focus of reptile collections and caregivers (Peaker 1969; Arena and Warwick 1995; Lillywhite and Gatten 1995). Although the general importance of providing appropriate thermal gradients in herpetological husbandry has long been emphasized (Peaker 1969; Arena and Warwick 1995), specific data on the thermal biology of most species are lacking, and as a result, captive environments may not provide the diversity and range of microclimates and microhabitats needed by reptiles to thermoregulate properly (Arena and Warwick 1995). Inappropriate thermal regimes, in turn, can have deleterious effects on the health and welfare of captive reptiles (Arena and Warwick 1995; Lillywhite and Gatten 1995).

Monitor lizards (family Varanidae, genus *Varanus*) occur throughout Africa, Asia, and Australia, and occupy a variety of habitats ranging from arid deserts to tropical lowland forests and mangrove swamps (Pianka and King 2004). Largely due to their size, activity levels, and observable intelligence, varanids are frequently maintained in zoos and private collections, where more than 55 species are currently kept in captivity (Eidenmüller 2007; Brown 2012). Despite having been maintained in numerous collections dating back more than 150 years, captive varanids continue to present significant husbandry challenges, with both zoos and private collections experiencing limited long-term maintenance and reproductive success relative to the number of specimens that have been kept (Bennett 1989, 1994; Bennett and Thakoordyal 2003; Mendyk, unpubl.). Recent assessments suggest that many varanid species may not be reaching their full lifespan potentials in captivity (Mendyk, unpubl.), and several authors have identified and discussed problematic areas of their captive management and reproduction (Horn and Visser 1989; Boyer and Boyer 1997; Horn and Visser 1997; Hartdegen 2002; Spelman 2002; Horn 2004; Mendyk et al. 2013). Of the various factors known to affect the health and welfare of varanid lizards in captivity, inappropriate thermal husbandry appears to be one of the most significant, yet highly overlooked issues (Bennett and Thakoordyal 2003; Mendyk et al. 2013). Inadequate thermal husbandry may not be easily recognized or understood, and as a result, some zoos, private herpetoculturists, and research laboratories may not be providing captives with the appropriate conditions needed to thrive.

In this article, we review several aspects of the thermal biology of wild varanid lizards and discuss how these parameters may relate to, and influence their maintenance in captivity. From a historical perspective, we highlight a significant paradigm shift in their thermal husbandry, and discuss how changing attitudes towards their captive management over the last few decades have helped improve keeping and reproductive success. Lastly, we discuss the implications and potential consequences that inadequate thermal husbandry can have on biological research.

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The Thermal Biology of *Varanus*

Varanids are unique among extant lizards regarding various aspects of their physiology. Relative to other reptile groups, varanids possess remarkably high aerobic capacities and unique lung morphology, with some of the highest rates of oxygen consumption documented among non-avian reptiles (Bartholomew and Tucker 1964; Bennett 1972; Earll 1982; Becker et al. 1989; Schachner et al. 2014). This, coupled with metabolic rates greater than many other reptiles and efficient behavioral control over heating and cooling, enables them to operate over a much wider temperature range and sustain greater activity levels than other lizards (Earll 1982; Auffenberg 1994; Thompson and Withers 1997; Thompson 1999; Sweet and Pianka 2007). The thermal biology of varanids has been a subject of much interest among researchers, and various aspects of their thermoregulation have been studied in depth through field (e.g., radiotelemetry, mark-recapture) and laboratory investigations over the past several decades (Bartholomew and Tucker 1964; Licht et al. 1966; Stebbins and Barwick 1968; Johnson 1972;

Brattstrom 1973; Sokolov 1975; McNab and Auffenberg 1976; Meek 1978; King 1980; Auffenberg 1981, 1988, 1994; Gleeson 1981; Buffenstein and Louw 1982; Earll 1982; King et al. 1989; Wikramanayake and Green 1989; Green et al. 1991; Thompson and Withers 1992, 1997; Wikramanayake and Dryden 1993, 1999; Christian and Weavers 1994; Traeholt 1995; Christian and Bedford 1996; Christian and Weavers 1996; Christian et al. 1996; Thompson 1997; King and Green 1999; Thompson et al. 1999; Walsh et al. 1999; Wikramanayake et al. 1999; Ibrahim 2000; Heger and Heger 2007; Smith et al. 2008; Harlow et al. 2010).

Field studies have shown that active varanid lizards have preferred, or average body temperatures (Tbs) which exceed those of many other lizard groups. With the exception of a few semi-aquatic species (*Varanus salvator*, *V. mertensi*, *V. niloticus* and *V. indicus*) which seem to prefer to maintain lower Tbs between 28.9 (84°F) and 34°C (93.2°F) (Wikramanayake and Green 1989; Traeholt 1995; Muhigwa 1998; King and Green 1999; Smith et al. 2008), the majority of varanid species looked at maintain optimal Tbs between 35 (95°F) and 39°C (102.2°F) (Licht et al. 1966; Stebbins and Barwick 1968; Pianka 1970, 1994a; King 1980; Vernet et al. 1988; King et al. 1989; Wikramanayake and Dryden 1993; Christian and Bedford 1996; Christian and Weavers 1996; King and Green 1999; Heger and Heger 2007), but for short periods can withstand core body temperatures above 40°C (104°F) (Auffenberg 1994; Pianka 1994a; King and Green 1999; King et al. 1999; Thompson et al. 1999; Ibrahim 2000). The critical thermal maximum - the core body temperature at which death occurs - has been studied in several species including *V. komodoensis*, *V. olivaceus* and *V. bengalensis*, and ranges between 41.6 (106.9°F) and 44.6°C (112.3°F) (McNab and Auffenberg 1976; Auffenberg 1981, 1988, 1994).

Although morphologically conservative, varanid lizards do exhibit considerable variation in body size between species, ranging in mass by nearly five orders of magnitude (Pianka 1995). Given this disparity, thermoregulation within the genus is heavily influenced by thermal inertia associated with body size (Brattstrom 1973; Harlow et al., 2010). Larger taxa, particularly *V. komodoensis*, semi-aquatic species such as *V. salvator*, *V. niloticus*, *V. mertensi*, and *V. indicus*, and dense forest-dwelling species such as *V. olivaceus*, typically maintain lower, but relatively stable body temperatures throughout the day and night (Auffenberg 1981, 1988; Wikramanayake and Green 1989; Wikramanayake and Dryden 1993; King and Green 1999; Smith et al. 2008). Adult individuals of some larger species can be independent of external heat input for several hours once their preferred Tbs are reached (Wikramanayake and Dryden 1993; Harlow et al. 2010), and some species can maintain relatively stable Tbs in nocturnal retreats and emerge the following morning with body temperatures warmer than ambient air conditions (Auffenberg 1981; Pianka and Vitt 2003). A lower thermal conductance in semi-aquatic species such as *V. salvator* is also believed to enable these animals to more effectively maintain stable Tbs while foraging, traveling, and sheltering in aquatic environments (King and Green 1999).

Not all larger varanids fit this general model. Adult *V. giganteus* (to 2 m in total length [TL]) and *V. bengalensis* (to 1.4 m TL) both experience considerable fluctuations in body temperature throughout the day (Wikramanayake and Dryden 1999; Heger and Heger 2007). In contrast to *V. komodoensis* and *V. salvator*, *V. bengalensis* and many smaller taxa have a higher thermal conductance which enables them to heat up and cool down more quickly, and also tend to experience greater daytime fluctuations in body temperature, that drop considerably at night (Wikramanayake and Green 1989; Wikramanayake and Dryden 1993; King and Green 1999). For this reason, smaller taxa and juveniles of larger species usually require a greater degree of shuttling between shaded and sunlit areas to achieve and maintain preferred Tbs throughout the day (King and Green 1999; Wikramanayake et al. 1999; Harlow et al. 2010).

To achieve and maintain body temperatures that are usually greater than that of the ambient air, varanids require access to fairly high surface basking temperatures (Pianka 1970). Although some varanids have been shown to increase body temperatures through metabolic activity (Bartholomew and Tucker 1964), such increases are negligible and not considered to be a significant factor in thermoregulation (Auffenberg 1981, 1988). As heliotherms, they typically elevate their body temperatures by increasing exposure to solar radiation, but also absorb significant conductive heat through physical contact with substrates, surfaces and shelters heated by the sun. Auffenberg (1994) noted that in open areas, radiation from heated substrates can have a greater impact on thermoregulation in varanids than solar radiation. Unfortunately, few field studies have investigated the actual surface temperatures selected by varanids for basking; therefore, specific data are scarce (Pandav and Choudhury 1996; Ibrahim 2000; Auliya 2006).

It is well established that daytime surface temperatures in sun-exposed environments inhabited by varanids usually exceed both ambient air temperatures and the animals' preferred body temperatures (Auffenberg 1981, 1988, 1994). For example, in open habitats utilized by *V. komodoensis*, daytime substrate temperatures can reach over 50°C (122°F) (Auffenberg 1981). In northern India, Auffenberg (1994) noted that ground temperatures in *V. bengalensis* habitat exceeded 60°C (140°F) for 72% of the species' activity period, and in varanid habitats of northern Australia, surfaces receiving full radiant energy from the sun can exceed 70°C (158°F) (Christian and Weavers 1996). While these temperatures would prove lethal if individuals were continuously exposed to them, varanids tend to only enter sunlit areas for brief periods for basking or while foraging. Wild *V. tristis orientalis* have been observed basking on rocks in exposed sunlit areas with recorded surface temperatures of 60°C (140°F) (J. Lemm, unpub. dat.), and wild *V. varius* have been observed basking atop sun-exposed leaf litter with recorded surface temperatures of 56°C (132.8°F) (D. Kirshner, pers. comm.; Fig. 1). Captive *V. semiremex* maintained outdoors under natural climatic conditions regularly sought out sunlit branches for basking, with surface temperatures as high as 56°C (132.8°F) (Jackson 2005). These limited data suggest that many varanid species select and utilize surface basking temperatures that are far greater than their preferential range of body temperatures.

Basking in exposed areas poses serious risks of predation for many heliothermic reptiles. Minimizing the time spent basking can be advantageous in terms of predator avoidance (Krebs 1999; Wikramanayake and Dryden 1999), and can also allow more time for other important activities such as foraging (Auffenberg 1988; Wikramanayake and Dryden 1999). Therefore, with access to a range of microhabitats and microclimates within their environment, varanids and other heliothermic reptiles can be expected to select greater temperatures for basking in order to facilitate a quicker transition to their optimal body temperatures (Krebs 1999).

Reptiles, including varanids, also regulate their body temperatures by seeking out cooler microhabitats. Accessing

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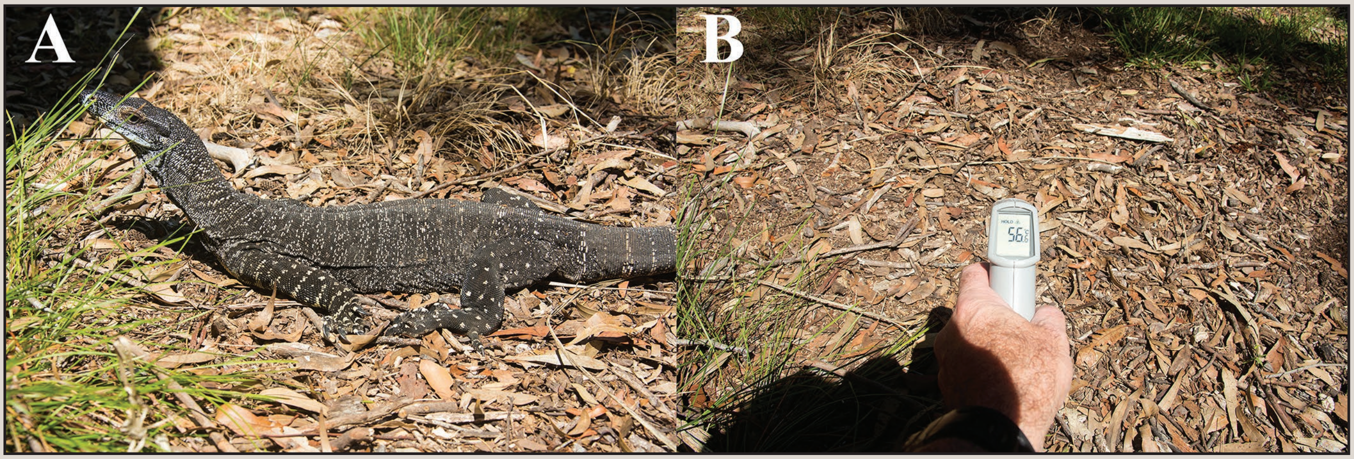

Fig. 1. A) Wild adult *Varanus varius* basking atop leaf litter in a forested area outside Sydney, New South Wales, Australia at 1500 h. B) Surface temperature of the basking site (56°C [132.8°F]; air temperature 26°C [78.8°F]) was recorded immediately after the lizard fled the area (D. Kirshner, pers. comm.).

cooler temperatures can serve as an energy-conserving measure (Huey and Stevenson 1979; Nagy 1983), a way to escape potentially life-threatening temperature extremes, or as a method of reducing evaporative water loss (Avery 1994). Depending on species and habitat, varanids employ various strategies for reducing body temperatures which include entering water (Auffenberg 1994; King and Green 1999; Auliya 2006), moving to shaded areas (Auffenberg 1994; King and Green 1999), seeking out breezy locations (Auffenberg 1994; Heger and Heger 2007), elevating their bodies up off of hot surfaces to increase convection to cool breezes (Heger and Heger 2007), resting atop cool, moist substrates (Auffenberg 1994), retreating to burrows and other refugia (Warburg 1965a; Auffenberg 1981, 1994; Christian and Weavers 1996), and gular pumping (Johnson 1972; Owerkowicz et al. 1999). Some species, particularly those inhabiting arid environments with limited vegetation and cover can be heavily reliant on burrows for regulating and lowering body temperature; for example, studies on the ecology of *V. gouldii* have shown that temperatures inside burrows can be more than 18°C (32.4°F) cooler than aboveground conditions (Warburg 1965a).

Thermal Husbandry of *Varanus*

Successful herpetological husbandry demands that the biological requirements of a species are met, and that the environmental conditions provided in captivity replicate, as closely as possible, those available and familiar to a species in nature (Arena and Warwick 1995; Guillette et al. 1995; Lillywhite and Gatten 1995). Although some reptile species may do well in captivity when provided with minimalistic or "reductionist" husbandry conditions, such conditions are probably inappropriate for most species as they offer less potential to fulfil biological needs (Warwick and Steedman 1995). Given what is known about the ecology and thermal biology of free-living varanid lizards, it is clear that captive specimens require a broad range of temperatures and humidity levels that can be selected as needed to satisfy various physiological needs. However, multiple lines of evidence from the literature suggest that historically, varanids as a whole have not been provided with sufficient thermal conditions in captivity.

From a health perspective, several diseases and complications observed in captive varanids can be linked to inadequate thermal husbandry. Obesity, which is often attributed to excessively rich captive diets in reptiles (Donoghue and Langenberg 1996; Brown 2012), is common among varanid lizards (Boyer and Boyer 1997; Bennett 1998; Bennett and Thakoordyal 2003), but may have deeper roots in chronic exposure to low temperatures (Anonymous 1997, 1998a; Good 1999; Vincent and Wilson 1999; Lemm 2001; Bennett and Thakoordyal 2003). Under conditions in which eating is possible but activity levels and metabolisms are impaired by cooler temperatures, energy from food may be stored as fat, rather than allocated towards growth or reproduction (Bennett and Thakoordyal 2003), and several authors have argued that captive varanids, especially younger individuals, rarely become obese when provided with an appropriate range of temperatures to facilitate efficient digestion, even when offered large quantities of food (Anonymous 1997, 1998a; Retes, in Good 1999; Bennett and Thakoordyal 2003). Although empirical studies are lacking, chronic exposure to inadequate temperatures is also suspected of being etiologically linked to common metabolic disorders of captive varanids such as gout (Mendyk et al. 2013), weakened immune systems (Mendyk et al. 2013), and gastrointestinal diseases (Bacon 1976; Brown 2012).

From an ethological standpoint, captive varanids have rarely exhibited the same levels of activity as their wild counterparts, and their overall behavior in captivity has been described as lethargic by several authors. For instance, Barbour (1943) and Marcellini (quoted in Cohn 1994) both characterized varanids as "phlegmatic" in captivity, and Oliver and Spencook (1956) likened two *V. komodoensis* at the Bronx Zoo to "lethargic dogs". Murphy (1969) remarked that few captives exhibited the "characteristic alertness and activity associated with wild specimens", and that their lethargy was "depressing even to the casual zoo visitor". More recently, Gupta (1997) reported that captive *V. bengalensis* spent an average of 68.2% of their activity period basking, and Walsh et al. (1999) recognized that captive *V. komodoensis* "did not become completely inactive", but never exhibited the foraging activity levels characteristic of wild individuals. Descriptors such as these contradict what has generally been observed in, and reported for wild varanid lizards, which tend to be highly alert and active by nature, with several species known to travel expansive distances each day (Stebbins and Barwick 1968; Auffenberg 1981; Pianka 1994b). While spatial constraints and associated boredom may play some contributing roles in the behavior of captive varanids,

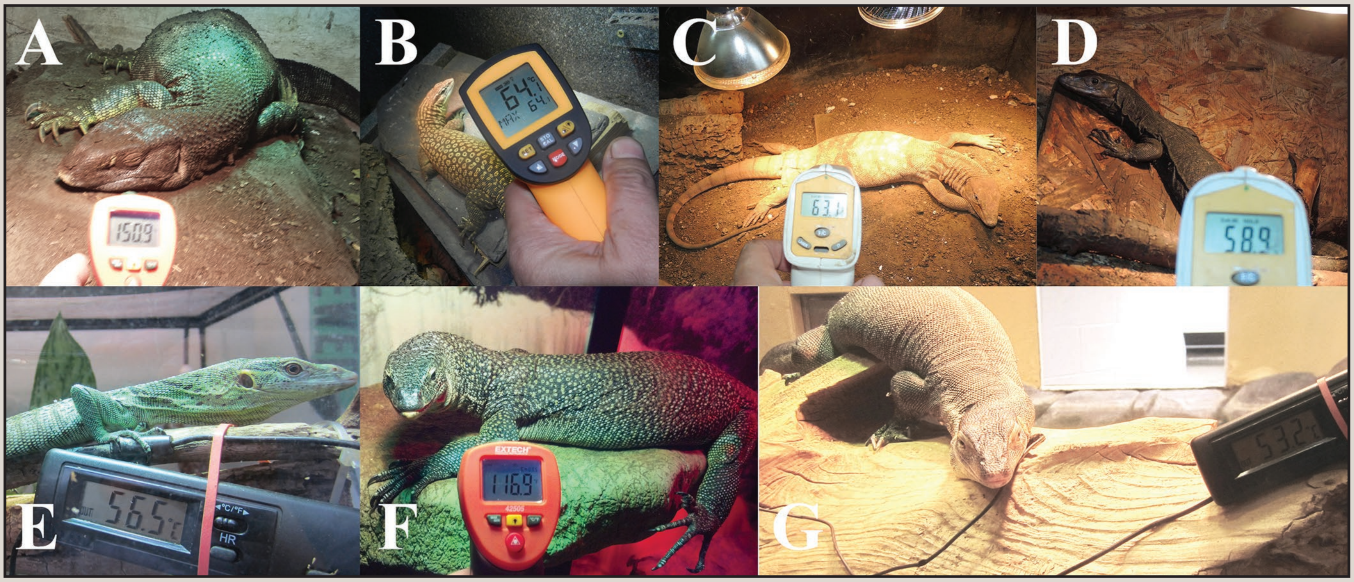

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Fig. 2. Examples of elevated surface basking temperatures selected and utilized by different varanid species in captivity. A) *Varanus albigularis* (66.1°C [150.9°F]), private collection; B) *V. acanthurus* (64.1°C [147.4°F]), private collection; C) *V. griseus* (63.1°C [145.6°F]), private collection; D) *V. salvator macromaculatus* (58.9°C [138°F]), private collection; E) *V. prasinus* (56.5°C [133.7°F]), Smithsonian National Zoological Park; F) *V. indicus* (47.2°C [116.9°F]), private collection; G) *V. mertensi* (53.2°C [127.8°F]), Smithsonian National Zoological Park.

lethargy and prolonged basking activity are largely symptomatic of animals experiencing difficulties achieving and maintaining preferred body temperatures (Arena and Warwick 1995).

Despite signs of inadequate thermal husbandry being present in captive collections for decades, there appears to have been little concern or inquiry into why captives behaved markedly different than their wild counterparts, and even less testing and experimentation with the actual thermal preferences and tolerances of specimens in captivity. Surprisingly, many published accounts describing varanid husbandry over the past several decades have not included the specific basking temperatures (Moehn 1984; Sprackland 1989, 2007; Chippendale 1991; Kok 1995; Card 1996; De Lisle 1996; Mehaffey and McGinnity 1996; Wick 1996; Bayless and Dwyer 1997; Kala 1998; McDonald 1999; Hairston-Adams and Reed 2000; Dwyer and Bayless 2001; Eidenmüller 2005; Ryman 2009) or thermal gradients (Moehn 1984; Kala 1998; Eidenmüller 2005, 2007) offered to, or recommended for captives. This general lack of attention or concern for specific basking temperatures and thermal gradients suggests that thermal husbandry has largely been overlooked as an important component of varanid husbandry, especially when compared to other frequently discussed keeping parameters such as enclosure dimensions, diets, lighting, and photoperiod.

Earlier husbandry accounts that have cited specific temperatures often described or recommended surface basking temperatures of 35–40°C (95–104° F) and below (Murphy 1969, 1971, 1972; Behrmann 1981; Barker 1984; Erdfelder 1984; Davis et al. 1986; Radford and Paine 1989; Thissen 1993; Card 1995; Fost 1996; Holmstrom 1996; O'Dell 1996; Strimple 1996; Hartdegen 1998; Kirschner 1999; Gorman 2000; Lee 2000; Lee and Friedman 2000; Grützner 2003). Considering that the preferred active body temperatures of most wild varanid lizards appear to exceed 35°C (95°F), and that active body temperatures over 40°C (104°F) are not uncommon in free-ranging individuals (Auffenberg 1981,1994; King et al. 1989; King and Green 1999; Thompson et al. 1999), surface basking temperatures of 40°C (104°F) and below may prohibit captives from reaching their preferred body temperatures, or prevent them from doing so within a reasonable timeframe. These values also contradict the surface temperatures generally experienced and utilized by varanids under natural conditions, which frequently exceed 50°C (122°F) (Auffenberg 1981, 1994; Christian and Bedford 1996; Christian and Weavers 1996; Jackson 2005; J. Lemm, unpub. dat., D. Kirshner, pers. comm.; Fig. 1). In some published accounts where thermal gradients have been discussed, ranges of less than 10°C (18°F) have been reported (Barker 1984; Zimmermann 1986; Radford and Paine 1989; Sprackland 1989; Card 1995; Kok 1995; Bayless and Dwyer 2001). Considering the heterogeneity of climatic and physical conditions present in wild varanid habitats (Warburg 1965a; Auffenberg 1981, 1988), such limited thermal gradients in captivity may not provide individuals with an appropriate range of temperatures to thermoregulate effectively or efficiently.

A Paradigm Shift.—Beginning in the mid-1990s, a novel approach to the thermal husbandry of varanid lizards began to emerge from the private keeping sector in North America, which focused more on the ecology and thermal biology of free-ranging animals than previous methodologies. American herpetoculturist Frank Retes is credited with pioneering and promoting the use of elevated surface basking temperatures which had not previously been used or considered for varanids (Anonymous 1997, 1998a; Good 1999; Retes and Bennett 2001), perhaps due to fears that they would prove lethal to captives. Retes showed that when given access to a broad range of temperatures, captive individuals of many different varanid species selected surface temperatures in excess of 60°C (140°F) for basking. These elevated basking temperatures reduced the amount of time needed for captives to reach their preferred body temperatures, and led to greater activity levels and faster rates of digestion, growth, and sexual maturation (Anonymous 1997; Retes and Bennett 2001). Additionally, these conditions, in conjunction with the offering of small, but frequent meals have been attributed to marked increases in Retes' captive breeding success not just with diminutive species belonging to the subgenus *Odatria* (Anonymous 1997, 1998a,b; Good 1999;

Retes and Bennett 2001), but larger species such as *V. varius* and *V. albigularis* as well (Anonymous 1998a; F. Retes, pers. comm.).

Captive breeding success with varanids had been experienced by zoos and private keepers prior to this innovation (see Horn and Visser 1989, 1997); however, most occurrences before the mid- to late-1990s were infrequent, and rarely repeated. When adopted, the use of elevated basking temperatures and broader thermal gradients has led to greater activity levels and reproductive success with many species in both zoos and private collections, including multiple captive-bred generations (Fyfe et al. 1999; Good 1999; Bennett 2001; Retes and Bennett 2001; Bennett and Thakoordyal 2003; Husband and Bonnett 2009). For example, Fyfe et al. (1999) reported that a group of *V. brevicauda* initially provided with a basking spot of 35°C (95°F) remained inactive, had poor appetites, and did not engage in any courtship or mating behaviors. Upon increasing the surface basking temperature to 45°C (113°F) following Retes' methodology, activity levels and appetites increased, and courtship was observed within just a few weeks (Fyfe et al. 1999). Today, surface basking temperatures as high as 60°C (140°F) are offered to *V. brevicauda* in captivity (Husband and Bonnett 2009), and similarly high basking temperatures are successfully used for many other varanid species as well (Tables 1 and 2; Fig. 2). Even species with lower preferred body temperatures such as *V. mertensi* and *V. salvator*, and dense-canopied forest dwellers such as *V. prasinus*, *V. rudicollis*, *V. dumerilii,* and *V. olivaceus* will actively seek out and bask at these elevated temperatures when given the option to do so (Fig. 2).

Surface basking temperatures in excess of 45°C (113°F) have been in use with captive varanids and extensively documented in the literature for more than a decade (Visser 1985; Anonymous 1997; Good 1999; Husband and Vincent 1999; Retes and Bennett 2001; Bennett and Thakoordyal 2003). Yet, it appears that many zoos and private keepers are unfamiliar with this innovation or are perhaps following older husbandry guidelines, and several authors have recently reported or recommended the use of substantially cooler basking temperatures and narrower thermal gradients (Downing 2007; Gaikhorst et al. 2010; Donovan 2012; Purser 2014). Preliminary investigations on the thermal husbandry offered to varanids in captivity have also shown that some North American zoos are currently offering surface basking temperatures as low as 25–30°C (77–86°F) (Mendyk et al., unpub. dat.), which are substantially lower than the actual preferred body temperatures of most species. This may be reflective of information presented within outdated taxon management accounts that are still in use today which recommend surface basking temperatures below 45°C (113°F) (Pfaff and Sprackland 1996) or do not recommend any specific basking temperatures at all (Card 1996; Mehaffey and McGinnity 1996; Hairston-Adams and Reed 2000). Moreover, these findings might also reflect a general unfamiliarity with current literature on the biology and husbandry of varanids as well as limited communication between zoos and private keepers. Zoos and private keepers that follow outdated information may be providing inappropriate husbandry that can directly affect the health, welfare and longevity of captive specimens.

Now widely practiced throughout many North American, Australian, and European collections, the use of elevated basking temperatures above 45°C (113°F) does not appear to have been as extensively adopted by zoos and private keepers in Germany, where lower surface basking temperatures continue to be used for many species (Moldovan 2007, 2008; Wesiak 2007, 2008; Berghof 2009; Ziegler et al. 2009, 2010; Mendyk et al., unpub. dat.). While this trend does appear to be changing (e.g., Fischer, 2012; Hörenberg 2013a,b; Ramm 2013a,b; Mendyk et al. unpub. dat.), this more traditional keeping approach may be popular because several pioneering varanid keepers in Germany have reported breeding success with lower basking temperatures and narrower thermal gradients (Stirnberg and Horn 1981; Eidenmüller and Horn 1985; Eidenmüller 1990; Eidenmüller and Wicker 1991,1993; Horn 1991; Kirschner 1999). Although successful reproduction may occur under such thermal conditions, consistent and repeated reproductive success, multi-clutching, and earlier sexual maturation appear to be rare. The elevated basking temperatures and broad thermal gradients highlighted in this, and other reports (see Tables 1 and 2) offer many biological benefits over these more traditional keeping methodologies, and more closely mirror the range of climatic conditions present and familiar to varanids in nature.

Biological Benefits of Elevated Basking Temperatures

When unable to achieve their preferred body temperature, varanids may exhibit reductions in food intake, digestive efficiency and energy conversion, thyroid activity, and growth rates (de Grijis 1899; Buffenstein and Louw 1982; Fyfe et al. 1999; Brown 2012). Whereas elevated body temperatures accelerate enzymatic and mechanical digestive functions in reptiles (Auffenberg 1981), colder temperatures impair digestive abilities (de Grijis 1899). Low temperatures can lead to the putrefaction of food within the gut (Auffenberg 1981) as well as gastrointestinal impactions (Brown 2012), and have also been implicated in two fatal cases of severe gastroenteritis in *V. komodoensis* (Bacon 1976). When given access to broad thermal gradients including elevated basking temperatures, captives exhibit increased activity levels, greater appetites, faster growth rates and earlier sexual maturation, as well as improved reproductive outputs (Fyfe et al. 1999; Retes and Bennett 2001).

Access to a broad range of temperatures can also benefit reproductively active females. For instance, Kuhn and Julander (1999) noted that female *V. acanthurus* bask extensively at higher surface temperatures (to 71°C [159.8°F]) when gravid. Given the histories of low egg viability in captive varanid lizards (Mendyk 2012, unpub. dat.) and inadequate thermal husbandry, it is possible that access to higher temperatures may be important for healthy egg development, as well as normal reproductive cycling (i.e., oogenesis, vitellogenesis and ovulation). Inadequate thermal conditions may also explain, to some extent, the high frequency of reproductive complications and disorders seen among captive females (Mendyk et al. 2013).

Gout, the accumulation of uric acid crystals in the joints and viscera, is a common metabolic disease of reptiles in captivity. Although comparative studies with other reptile groups are lacking, captive varanid lizards have shown a particular susceptibility to gout (Köhler 1992; Hartdegen 2002; Mendyk et al. 2013). Exposure to cold temperatures can inhibit renal tubular function and increase uric acid levels in reptiles (Hernandez and Coulson 1957), and may explain elevated levels of uric acid seen in *V. griseus* during brumation (Haggag et al. 1966; Dessauer 1970) as well as cases of gout in captive varanids, although chronic dehydration has also been proposed as an important causative agent of the disease (Card 1996; Yuyek 2012; Mendyk et al. 2013).

Immunocompromised reptiles often elevate their body temperatures beyond their preferred Tbs, when ill (Kluger

1979; Warwick 1991; Hutchinson and Dupre 1992; Lillywhite and Gatten 1995). Similar observations of wild-caught varanids in captivity suggest that captives select higher basking temperatures for eliminating parasite loads (Sprackland 1989; Mendyk, pers. observ.), perhaps by increasing body temperature beyond the critical thermal maximum of the infective agent. There is also evidence that suggests reptiles purposely seek out colder temperatures during certain stages of illness, perhaps as a way to cope with stress associated with disease (Warwick 1991). Therefore, providing access to a broad thermal matrix including cooler temperatures and elevated basking spots that animals can actively select from as needed is important for facilitating a healthy immune response.

Health Concerns Associated with Elevated Basking Temperatures

Without testing the thermal preferences and tolerances of captive specimens under one's care, it is easy to see why some zoos and private varanid keepers may be reluctant to provide surface basking temperatures in excess of 45°C (113°F), for fear that death or thermal burns might occur (Retes, in Good 1999). Although some varanid groups and species appear to seek out greater surface basking temperatures than others, particularly members of the subgenus *Odatria* (Table 1), if surface basking temperatures are too hot, animals will usually bask at the site's periphery where temperatures are slightly lower. Most burns in captive varanids appear to be related to animals coming into

Table 1. Elevated surface basking temperatures and broad thermal gradients documented in the literature for varanid lizards belonging to the subgenus *Odatria*. Species are clustered based on phylogenetic relatedness (Ast 2001; Fitch et al. 2006; Ziegler et al. 2007). Abbreviations: LT = lowest temperature available in terrarium; MSBT = maximum surface basking temperature; TG = thermal gradient. Temperatures are expressed as: °C (°F).

Taxon	LT	MSBT	TG	Reference
acanthurus	24 (75.2)	71 (159.8)	47 (84.6)	Kuhn and Julander 1999
	25 (77.0)	76 (168.8)	51 (91.8)	Lemm 1999
	28 (82.4)	70 (158.0)	42 (75.6)	Brown 2012
	15 (59)	78 (172.4)	63 (113.4)	van der Reijden 2006
	28 (82.4)	70 (158.0)	42 (75.6)	Brown 2008
baritji	28 (82.4)	70 (158.0)	42 (75.6)	Brown 2012
primordius	28 (82.4)	70 (158)	42 (75.6)	Brown 2012
	—	50 (122)	—	Husband 2001
	—	50 (122)	—	Husband and Bonnett 2008
storri	< 30 (< 86)	50 (122)	20+ (36+)	Richmond 2005
	28 (82.4)	70 (158)	42 (75.6)	Brown 2012
bushi	28 (82.4)	60 (140)	32 (57.6)	Brown 2012
		50 (122)		Husband and Bonnett 2008
caudolineatus	28 (82.4)	60 (140)	32 (57.6)	Brown 2012
	28 (82.4)	66 (150.8)	38 68.4)	Retes and Bennett 2001
	—	50 (122)	—	Husband and Bonnett 2008
gilleni	25 (77)	70+ (158+)	45+ (81+)	Deutscher 2006
	28 (82.4)	60 (140)	32 (57.6)	Brown 2012
	—	50 (122)	—	Husband and Bonnett 2008
brevicauda	—	45 (113)	—	Fyfe et al. 1999
	—	60 (140)	—	Standon 2008
	—	60 (140)	—	Husband and Bonnett 2008
eremius	28 (82.4)	70 (158)	42 (75.6)	Brown 2012
	—	60 (140)	—	Husband and Bonnett 2008
kingorum	28 (82.4)	60 (140)	32 (57.6)	Brown 2012
	28 (82.4)	66 (150.8)	38 (68.4)	Retes and Bennett 2001
glebopalma	28 (82.4)	60 (140)	32 (57.6)	Brown 2012
	< 30 (< 86)	60 (140)	30+ (54+)	Husband and Bonnett 2008
pilbarensis	28 (82.4)	60 (140)	32 (57.6)	Brown 2012
	28 (82.4)	66 (150.8)	38 (68.4)	Retes and Bennett 2001
	24 (75.2)	50 (122)	26 (46.8)	Hörenberg 2013a
glauerti	28 (82.4)	66 (150.8)	38 (68.4)	Retes and Bennett 2001
	28 (82.4)	60 (140)	32 (57.6)	Brown 2012
	26 (78.8)	55 (131)	29 (52.2)	de Zeeuw 2010
	< 30 (< 86)	60 (140)	30+ (54+)	Husband and Bonnett 2008
	28 (82.4)	55 (131)	27 (48.6)	Ramm 2013a
tristis	28 (82.4)	60 (140)	32 (57.6)	Brown 2012
	—	50 (122)	—	Husband and Bonnett 2008
scalaris	28 (82.4)	60 (140)	32 (57.6)	Brown 2012
	—	50 (122)	—	Husband and Bonnett 2008

Table 2. Elevated surface basking temperatures and broad thermal gradients documented in the literature for varanid lizards belonging to the subgenera *Varanus*, *Soterosaurus*, *Euprepiosaurus*, *Empagusia*, and *Polydaedelus*. Species are clustered based on phylogenetic relatedness (Ast 2001; Fitch et al. 2006; Ziegler et al. 2007). Abbreviations: LT = lowest temperature available in terrarium; MSBT = maximum surface basking temperature; TG = thermal gradient. Temperatures are expressed as: °C (°F).

Subgenus	Taxon	LT	MSBT	TG	Reference
Varanus	*giganteus*	28 (82.4)	55 (131)	27 (48.6)	Brown 2012
		high 20s (low 80s)	60 (140)	30+ (55+)	Husband and Bonnett 2008
	mertensi	28 (82.4)	60 (140)	32 (57.6)	Brown 2012
	mitchelli	28 (82.4)	60 (140)	32 (57.6)	Brown 2012
	gouldii	28 (82.4)	55 (131)	27 (48.6)	Brown 2012
		high 20s (low 80s)	60 (140)	30+ (55+)	Husband and Bonnett 2008
	panoptes	28 (82.4)	55 (131)	27 (48.6)	Brown 2012
		24 (75.2)	62.8 (145)	38.8 (69.8)	Burokas 2012
		high 20s (low 80s)	60 (140)	30+ (55+)	Husband and Bonnett 2008
	rosenbergi	28 (82.4)	55 (131)	27 (48.6)	Brown 2012
		high 20s (low 80s)	60 (140)	30+ (55+)	Husband and Bonnett 2008
	semiremex	24 (75.2)	56 (132.8)	32 (57.6)	Jackson 2005
		28 (82.4)	60 (140)	32 (57.6)	Brown 2012
	spenceri	28 (82.4)	55 (131)	27 (48.6)	Brown 2012
		high 20s (low 80s)	60 (140)	30+ (55+)	Husband and Bonnett 2008
	komodoensis	25 (77)	45 (113)	20 (36)	Sunter 2008
	varius	—	60 (140)	—	Kirshner 2007
		28 (82.4)	55 (131)	27 (48.6)	Brown 2012
		—	60 (140)	—	Husband and Bonnett 2008
	salvadorii	21 (69.8)	49 (120.2)	28 (50.4)	Waterloo and Bayless 2006
		high 20s (low 80s)	65 (149)	35+ (64+)	Trout 2007
Soterosaurus	*salvator*	—	48.9 (120)	—	Rodriguez 2009
Euprepiosaurus	*beccarii*	28 (82.4)	46 (114.8)	18 (32.4)	Gamble and Hartdegen 2000
		24 (75.2)	45+ (113+)	21+ (37.8+)	Fischer 2012
		23.8 (74.8)	49 (120)	25.2 (45.4)	Mendyk and Horn 2011
	keithhornei	—	50 (122)	—	Husband and Bonnett 2008
	prasinus	27 (80.6)	54 (129.2)	27 (48.6)	Mendyk 2006
		28 (82.4)	54.4 (130)	26.4 (47.6)	Mendyk 2008
		—	50 (122)	—	Husband and Bonnett 2008
	indicus	28 (82.4)	60 (140)	32 (57.6)	Brown 2012
	jobiensis	26 (78.8)	54.4 (130)	28.4 (51.2)	Stefani 2008
	juxtindicus	27 (80.6)	45 (113)	18 (32.4)	Wesiak and Koch 2009
	melinus	29 (84.2)	45 (113)	16 (28.8)	Dedlmar and Böhme 2000
Empagusia	*flavescens*	24 (75.2)	45 (113)	21 (37.8)	Visser 1985
Polydaedelus	*albigularis*	29.4 (85)	54.4 (130)	25 (45)	Markland and Brown 2009
	exanthematicus	24 (75.2)	60 (140)	36 (64.8)	Bennett 2001
		—	66 (150.8)	—	Bennett 2000
		28 (82.4)	57 (134.6)	29 (52.2)	Coiro 2007
		24 (75.2)	63 (145.4)	39 (70.2)	Bennett and Thakoordyal 2003
		21 (69.8)	63 (145.4)	42 (75.6)	Sprackland 2010
	ornatus	25 (77)	45 (113)	20 (36)	Hennessy 2010

direct physical contact with heating elements or protective wire cages surrounding heating elements (Horn and Schurer 1978; Greek 2010; Brown 2012), rather than the heated surfaces themselves. Burns arising through contact with extreme surface temperatures, although rare, may be possible only in certain circumstances where cold lizards maintained under cold ambient conditions are exposed to concentrated hot spots that cover too little an area of an animal's body (Good 1999; Vincent and Wilson 1999; Husband and Bonnett 2008; Brown 2012). An animal's body size should therefore dictate the size and coverage of basking areas, and for larger species, clusters or rows of multiple heating elements, as opposed to just a single fixture, have successfully been used to generate evenly distributed, elevated basking spots which provide entire body coverage (Good 1999; Bennett and Thakoordyal 2003; Kirshner 2007; Burokas 2012). Another potential concern is that some halogen flood lamps feature a clear lens in the center of the bulb which can direct a concentrated, magnified beam of light on a relatively small focal point, and are best avoided as heating fixtures.

Concerns of captives overheating can be dismissed, provided that access to a sufficiently broad range of temperatures is available (see below). A growing trend among private varanid keepers, which seeks to further replicate the conditions familiar to many species in nature, is the use of deep (sometimes up to 1 m), naturally-occurring substrates such as soil, sand, and loam which facilitate burrowing. Deep burrows and similar refuge sites can provide relief from warmer ambient air temperatures, and greatly increase thermal variation within an enclosure. Some zoos, however, may be unable, or reluctant to provide deep substrates for burrowing species, as burrows can interfere with the observation of specimens maintained on public display. In such circumstances, providing cooler refugia may require novel and innovative approaches which take into consideration the ecology and biological requirements of the species as well as display values. Similarly, since most private keepers are unable to accommodate spacious enclosures in their households, creating broad thermal gradients in diminutively sized enclosures presents its own set of logistical challenges, but is possible with careful planning and design.

The relationship between temperature and humidity is often overlooked in herpetological husbandry, even though it is widely established that water loss in reptiles is strongly influenced by both of these environmental factors (Warburg 1965b; Cohen 1975; Thomspon and Withers 1997; DeNardo et al. 2004). Enclosures with liberal screen or wire mesh coverage, and warmer than room temperatures (especially those used for basking) can create a significant air-flow, leading to a loss of humidity, and ultimately drier ambient conditions within the enclosure. Without access to high humidity levels, animals lose water to the captive environment through cutaneous evaporation and respiration, which can lead to dehydration, related health complications, and death. Reducing the amount of ventilation and incorporating deep, moisture-retaining natural substrates can help maintain appropriate ambient humidity levels within enclosures (Mendyk et al. 2013), provided that drainage and airflow are adequate for preventing microbial growth and associated health issues. Moreover, providing a variety of refuge sites with varying levels of humidity that captives can select from as needed further replicates the variation in microhabitats and microclimates experienced in nature, and can help further reduce the risk and health consequences of dehydration.

Implications for Biological Research

Ex situ investigations are frequently used by herpetologists to study various aspects of reptilian biology, particularly biological parameters that may not be possible or logistically feasible to study in the field. Although short-term laboratory investigations typically do not require the longevity that keeping reptiles in zoos and private collections does, biologically appropriate husbandry practices are still necessary for maintaining healthy research subjects. Captive varanid lizards have served as important study subjects in numerous investigations on reptilian physiology, psychology, and behavior (Bartholomew and Tucker 1964; Bennett 1972, 1973; Green 1972; Loop 1974, 1976; Berger and Heisler 1977; Meek 1978; Earll 1982; Cooper 1989a,b; Thompson and Withers 1992; Christian et al. 1996; Kaufman et al. 1996; Secor and Phillips 1997; Thompson 1997; Bennett et al. 2000; Frappell et al. 2002; Clemente et al. 2009; Gaalema 2011; Schachner et al. 2014). The fact that basking temperatures and thermal gradients offered to varanids in captivity have historically been inadequate could have far-reaching consequences which cross over into biological research. Captive conditions that prevent or discourage animals from reaching their preferred body temperatures can have direct effects on their activity levels, behavior, and performance (Christian and Weavers 1996). As a result, thermally compromised individuals may not be operating under optimal physiological conditions, which can skew experimental results and their interpretations.

One particular study, in which thermal husbandry practices may have had an unintended effect on its results and interpretations, compared the active body temperatures of captive *V. komodoensis* to free-ranging wild individuals (Walsh et al. 1999). This study found that captive *V. komodoensis* maintained active body temperatures that were significantly cooler than those recorded from wild conspecifics. Two potentially feasible explanations were offered for these unusual results. The first suggested that captives may have chosen to operate at lower body temperatures because of the reduced energy demands of captivity created by confinement and food provisioning (Walsh et al. 1999). The other suggested that the lower body temperatures in captives may have been a physiological response to the smaller size of prey items and greater frequency at which they are fed when compared to the larger and less frequent meals typical of wild *V. komodoensis*, which might require higher temperatures for digestion (Walsh et al. 1999).

A possible alternative hypothesis, not discussed by Walsh et al. (1999), relates to the range of temperatures available to captives for thermoregulation. Since the 40°C (104°F) maximum surface basking temperature offered to captives in the study (Walsh et al. 1999) is substantially cooler than the surface temperatures individuals would normally have access to for basking in nature (Auffenberg 1981), heating rates among captives were probably slower than in free-living wild individuals. Considering the activity levels, foraging habits, and general inquisitiveness of varanid lizards, particularly *V. komodoensis* (Auffenberg 1981; Burghardt et al. 2002), it is possible that captives chose to forgo reaching their optimal Tbs for other activities simply because it was taking too long to heat up. Field studies on seasonal body temperature variation in varanid lizards have reported similar findings, where several species maintain year-round activity, but operate at lower body temperatures than their optimal range during colder weather (Auffenberg 1994; Christian and Weavers 1996; King and Green 1999; Ibrahim 2000; Rathnayake et al. 2003). King and Green (1999) showed that wild *V. rosenbergi* spent nearly three times as much time basking to elevate Tbs during colder winter months than in summer, yet never achieved the same active Tbs as in summer (29.3 vs 32.0°C [84.7 vs 89.6°F], respectively). The inability to reach optimal Tbs, or an inability to reach them within a reasonable timeframe would explain why varanids operate at lower Tbs during colder weather, and may explain a similar phenomenon in captive *V. komodoensis*.

Another important consideration is that as heliotherms, varanids largely rely on heat generated by the sun, a visible heat source, for elevating their body temperatures and typically thermoregulate by moving between sunlit and covered areas. Although empirical studies have yet to compare the thermoregulatory behaviors of varanids when given a choice between visible (i.e., natural sunlight, mercury vapor lamps, incandescent lamps, etc.) and non-visible (i.e. infrared heat emitters) heat sources for basking, observations from captivity suggest that at least some species respond differently to basking sites generated by different wavelengths of light (Laszlo 1969; Vincent and Wilson 1999; Deutscher 2006). For instance, when given access to both a non-heat emitting fluorescent coil lamp and a heat-producing halogen flood lamp, two *V. similis* repeatedly sought out and basked for extended periods under the fluorescent lamp, even though it did not emit any heat (Mendyk, unpub. obs.). Similar observations of basking behavior have also been reported for *V. timorensis* when given access to full-spectrum fluorescent lighting (Laszlo 1969). The infrared quartz heaters used by Walsh et al. (1999) to create a basking site for their *V. komodoensis* generated heat without producing visible light, and may have had some unintended effect on basking behavior. Several authors have suggested that captive varanids may not receive the same behavioral cues from non-visible, light-emitting heat sources as they do when basking under a visible light source (Card 1995; Vincent and Wilson 1999; Eidenmüller 2005), and while Walsh et al. (1999) noted that *V. komodoensis* occasionally entered the basking spot during the study period, it is possible that the animals may have been more drawn to basking in natural sunlight filtered through the exhibit's extensive skylights and windows than under the heater itself, which could have also had an effect on selected body temperatures. The tendency of diurnal reptiles to seek out filtered natural sunlight over infrared heat for basking has been observed in other species in captivity including *Astrochelys radiata* and *Phelsuma madagascariensis* (R.W.M. and L.A., pers. observ.), and warrants further investigation, especially since these types of behavioral observations can illustrate the taxon-specific appropriateness of different types of heating elements in herpetological husbandry.

Concluding Remarks

Since captive reptiles are often provided with narrow and inadequate temperature ranges that are based on human-estimated requirements (Arena and Warwick 1995), it is important for keepers to approach herpetological husbandry with an open mind and experimental methodology. By ignoring baseless long-term keeping traditions and "folklore husbandry" (Arbuckle 2013), and actually testing the preferences and tolerances of specimens under their care, keepers can develop and employ more effective biologically-appropriate husbandry practices. Based on our review of the thermal biology and captive maintenance of varanid lizards, several conclusions (see below) can be reached about their thermal husbandry. Applying this information towards current keeping methodologies can help zoos, private keepers, and research laboratories improve the welfare, keeping, and reproductive success of specimens in their care.

1) Surface basking temperatures below 45°C (113°F) and narrow thermal gradients may prohibit animals from reaching their preferred Tbs or prevent them from achieving them within a reasonable timeframe.

2) Broad thermal gradients which extend from 22°C (71.6°F) to elevated basking temperatures in excess of 45°C (113°F) (sometimes as high as 70°C [158°F] for some species) allow captives to select from a wide range of temperatures as needed to satisfy various physiological requirements, and offer many biological benefits over older, traditional keeping methodologies.

3) Access to a range of elevated humidity levels, including those near or at the point of saturation is important for captives to reduce and control evaporative water loss to their environment, and prevent dehydration.

4) Biological research carried out in captivity should consider the ecology and thermal biology of varanids when developing keeping methodologies to ensure that study subjects are provided with climatic conditions that allow them to reach their preferred Tbs and operate under optimal physiological condition.

Finally, in addition to establishing a target set of parameters for zoos, private keepers, and research laboratories to follow and incorporate into existing captive management practices, this study raises many additional questions relating to the thermal biology and thermal husbandry of varanid lizards. For instance, when provided with an unlimited range of basking temperatures, what is the highest temperature that a particular species will select for basking, and do these preferences vary with sex, age, or body size? How does basking behavior and the temperatures selected for basking differ under different ambient humidity levels, and is there a single, optimal body temperature for an individual, or do individual thermal preferences vary with age, reproductive state, physical condition, or season? These questions and others can be answered through carefully designed, captivity-based experiments, and represent a possible avenue for zoos and related facilities to contribute to research.

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Literature Cited

Anonymous. 1997. Secrets of the goanna man, part 1. Vivarium 9(2):16–17, 65–66.

———. 1998a. Secrets of the goanna man, part 2. Vivarium 9(3):65–66.

———. 1998b. Secrets of the goanna man, part 3. Vivarium 9(4):60–61.

Arbuckle, K. 2013. Folklore husbandry and a philosophical model for the design of captive management regimes. Herpetol. Rev. 44:448–452.

Arena, P. C., and C. Warwick. 1995. Miscellaneous factors affecting health and welfare. *In* C. Warwick, F. L. Frye, and J. B. Murphy (eds.), Health and Welfare of Captive Reptiles, pp. 263–283. Chapman and Hall, London.

Ast, J. C. 2001. Mitochondrial DNA evidence and evolution in Varanoidea (Squamata). Cladistics 17:211–226.

Auffenberg, W. 1981. The Behavioral Ecology of the Komodo Monitor. University Press of Florida, Gainesville. 406 pp.

———. 1988. Gray's Monitor Lizard. University Press of Florida, Gainesville. 419 pp.

———. 1994. The Bengal Monitor. University Press of Florida, Gainesville. 560 pp.

Auliya, M. A. 2006. Taxonomy, Life History and Conservation of Giant Reptiles in West Kalimantan. Natur und Tier Verlag GmbH, Münster. 432 pp.

Avery, R. A. 1994. The effects of temperature on captive amphibians and reptiles. *In* J. B. Murphy, K. Adler, and J. T. Collins (eds.), Captive Management and Conservation of Amphibians and Reptiles, pp. 47–51. Society for the Study of Amphibians and Reptiles, Ithaca, New York.

Bacon, J. P. 1976. Thermoregulation in *Varanus komodoensis* in captivity—a preliminary report. Proc. Amer. Assoc. Zool. Parks and Aquar. 1976:211–214.

Barbour, T. 1943. Defense posture of *Varanus gouldii*. Copeia 1943:56–57.

Barker, D. G. 1984. Maintenance and reproduction of *Varanus prasinus kordensis* at the Dallas Zoo. *In* R. A. Hahn (ed.), 8th International Herpetological Symposium on Captive Propagationand Husbandry, pp. 91–92. International Herpetological Symposium, Thurmont, Maryland.

Bartholomew, G. A., and V. A. Tucker. 1964. Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards. Physiol. Zool. 37:341–354.

Bayless, M. K., and Q. Dwyer. 1997. Notes on the peach-throated monitor. Reptile and Amphibian Magazine 47:26–30.

Becker, H. -O., W. Böhme, and S. F. Perry. 1989. Die Lungenmorphologie der Warane (Reptilia: Varanidae) und ihre systematisch-stamesgeschichtliche Bedeutung. Bonn. Zool. Beitr. 40:27–56.

Behrmann, H. -J. 1981. Haltung und Nachzucht von *Varanus t. timorensis* (Reptilia: Sauria: Varanidae). Salamandra 17:198–201.

Bennett, A. F. 1972. The effect of activity on oxygen consumption, oxygen debt, and heart rate in the lizards *Varanus gouldii* and *Sauromalus hispidus*. J. Comp. Physiol. 79:259–280.

———. 1973. Blood physiology and oxygen transport during activity in two lizards, *Varanus gouldii* and *Sauromalus hispidus*. Comp. Biochem. Physiol. 46A: 673–690.

———, J. W. Hicks, and A. J. Cullum. 2000. An experimental test of the thermoregulatory hypothesis for the evolution of endothermy. Evolution 54:1768–1773.

Bennett, D. 1989. Monitor lizards. Brit. Herpetol. Soc. Bull. 28:3–5.

———. 1994. Some remarks on longevity in monitor lizards. SW Herpetol. Soc. J. 2(3):27–29.

———. 1998. Monitor Lizards: Natural History, Biology and Husbandry. Edition Chimaira, Frankfurt am Main. 352 pp.

———. 2001. A very misunderstood lizard *Varanus exanthematicus*. Reptilia 19:43–47.

———, and R. Thakoordyal. 2003. The Savannah Monitor Lizard—The Truth About *Varanus exanthematicus*. Viper Press, Aberdeen. 83 pp.

Berger, P. J., and N. Heisler**.** 1977. Estimation of shunting, systematics and pulmonary output of the heart, and regional blood flow distribution in unanaesthetized lizards, *Varanus exanthematicus* by injection of radioactivity labelled microspheres. J. Exper. Biol. 71:111–121.

Berghof, H. -P. 2009. Der Getüpfelte Baumwaran *Varanus* (*Odatria*) *similis*. Natur und Tier Verlag GmbH, Münster. 61 pp.

Bogert, C. M. 1949. Thermoregulation in reptiles, a factor in evolution. Evolution 3:195–211.

———. 1959. How reptiles regulate their body temperature. Sci. Amer. 200:105–120.

Boyer, D., and T. H. Boyer. 1997. Comments on husbandry and medical problems in captive varanids. Varanids 1(1):4–11.

Brattstrom, B. H. 1973. Rate of heat loss by large Australian monitor lizards. Bull. S. California Acad. Sci. 72:52–54.

Brown, D. 2008. A case of hermaphroditism in the ridge tailed monitor (*Varanus acanthurus*). Biawak 2:87–88.

———. 2012. A Guide to Australian Monitors in Captivity. Reptile Publications, Burleigh. 263 pp.

Buffenstein, R., and G. Louw. 1982. Temperature effects on bioenergetics of growth, assimilation efficiency and thyroid activity in juvenile varanid lizards. J. Therm. Biol. 7:197–200.

Burghardt, G. M., D. Chiszar, J. B. Murphy, J. Romano, T. Walsh, and J. Manrod. 2002. Behavioral complexity, behavioral development, and play. *In* J. B. Murphy, C. Ciofi, C. de la Panouse, and T. Walsh (eds.), Komodo Dragons: Biology and Conservation, pp. 78–117. Smithsonian Institution Press, Washington, DC.

Burokas, J. 2012. An owner's guide to the Argus monitor. Reptiles 20(3):5257.

Card, W. 1995. Monitor lizard husbandry. Bull. Assoc. Reptil. Amphib. Vet. 5(3):917.

———. 1996. Taxon management account—Gray's monitor or Butaan *Varanus olivaceus*. *In* S. H. Hammack (ed.), American Zoo and Aquarium Association Lizard Advisory Group, Taxon Management Accounts, 4 pp. Fort Worth Zoological Park, Fort Worth.

Chippendale, P. 1991. Captive breeding of the Timor monitor (*Varanus timorensis similis*). Herpetol. Rev. 22:52–53.

Christian, K., and G. Bedford. 1996. Thermoregulation by the spotted tree monitor, *Varanus scalaris*, in the seasonal tropics of Australia. J. Therm. Biol. 21:67–73.

———, ———, and S. T. Shannahan. 1996. Solar absorptance of some Australian lizards and its relationship to temperature. Austral. J. Zool. 44:59–67.

———, and B. Weavers. 1994. Analysis of the activity and energetics of the lizard *Varanusrosenbergi*. Copeia 1994:289–295.

———, and ———. 1996. Thermoregulation of monitor lizards in Australia: An evaluation of methods in thermal biology. Ecol. Monogr. 66:139–157.

Clemente, C. J., P. C. Withers, and G. G. Thompson. 2009. Metabolic rate and endurance capacity in Australian varanid lizards (Squamata: Varanidae: *Varanus*). Biol. J. Linn. Soc. 97:664–676.

Cohen, A. C. 1975. Some factors affecting water economy in snakes. Comp. Biochem. Physiol. 51A:361–368

Cohn, J. P. 1994. Indonesian treasure has a Jurassic appeal. Bioscience 44(1):4–7.

Coiro, J. 2007. Captive breeding of *Varanus exanthematicus*. Biawak 1:29–33.

Cooper, W. E. 1989a. Prey odor discrimination in the varanoid lizards *Heloderma suspectum* and *Varanus exanthematicus*. Ethology 81:250–258.

———. 1989b. Strike induced chemosensory searching occurs in lizards. J. Chem. Ecol. 15:1311–1320.

Cowles, R. B., and C. M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Amer. Mus. Nat. Hist. 83:261–296.

Davis, R., R. Darling, and A. Darlington. 1986. Ritualized combat in the Dumeril's monitor. Herpetol. Rev. 17:85–88.

Dedlmar, A., and W. Böhme. 2000. Erster Nachzuchterfolg beim Quittenwaran, *Varanus melinus* Böhme and Ziegler, 1997. Herpetofauna 22:29–34.

De Grijis, P. 1899. Beobachtungen an Reptilien in der Gefangenschaft. Der Zool. Gart. 40:175–191.

De Lisle, H. F. 1996. The Natural History of Monitor Lizards. Krieger Publ. Co., Malabar, Florida. 201 pp.

DeNardo, D. F., T. E. Zubal, and T. C. M. Hoffman. 2004. Cloacal evaporative cooling: A previously undescribed means of increasing evaporative water loss at higher temperatures in a desert ectotherm, the Gila monster *Heloderma suspectum*. J. Exp. Biol. 207:945–953.

Dessauer, H. C. 1970. Blood chemistry of reptiles: Physiological and evolutionary aspects. *In* C. Gans (ed.), Biology of the Reptilia, pp. 1–72. Academic Press, San Diego, California.

Deutscher, J. 2006. Husbandry and reproduction of captive pygmy mulga monitors *Varanus gilleni*. Reptil. Austral. 3(1):20–25.

De Zeeuw, M. 2010. Husbandry and reproduction of *Varanus glauerti* in captivity. Biawak 4:103–107.

Donoghue, S., and J. Langenberg. 1996. Nutrition. *In* D. R. Mader (ed.), Reptile Medicine and Surgery, pp. 148–174. W. B. Saunders, Philadelphia, Pennsylvania.

Donovan, P. 2012. Out of Africa: The white-throated or rock monitor. Practical Reptile Keeping (April):52–55.

Downing, A. 2007. Dragons of Komodo. EAZA News 59:2–4.

Dwyer, Q., and M. K. Bayless. 2001. The peach-throated monitor: notes on husbandry and reproductive behavior. Reptile & Amphibian Hobbyist 7(1):18–24.

Earll, C. R. 1982. Heating, cooling and oxygen consumption rates in *Varanus bengalensis*. Comp. Biochem. Physiol. A: Physiol. 72:377–381.

Eidenmüller, B. 1990. Beobachtungen bei der Haltung und Nachzucht von *Varanus* (*Varanus*) *mertensi* Glauert, 1951. Salamandra 26:132–139

———. 2005. Captive care of monitors. Part I: Introduction and housing. Iguana 12:177–181.

———. 2007. Monitor Lizards: Natural History, Captive Care and Breeding. Edition Chimaira, Frankfurt am Main. 176 pp.

———, and H. -G. Horn. 1985. Eigene Nachzuchten und der gegenwartige Stand der Nachzucht von *Varanus* (*Odatria*) *storri* Mertens, 1966. Salamandra 21:55–61.

———, and R. Wicker. 1991. Einige Beobachtungen bei der Pflege und Nachzucht von *Varanus* (*Odatria*) *timorensis similis* Mertens, 1958. Salamandra 27:187–193.

———, and ———. 1993. *Varanus* (*Odatria*) *prasinus beccarii* (Doria, 1874), Pflege und Zucht. Salamandra 28:171–178.

Erdfelder, K. -H. 1984. Haltung und Zucht des Stachelschwanzwarans, *Varanus acanthurus* Boulenger, 1885. Sauria 1:911.

Fischer, D. 2012. Notes on the husbandry and breeding of the black tree monitor *Varanus* (*Euprepiosaurus*) *beccarii* (Doria, 1874). Biawak 6:79–87.

Fitch, A. J., A. E. Goodman, and S. C. Donnellan. 2006. A molecular phylogeny of the Australian monitor lizards (Squamata: Varanidae) inferred from mitochondrial DNA sequences. Austral. J. Zool. 54:253–269.

Fost, M. 1996. Taxon management account: Timor monitor (spotted tree monitor) *Varanus timorensis* and *Varanus similis* (=*scalaris*). *In* S. H. Hammack (ed.), American Zoo and Aquarium Association Lizard Advisory Group, Taxon Management Accounts, 14 pp. Fort Worth Zoological Park, Fort Worth, Texas.

Frappell, P., T. Schultz, and K. Christian. 2002. Oxygen transfer during aerobic exercise in a varanid lizard *Varanus mertensi* is limited by the circulation. J. Exp. Biol. 205:2725–2736.

Fyfe, G., B. Munday, and J. Comber. 1999. Captive husbandry and breeding of the short-tailed goanna, *Varanus brevicauda* at the Alice Springs Desert Park. Herpetofauna (Sydney) 29:31–36.

Gaikhorst, G., J. McLaughlin, B. Larkin, and M. McPharlin. 2010. Successful captive breeding of Mitchell's water monitor, *Varanus mitchelli* (Mertens 1958), at Perth Zoo. Zoo Biol. 28:615–625.

Gaalema, D. E. 2011. Visual discrimination and reversal learning in rough-necked monitor lizards (*Varanus rudicollis*). J. Comp. Psychol. 125:246–249.

Gamble, K. C., and R. Hartdegen. 2000. What's your diagnosis? J. Herpetol. Med. Surg. 10:31–32.

Gleeson, T. T. 1981. Preferred body temperature, aerobic scope, and activity capacity in the monitor lizard, *Varanus salvator*. Physiol. Zool. 54:423–429.

Good, D. H. 1999. An interview with Frank Retes. Reptiles 7(5):32–47.

Gorman, D. 2000. Notes on the green tree monitor (*Varanus prasinus*). Reptiles 8(2):68–73.

Greek, T. 2012. Heat things up. Reptiles 20(8):46–49.

Green, B. 1972. Water losses of the sand goanna (*Varanus gouldii*) in its natural environments. Ecology 53:452–457.

———, D. King, M. Braysher, and A. Saim. 1991. Thermoregulation, water turnover and energetics of free-living Komodo dragons, *Varanus komodoensis*. Comp. Biochem Physiol A: Physiol. 99:97–101.

Grützner, T. 2003. Nachzucht von *Varanus ornatus* (Daudin 1803). Elaphe 11:25–34.

Guillette, L. J., A. Cree, and A. A. Rooney. 1995. Biology of stress: Interactions with reproduction, immunology and intermediary metabolism. *In* C. Warwick, F. L. Frye, and J. B. Murphy (eds.), Health and Welfare of Captive Reptiles, pp. 32–81. Chapman and Hall, London.

Gupta, B. 1997. The captive maintenance of the Indian monitor (*Varanus bengalensis*) Daudin in India. Animal Keepers' Forum 24:309–313.

Haggag, G., K. A. Raheem, and F. Khallil. 1966. Hibernation in reptiles II. Changes in blood glucose, haemoglobin, red blood cell count, protein and non-protein nitrogen. Comp. Biochem. Physiol. 17:335–339.

Hairston-Adams, C., and R. Reed. 2000. Taxon management account: crocodile or Papuan monitor *Varanus salvadorii*. *In* R. Hartdegen (ed.), 1999 Asian Forest Monitor North American Regional Studbook, pp. 35–41. Dallas Zoo, Dallas, Texas.

Harlow, H. J., D. Purwandana, T. S. Jessop, and J. A. Phillips. 2010. Size-related differences in the thermoregulatory habits of free-ranging Komodo dragons. Int. J. Zool. 2010: Article ID 921371.

Hartdegen, R. 1998. Black rough-necked monitors (*Varanus rudicollis*). Reptiles 6(10):68–74.

Hartdegen, R. W. 2002. 2002 Asian Forest Monitor North American Regional Studbook. Dallas Zoo, Dallas, Texas. 123 pp.

Heger, N. A., and T. G. Heger. 2007. Behavior, ecology, and thermal physiology of *Varanus giganteus*: a field study of Australia's largest monitor lizard. *In* H. -G. Horn, W. Böhme, and U. Krebs (eds.), Advances in Monitor Research 3, Mertensiella 16, pp. 255–290. Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V., Rheinbach.

Hennessy, J. 2010. Parthenogenesis in an ornate Nile monitor, *Varanus ornatus*. Biawak 4:26–30.

Hernandez, T., and R. A. Coulson. 1957. Inhibition of renal tubular function by cold. Amer. J. Physiol. 188:485–489.

Holmstrom, W. 1996. Taxon management account, desert monitor *Varanus griseus*. *In* S. H. Hammack (ed.), American Zoo and Aquarium Association Lizard Advisory Group, Taxon Management Accounts, 6 pp. Fort Worth Zoological Park, Fort Worth, Texas.

Hörenberg, T. 2013a. Der Pilbara-Waran, *Varanus pilbarensis* - Haltung und Nachzucht. Draco 53:31–36.

———. 2013b. Erfarungen bei der Pflege und Nachzucht des Schwarzkopfwarans, *Varanus tristis tristis*. Draco 53:69–77.

Horn, H. –G. 1991. Breeding of the lace monitor (*Varanus varius*) for the first time outside of Australia (Reptilia: Sauria: Varanidae). *In* W. Böhme, and H. –G. Horn (eds.), Advances in Monitor Research, Mertensiella 2, pp. 168–175. Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V., Rheinbach.

———. 2004. Keeping monitors in captivity: A biological, technical, and legislative problem. *In* E. R. Pianka, D. R. King, and R. A. King (eds.), Varanoid Lizards of the World, pp. 556–570. Indiana University Press, Indianapolis, Indiana.

———, and U. Schurer. 1978. Bemerkungen zu *Varanus* (*Odatria*) *glebopalma* (Mitchell, 1955). Salamandra 14:105–116.

———, and G. J. Visser. 1989. Review of reproduction of monitor lizards *Varanus* spp. in captivity. Int. Zoo Yb. 28:140–150.

———, and ———. 1997. Review of reproduction of monitor lizards *Varanus* spp. in captivity II. Int. Zoo Yb. 35:227–246.

Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. Amer. Zool. 19:357–366.

Husband, G., and M. Bonnett. 2009. Monitors. *In* M. Swan (ed.), Keeping and Breeding Australian Lizards, pp. 484–583. Mike Swan Herp Books, Lilydale.
———, and M. Vincent. 1999. The pygmy mulga monitor *Varanus gilleni*—take a look at one of Australia's fascinating diminutive monitor species. Reptiles 7(5):10–18.
Hutchinson, V. H., and R. K. Dupre, 1992. Thermoregulation. *In* M. Feder and W. Burggren (eds.), Environmental Physiology of the Amphibia, pp. 206–249. University of Chicago Press, Chicago, Illinois.
Ibrahim, A. A. 2000. A radiotelemetric study of the body temperature of *Varanus griseus* (Sauria: Varanidae) in Zaranik Protected Area, North Sinai, Egypt. Egypt. J. Biol. 2:57–66.
Jackson, R. 2005. The poorly known rusty monitor *Varanus semiremex*: history, natural history, captive breeding and husbandry. Herpetofauna (Sydney) 35:15–24.
Johnson, C. R. 1972. Head-body temperature differences in *Varanus gouldii* (Sauria: Varanidae). Comp. Biochem. Physiol. A: Physiol. 43:1025–1029.
Kala, N. 1998. Captive breeding of *Varanus salvator andamanensis* Deraniyagala, 1944. Hamadryad 22:122–123.
Kaufman, J. D., G. M. Burghardt, and J. A. Phillips. 1996. Sensory cues and foraging decisions in a large carnivorous lizard, *Varanus albigularis*. Anim. Behav. 52:727–736.
King, D. 1980. The thermal biology of free-living sand goannas (*Varanus gouldii*) in southern Australia. Copeia 1980:755–767.
———, and B. Green. 1999. Monitors: The Biology of Varanid Lizards. Krieger Publ. Co., Malabar, Florida. 116 pp.
King, D., B. Green, and H. Butler. 1989. The activity pattern, temperature regulation and diet of *Varanus giganteus* on Barrow Island, Western Australia. Austral. Wild. Res. 16:41–47.
Kirschner, A. 1999. Bemerkungen zur Pflege und Zucht vom Timorwaran der Insel Roti, Indonesien. Herpetofauna (Weinstadt) 21:13–18.
Kirshner, D. S. 2007. Multiclutching in captive lace monitors (*Varanus varius*). *In* H. -G. Horn, W. Böhme, and U. Krebs (eds.), Advances in Monitor Research III, Mertensiella 16, pp. 403–421. Deutsche Geselleschaft für Herpetologie und Terrarienkunde e.V., Rheinbach.
Kluger, M. J. 1979. Fever in ectotherms: evolutionary implications. Amer. Zool. 19:295–304.
Köhler, G. 1992. Häufige Todesursachen bei Waranen und Krustenechsen. Monitor 1(1):38–41.
Kok, R. 1995. Zur Haltung und Nachzucht des Pazifikwarans (*Varanus indicus*). Salamandra 31:129–136.
Krebs, U. 1999. Experimental variation of breeding season and incubation time in the spiny-tailed monitor (*Varanus acanthurus*). *In* H. -G. Horn, and W. Böhme (eds.), Advances in Monitor Research II, Mertensiella 11, pp. 227–238. Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V., Rheinbach.
Kuhn, P., and J. Julander. 1999. Husbandry and captive breeding of the red acanthurus monitor *Varanus acanthurus*: A giant dwarf. Vivarium 10(3):23–26
Laszlo, J. 1969. Observations on two new artificial lights for reptile displays. Int. Zoo Yb. 9:12–13.
Lee, S. M. 2000. The captive maintenance and propagation of the ornate monitor, *Varanus ornatus* (Daudin, 1803) and Merten's water monitor, *Varanus mertensi* (Glauert, 1951) at the Wildlife Conservation Park (Bronx Zoo). *In* J. Ettling (ed.), Proceedings of the 24th Internationa Herpetological Symposium, pp. 53–77. Audubon Park and Zoological Gardens, New Orleans, Louisiana.
———, and J. Friedman. 2000. Captive maintenance and propagation of the Merten's water monitor (*Varanus mertensi*). Reptiles 8(8):70–88.
Lemm, J. 1999. Ackies: The natural history and captive husbandry of the spiny-tailed monitor (*Varanus acanthurus*). Reptiles 7(6):4865.
———. 2001. Die Aufigsten Warane im Tierhandel- Arten und Grundlagen der Haltung. Draco 7:20–29.
Licht, P., W. R. Dawson, V. H. Shoemaker, and A. R. Main. 1966. Observations on the thermal relations of western Australian lizards. Copeia 1966:97–110.
Lillywhite, H. B., and R. E. Gatten. 1995. Physiology and functional anatomy. *In* C. Warwick, F. L. Frye and J. B. Murphy (eds.), Health and Welfare of Captive Reptiles, pp. 5–31. Chapman and Hall, London.
Loop, M. S. 1974. The effect of relative prey size on the ingestion behavior of the Bengal monitor, *Varanus bengalensis* (Sauria: Varanidae). Herpetologica 30:123–127.
———. 1976. Auto-shaping—a simple technique for teaching a lizard to perform a visual discrimination task. Copeia 1976:574–576.
Markland, R., and C. Brown. 2009. Keeping and breeding *Varanus albigularis*. *In* R. G. Sprackland, Giant Lizards, pp. 220–221. TFH Publications, Neptune, New Jersey.
McDonald, B. 1999. Captive husbandry and reproduction of the freckled monitor (*Varanus tristisorientalis*) (Fry 1913). Monitor 10:69–75.
McNab, B. K., and W. Auffenberg. 1976. The effect of large body size on the temperature regulation of the Komodo dragon, *Varanus komodoensis*. Comp. Biochem. Physiol. A: Physiol. 55:345–350.
Meek, R. 1978. On the thermal relations of two oriental varanids: *Varanus bengalensis nebulosus* and *Varanus salvator*. Cotswold Herpetol. Symp. Rep. 1978:32–47.
Mehaffey, D., and D. McGinnity. 1996. Taxon management account: Black roughneck monitor *Varanus rudicollis*. *In* S. H. Hammack (ed.), American Zoo and Aquarium Association Lizard Advisory Group, Taxon Management Accounts, 8 pp. Fort Worth Zoological Park, Fort Worth, Texas.
Mendyk, R. W. 2006. Keeping the green tree monitor: a herpetological gem. Reptiles 14(8):44–53.
———. 2008. Remarks on osteological deformities in a captive-bred emerald tree monitor, *Varanus prasinus*. Biawak 2:72–79.
———. 2012. Reproduction of varanid lizards (Reptilia: Squamata: Varanidae) at the Bronx Zoo. Zoo Biol. 31:374–389.
———, and H. -G. Horn. 2012. Skilled forelimb movements and extractive foraging in the arboreal monitor lizard *Varanus beccarii*. (Doria, 1874). Herpetol. Rev. 42:343–349.
———, A. L. Newton, and M. Baumer. 2013. A retrospective study of mortality in varanid lizards (Reptilia: Squamata: Varanidae) at the Bronx Zoo: Implications for husbandry and reproductive management in zoos. Zoo Biol. 32:152–162.
Moehn, L. D. 1984. Courtship and copulation in *Varanus timorensis*. Herpetol. Rev. 15:14–16.
Moldovan, D. 2007. Haltung und Zucht von *Varanus* (*Odatria*) *similis* Mertens, 1958. Sauria 29(3):21–26.
———. 2008. Haltung und Zucht von *Varanus* (*Euprepiosaurus*) *macraei* Böhme and Jacobs, 2002. Sauria 30(4):5–10.
Muhigwa, J.B. 1998. Diel activity and biotope choices of the Nile monitor lizard in western Kenya. Afr. J. Ecol. 36:271–275.
Murphy, J. B. 1969. Notes on iguanids and varanids in a mixed exhibit at Dallas Zoo. Int. Zoo Yb. 9:39–41.
———. 1971. Notes on the care of the ridge-tailed monitor *Varanus acanthurus brachyurus* at Dallas Zoo. Int. Zoo Yb. 11:230–231.
———. 1972. Notes on some Indo-Australian varanids in captivity. Int. Zoo Yb. 12:199–202.
Nagy, K. A. 1983. Ecological energetics. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), Lizard Ecology, pp. 25–54. Harvard University Press, Cambridge, Massachusetts.
O'Dell, J. 1996. The freckled monitor. Reptiles 4(7):32–38.
Oliver, J. A., and S. Spencook. 1956. Department of reptiles. *In* 61st Annual Report of the New York Zoological Society, pp. 17–22. New York Zoological Society, New York.
Owerkowicz, T., C. G. Farmer, J. W. Hicks, and E. L. Brainerd. 1999. Contribution of gular pumping to lung ventilation in monitor lizards. Science 284:1661–1663.
Pandav, B., and B. C. Choudhury. 1996. Diurnal seasonal activity patterns of water monitor (*Varanus salvator*) in the Bhitarkanika mangroves, Orissa, India. Hamadryad 21:4–12.
Peaker, M. 1969. Some aspects of the thermal requirements of reptiles in captivity. Int. Zoo Yb. 9:3–8.

Pfaff, S., and R .G. Sprackland. 1996. Taxon management account: green tree monitor/emerald tree monitor *Varanus prasinus*. *In* S. H. Hammack (ed.), American Zoo and Aquarium Association Lizard Advisory Group, Taxon Management Accounts, 5 pp. Fort Worth Zoological Park, Fort Worth, Texas.

Pianka, E. R. 1970. Notes on the biology of *Varanus gouldi flavirufus*. W. Austral. Nat. 11:141–144.

———. 1994a. Comparative ecology of *Varanus* in the Great Victoria Desert. Austral. J. Ecol. 19:395–408.

———. 1994b. The Lizard Man Speaks. University of Texas Press, Austin. 179 pp.

———. 1995. Evolution of body size: varanid lizards as a model system. Amer. Nat. 146:398–414.

———, and D. R. King. 2004. Introduction. *In* E. R. Pianka, D. R. King, and R. A. King (eds.), Varanoid Lizards of the World, pp. 3–9. Indiana University Press, Bloomington, Indiana.

———, and L. J. Vitt. 2003. Lizards: Windows to the Evolution of Diversity. University of California Press, Berkeley and Los Angeles. 333 pp.

Purser, P. 2014. A monitor foursome. Reptiles 22(1):38–45.

Radford, L., and F. L. Paine. 1989. The reproduction and management of the Dumeril's monitor *Varanus dumerilii* at the Buffalo Zoo. Int. Zoo Yb. 28:153–155.

Ramm, T. 2013a. Haltung und erfolgreiche Nachzucht des Kimberley-Felswarans, *Varanus glauerti*. Draco 53:20–28.

———. 2013b. Die erfolgreichte Haltung und Nachzucht von Gillens Zwergwaran (*Varanus gilleni*) im Terrarium. Draco 53:45–50.

Rathnayake, N. D., N. D. Herath, K. K. Hewamathes, and S. Jayalath. 2003. The thermal behavior, diurnal activity pattern and body temperature of *Varanus salvator* in central Sri Lanka. Hamadryad 27:179–184.

Retes, F., and D. Bennett. 2001. Multiple generations, multiple clutches, and early maturity in four species of monitor lizards (Varanidae) bred in captivity. Herpetol. Rev. 32:244–245.

Richmond, M. 2005. Captive breeding of Storr's monitor *Varanus storri*. Reptil. Austral. 5(2):40–43.

Rodriguez, P. 2009. Keeping and breeding *Varanus salvator. In* R. G. Sprackland, Giant Lizards, pp. 257–259. TFH Publications, Neptune, New Jersey.

Ryman, R. 2009. Husbandry Guidelines for Perentie *Varanus giganteus*, Gray 1945 Reptilia: Varanidae. Western Sydney Institute of TAFE, Richmond. 71 pp.

Schachner, E. R., R. L. Cieri, J. P. Butler, and C. G. Farmer. 2014. Unidirectional pulmonary airflow patterns in the savannah monitor lizard. Nature 506:367–370.

Secor, S. M., and J. A. Phillips. 1997. Specific dynamic action of a large carnivorous lizard, *Varanus albigularis*. Comp. Biochem. Physiol. A: Physiol. 117:515–522.

Sokolov, V. E., V. P. Sukhov, and Y. M. Chernyshov. 1975. A radiotelemetric study of diurnal fluctuations of body temperature in the desert monitor (*Varanus griseus*). Zoological Zhurnal 54:1347–1356.

Smith, J. G., K. Christian, and B. Green. 2008. Physiological ecology of the mangrove-dwelling varanid *Varanus indicus*. Physiol. Biochem. Zool. 81:561–569.

Spelman, L. H. 2002. Medical Management. *In* J. B. Murphy, C. Ciofi, C. de La Panouse, and T. Walsh (eds.), Komodo Dragons: Biology and Conservation, pp. 196–210. Smithsonian Institution Press, Washington, DC.

Sprackland, R. G. 1989. Captive maintenance of green tree monitors (*Varanus prasinus*) and their kin. Proc. N. California Herpetol. Soc. 1989:49–56.

———. 2007. Peach-throat monitors. Reptiles 15(2):40–47.

———. 2010. Savannah savvy. Reptiles 18(2):32–41.

Standon, W. 2008. Husbandry manual for the short tailed monitor *Varanus brevicauda* (Reptilia: Varanidae). Western Sydney Institute of TAFE, Sydney. 43 pp.

Stebbins, R. C., and R. E. Barwick. 1968. Radiotelemetric study of thermoregulation in a lace monitor. Copeia 1968:541–547.

Stefani, M. 2008. Husbandry and reproduction of the peach-throated monitor *Varanus jobiensis* in captivity. Biawak 2:124–130.

Stirnberg, E., and H. -G. Horn. 1981. Eine unerwartete Nachzucht im Terrarium: *Varanus* (*Odatria*) *storri*. Salamandra 17:55–62.

Strimple, P. D. 1996. Natural history and captive husbandry of selected monitor species. Reptiles USA Annual 1996:136–153.

Sunter, G. 2008. Management and reproduction of the Komodo dragon *Varanus komodoensis* Ouwens 1912 at ZSL London Zoo. Int. Zoo Yb. 42:172–182.

Sweet, S. S., and E. R. Pianka. 2007. Monitors, mammals, and Wallace's Line. *In* H. -G. Horn, W. Böhme, and U. Krebs (eds.), Advances in Monitor Research III, Mertensiella 16, pp. 79–99. Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V., Rheinbach.

Thissen, R. 1993. Haltung und Zucht des Stachelschwanzwarans *Varanus acanthurus* (Boulenger, 1885). Elaphe 1(3):4–9.

Thompson, G. G. 1997. Do training and captivity affect maximal metabolic rate of *Varanus gouldii* (Squamata: Varanidae)? Amphibia-Reptilia 18:112–116.

———. 1999. Goanna metabolism: Is it different to other lizards and if so what are the ecological consequences. *In* H. –G. Horn, and W. Böhme (eds.), Advances in Monitor Research II, Mertensiella 11, pp. 79–90. Deutsch Gesellschaft für Herpetologie und Terrarienkunde e.V., Rheinbach.

———, E. R. Pianka, and M. de Boer. 1999. Body temperatures of an arboreal monitor lizard, *Varanus tristis* (Squamata: Varanidae), during the breeding season. Amphibia-Reptilia 20:82–88.

———, and P. C. Withers. 1992. Effects of body mass and temperature on standard metabolic rates for two Australian varanid lizards (*Varanus gouldii* and *V. panoptes*). Copeia 1992:343–350.

———, and ———. 1997. Standard and maximal metabolic rates of goannas (Squamata: Varanidae). Physiol. Zool. 70:307–323.

Traeholt, C. 1995. A radio-telemetric study of the thermoregulation of free living water monitor lizards, *Varanus s. salvator*. J. Comp. Physiol. B 165:125–131.

Trout, T. 2007. Observations of breeding and nesting behaviors in captive *Varanus salvadorii*. *In* H. -G. Horn, W. Böhme, and U. Krebs (eds.), Advances in Monitor Research III, Mertensiella 16, pp. 441–447. Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V., Rheinbach.

van der Reijden, J. 2006. Captive husbandry and breeding of the ridge-tailed monitor *Varanus acanthurus*. Reptil. Austral. 3(1):6–11.

Vernet, R., M. Lemire, C. Grenot, and J. Francaz. 1988. Ecophysiological comparisons between two large Saharan lizards, *Uromastix acanthinurus* (Agamidae) and *Varanus griseus* (Varanidae). J. Arid. Environ. 14:187–200.

Vincent, M., and S. Wilson. 1999. Australian Goannas. New Holland Publishers, Sydney. 152 pp.

Visser, G. J. 1985. Notizen zur Brutbiologie des Gelbwarans *Varanus* (*Empagusia*) *flavescens* (Hardwicke & Gray, 1827) im Zoo Rotterdam. Salamandra 21:161–168.

Walsh, T., D. Chiszar, E. Wikramanayake, H. M. Smith, and J. B. Murphy. 1999. The thermal biology of captive and free ranging wild Komodo dragons, *Varanus komodoensis* (Reptilia: Sauria:Varanidae). *In* H. -G. Horn, and W. Böhme (eds.), Advances in Monitor Research II, Mertensiella 11, pp. 239–246. Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V., Rheinbach.

Warburg, M. R. 1965a. Studies on the environmental physiology of some Australian lizards from arid and semi-arid habitats. Austral. J. Zool. 13:563–575.

———. 1965b. The influence of ambient temperature and humidity on the body temperature and water loss from two Australian lizards, *Tiliqua rugosa* (Gray) (Scincidae) and *Amphibolurus barbatus* Cuvier (Agamidae). Austral. J. Zool. 13:331–350.

Warwick, C. 1991. Observation on disease-associated preferred body temperatures in reptiles. Appl. Anim. Behav. Sci. 28:375–380.

———, and C. Steedman. 1995. Naturalistic versus clinical environments in husbandry and research. *In* C. Warwick, F. L. Frye, and

J. B. Murphy (eds.), Health and Welfare of Captive Reptiles, pp. 113–130. Chapman and Hall, London.

Waterloo, B., and M. K. Bayless. 2006. Notes on the breeding behaviour of the crocodile monitor (*Varanus salvadorii)* in captivity. Herpetol. Bull. 98:2–6.

Wesiak, K. 2007. Die Nachzucht des Getüpfelten Baumwarans *Varanus* (*Odatria*) *tristis orientalis* Fry, 1913, als Resultat einer konstruktiven Zusammenarbeit. Sauria 29:49–52.

———. 2008. Unterbringung, Pflege und Nachzucht von *Varanus* (*Odatria*) *auffenbergi* Sprackland, 1999. Elaphe 16:37–47.

———, and A. Koch. 2009. Successful husbandry and first breeding of *Varanus juxtindicus* Böhme et al., 2002, with remarks on the development of juveniles of this "rarely-kept" endemic Solomon monitor species. Biawak 3:106–121.

Wick, W. 1996. Erfahrungen bei der Haltung und Zucht des Australischen Stachelschwanzwaranes *Varanus* (*Odatria*) *acanthurus brachyurus*. Monitor 4(2):5–18.

Wikramanayake, E. D., and G. L. Dryden. 1993. Thermal ecology of habitat and microhabitat use by sympatric *Varanus bengalensis* and *V. salvator* in Sri Lanka. Copeia 1993:709–714.

———, and ———. 1999. Implications of heating and cooling rates in *Varanus bengalensis* and *V. salvator*. *In* H. -G. Horn, and W. Böhme (eds.), Advances in Monitor Research II, Mertensiella 11, pp. 149–156. Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V., Rheinbach.

———, and B. Green. 1989. Thermoregulatory influences on the ecology of two sympatric varanids in Sri Lanka. Biotropica 21:74–79.

———, W. Ridwan, and D. Marcellini. 1999. The thermal ecology of free-ranging Komodo dragons, *Varanus komodoensis*, on Komodo Island, Indonesia. *In* H. -G. Horn, and W. Böhme (eds.), Advances in Monitor Research II, Mertensiella 11, pp. 157–166. Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V., Rheinbach.

Yuyek, M. D. 2012. Husbandry and reproduction of *Varanus olivaceus* Hallowell (Sauria: Varanidae) at the Avilon Montalban Zoological Park. Biawak 6:39–53.

Ziegler, T., N. Rütz, J. Oberreuter, and S. Holst. 2010. First F2 breeding of the quince monitor lizard *Varanus melinus* Böhme & Ziegler, 1997 at the Cologne Zoo Aquarium. Biawak 4:82–92.

———, A. Schmitz, A. Koch, and W. Böhme. 2007. A review of the subgenus *Euprepiosaurus* of *Varanus* (Squamata: Varanidae): Morphological and molecular phylogeny, distribution and zoogeograpy, with an identification key for the members of the *V. indicus* and *V. prasinus* species groups. Zootaxa 1472:1–28.

———, M. Strauch, T. Pes, J. Konas, T. Jirasek, N. Rütz, J. Oberreuter, and S. Holst. 2009. First captive breeding of the blue tree monitor *Varanus macraei* Böhme & Jacobs, 2001 at the Plzen and Cologne Zoos. Biawak 3:122–133.

Zimmermann, E. 1986. Breeding Terrarium Animals. TFH Publications, Neptune, New Jersey. 384 pp.