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Skilled Forelimb Movements and Extractive Foraging in the Arboreal Monitor Lizard *Varanus beccarii* (Doria, 1874)

Scientists and enthusiasts who have studied, kept, or observed monitor lizards (Varanidae: *Varanus*) for extended periods of time usually recognize that monitors possess considerable intelligence when compared to other reptile groups. Scientific testaments to their "higher intelligence" date back more than a century, with both Ditmars (1902) and Werner (1904) recognizing monitors as the pinnacle of lizard intelligence. Since then, many herpetologists have followed suit in this claim (e.g., Burghardt et al. 2002; Mertens 1942; Phillips 1994; Pianka and King 2004; Sweet and Pianka 2003), supported by research and behavioral observations of their own as well as a growing number of published accounts describing unusual and insightful behaviors in the group (see reviews by Horn 1999 and Krebs 2007). Formal research on the memory and learning capacities of monitors has also contributed to the general understanding of their intelligence (Loop 1976; Manrod et al. 2008).

Despite numerous published accounts on monitor behavior, the insight and behavioral complexity of some species are better understood than others. It is not surprising, given their size and conspicuousness when compared to smaller tree-dwelling taxa, that large terrestrial species (> 1.5 m in total length [TL]) account for most behavioral observations which have led to the idea of intelligence in monitors (Horn 1999; Krebs 2007). Even captivity-based studies on learning and behavioral complexity have focused primarily on large terrestrial species (e.g., Burghardt et al. 2002; Firth et al. 2003; Loop 1976; Manrod et al. 2008). Thus, little is known about the problem-solving abilities and behavioral specializations of the more diminutive monitors, particularly arboreal taxa belonging to the subgenera *Odatria* and *Euprepiosaurus*.

Within *Euprepiosaurus*, the *Varanus prasinus* complex is currently comprised of nine highly arboreal species (to ca. 100 cm TL) endemic to tropical lowland environments of northeastern Australia, New Guinea, and adjacent islands (Ziegler et al. 2007). Behavioral observations on these species in the wild (e.g., Clarke 2004; Irwin 1994, 1996; Pattiselanno et al. 2007; Whittier and Moeller 1993) and in captivity (e.g., Eidenmüller and Wicker 1992; Garrett and Peterson 1991; Hartdegen et al. 1999, 2000; Irwin 1996; Kiehlmann 1999) are rather limited, but specific references to insightful behaviors are scant (Holmstrom 1993). Krebs (1991) doubted the insight of *V. prasinus*, grouping it together with "less-specialized" monitor species on account of a presumed "lower specialized learning ability." This was before several published reports describing diverse prey-handling tactics used by the *V. prasinus* complex (Hartdegen et al. 1999, 2000; Kiehlmann 1999), which Greene (2004) later recognized as highly specialized behaviors. Here, we call special attention to the insight and behavioral complexity of the *V. prasinus* complex by describing a remarkable prey extraction behavior used by the Black Tree Monitor, *V. beccarii* (Doria, 1874), which demonstrates complex problem solving abilities, fine motor coordination, and skilled forelimb movements.

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METHODS

History and husbandry of specimens.—An adult male (242 mm in snout to vent length [SVL]) and female (270 mm SVL) *Varanus beccarii* of unknown ages and of wild-caught origin have been maintained for several years in the private collection of RWM. Both specimens are housed in separate terraria each measuring 90 x 60 x 180 cm (l x w x h). A 6 mm thick sheet of acrylic doubles as a viewing window and access door for each terrarium. Each terrarium is furnished with large tree limbs and the walls are covered with cork sheeting and virgin cork slabs. Live *Pothos* plants provide additional cover. A basking spot of ca. 49°C is provided in each terrarium by outdoor Sylvania® 100 watt halogen flood lamps, which also provide ambient lighting. Daytime ambient temperatures range in a vertical gradient from 23.8°C at the floor to 40.6°C at the ceiling. Nighttime ambient temperatures drop to 30°C. A small access door connecting the terraria is periodically opened to allow the monitors access to one another for breeding.

Since their acquisition, both specimens have been fed a rotating daily diet of *Zophobas morio* larvae, domestic crickets (*Acheta domesticus*), wood cockroaches (*Nauphoeta cinerea*), wax moth larvae (*Achroia grisella*), and frozen-thawed neonatal mice. Typical of many male monitor lizards in captivity, the male *Varanus beccarii* quickly developed a strong feeding response, and feeds aggressively from forceps. The female has remained timid with a weaker feeding response, and only occasionally accepts prey from forceps. Each specimen is fed at alternating locations throughout its terrarium to prevent habitual feeding locations and associated feeding aggression.

Beginning around April 2009, the male was infrequently offered neonatal mice and *Zophobas morio* larvae through a permanent 15 mm gap which had formed in the upper left corner of its terrarium between the acrylic door and the door frame. The gap, created by the warping of the acrylic door over time, was large enough to pass prey items through using forceps, but not large enough for the monitor to fit its head through.

OBSERVATIONS AND RESULTS

Initial behavioral observations.—On 25 January 2010, the male *Varanus beccarii* was fed a neonatal mouse through the gap in the terrarium door. Following its consumption, the monitor showed continued interest in the gap, now scented with mouse odor, by repeatedly tongue-flicking the area. After ca. 15 seconds of tongue-flicking, the lizard extended its right forearm through the opening, and began reaching around the outside frame of the terrarium with its forehand. The lizard retracted its arm back into the terrarium, then after another series of tongue flicks, it extended its left forearm through the opening, performing the same reaching arm movements as before, but reaching a farther extension than with the right arm. This sequence of behaviors was repeated several more times over the next minute until the monitor apparently lost interest.

To determine if this behavior was intended to locate or retrieve prey, a neonatal mouse was held by forceps just outside the gap of the male's terrarium, visible to the lizard. Once the monitor noticed the mouse and recognized its scent, it immediately extended its left forearm through the gap, and began reaching and clawing at the mouse with its forehand. These efforts appeared frantic and were noticeably more coordinated than earlier attempts when a prey item was not present. After keeping the mouse out of reach for several unsuccessful retrieval attempts, it was moved within reach of the monitor. The *Varanus beccarii* hooked the prey with its claws using a grasping forehand movement, then quickly pulled it back into the enclosure where it was seized from the claws with the jaws and swallowed. Additional trials were successfully repeated with both the male and female (through a gap created by partially-opening the female's terrarium door), as well as with *Zophobas morio* larvae offered as prey (Fig. 1).

It is important to note that these reaching and grasping forearm movements involved highly coordinated wrist and digit manipulations (Fig. 1). A similar reaching behavior was observed at the base of the male's terrarium door whenever *Zophobas morio* larvae would fall into a 7 mm wide, 30 mm deep channel running along the length of the door (56 cm) between the door, frame, and weather stripping. Alternating use of both forelimbs, the male was able to retrieve the prey by inserting its forearm into this groove then using a series of side-swiping arm movements until the prey became snagged on a claw or was able to be pulled upwards and out of the opening.

Semi-natural experiments.—Following these initial trials and observations, a simple experiment was carried out to test the use of this behavior in a semi-natural situation. A series of four holes narrower than the width of the monitors' heads measuring 15 x 35, 15 x 65, 20 x 35, and 20 x 65 mm (width x depth) was drilled into one vertically-oriented and one horizontally-oriented tree trunk (trunks ca. 15 cm in diameter) in each terrarium. A variety of prey items, including *Zophobas morio* and *Achroia grisella* larvae,

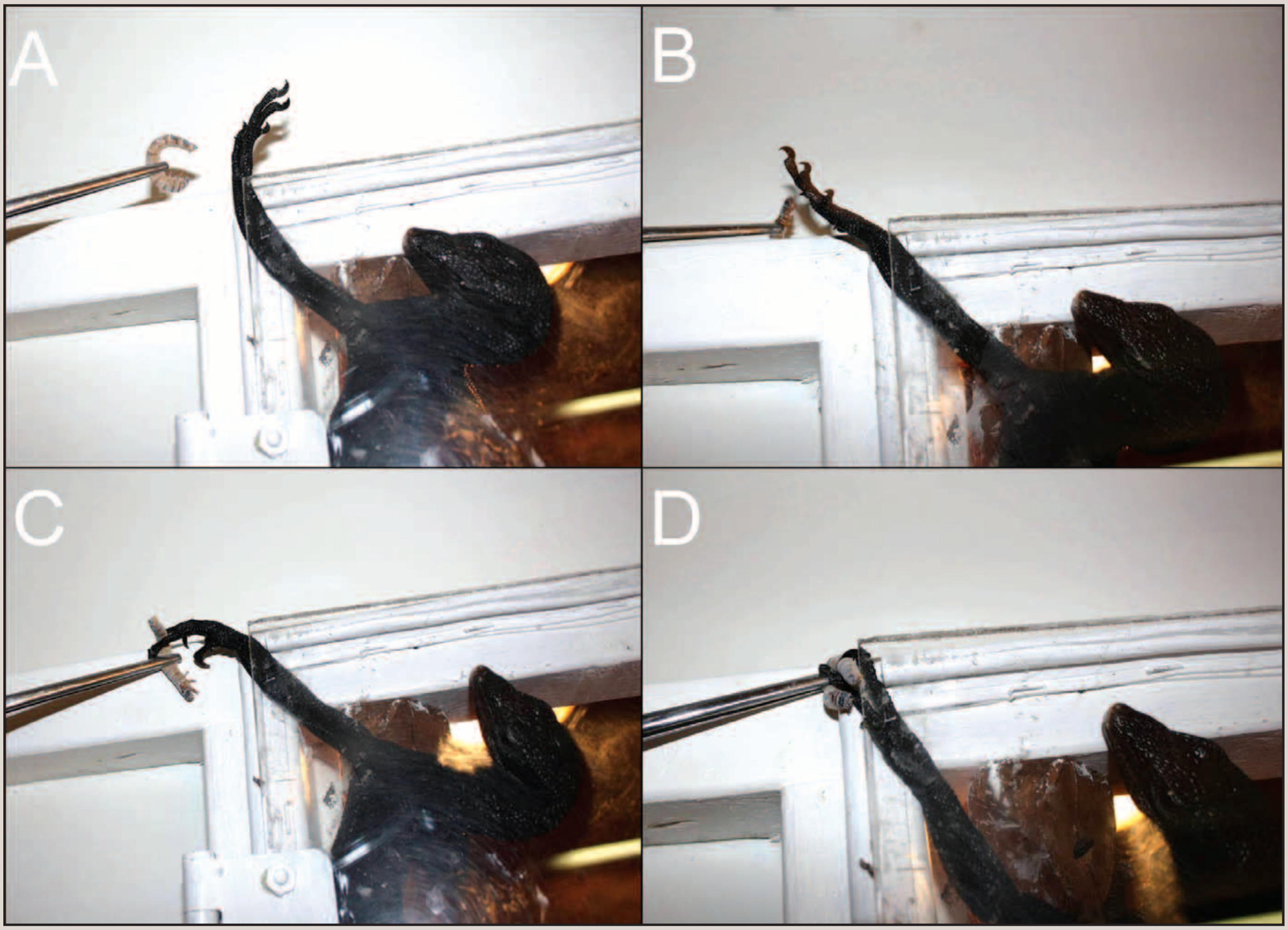

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Fig. 1. Male *Varanus beccarii* using reaching arm movements to retrieve a *Zophobas morio* larva through a gap in the terrarium door. A) The forearm is extended through the opening, with the wrist angled back and the digits close together; B) the forearm reaches its furthest extension, with the wrist angled downward and the digits spread apart; C) contact is made with the prey item, and the digits are curled around the prey; D) the prey is pulled through the opening with the claws to be seized with jaws and swallowed.

neonatal mice, and *Acheta domesticus* were placed inside these holes during feedings to test whether each *V. beccarii* specimen was capable and willing to use its forelimbs to retrieve the prey.

Using coordinated forearm movements, both *V. beccarii* successfully retrieved all prey types from all four holes located in each tree trunk. Both individuals used identical extraction behaviors, including the same body positioning, reaching arm movements, and sequences of movements.

Prey is extracted from the holes in vertically-oriented trunks when the monitors are positioned either upright or inverted on the trunk. Once a prey item is detected in a hole either by sight (prey was seen as it was placed inside the hole) or smell, the monitor carefully inspects the hole with a series of tongue-flicks. After unsuccessfully attempting to enter the hole with its head, the forearm is skillfully inserted into the opening, all while maintaining eye contact with the prey inside (Fig. 2). The prey is then either flushed from the hole or pulled out with the foreclaws, where it is seized with the jaws and swallowed. The same behaviors are used on horizontally-oriented trunks (Fig. 3), though when extracting prey, the monitor must lift the prey upwards and out of the hole, requiring slightly different muscular movements and greater coordination, which appeared to take more concentration and effort than with holes in vertically-oriented trunks. Occasionally, prey items are impaled and extracted from the opening while still attached to the claws, where they are then seized with the jaws and swallowed. Both individuals regularly switch usage of each forelimb to maximize its depth of penetration into the hole, depending on its body positioning at the time.

Additional specimens.—Once this behavior was observed in both *Varanus beccarii* specimens in RWM's collection, another keeper of the species was asked to test for the usage of this behavior in an additional adult female (265 mm SVL). When offered mice through a small (ca. 13 mm) opening in the terrarium door, the monitor repeatedly used the same reaching forearm movements described herein to successfully retrieve the prey (S. Sweet, pers. comm.). Likewise, this female also used its forearms to successfully extract mouse parts from a 15 mm x 70 mm deep hole drilled into a 15 cm thick, diagonally-oriented tree trunk (Fig. 4).

DISCUSSION

Initial remarks.—Extractive foraging, the location and retrieval of food items from embedded matrices (Gibson 1986), is rarely performed by non-avian reptiles, limited mostly to

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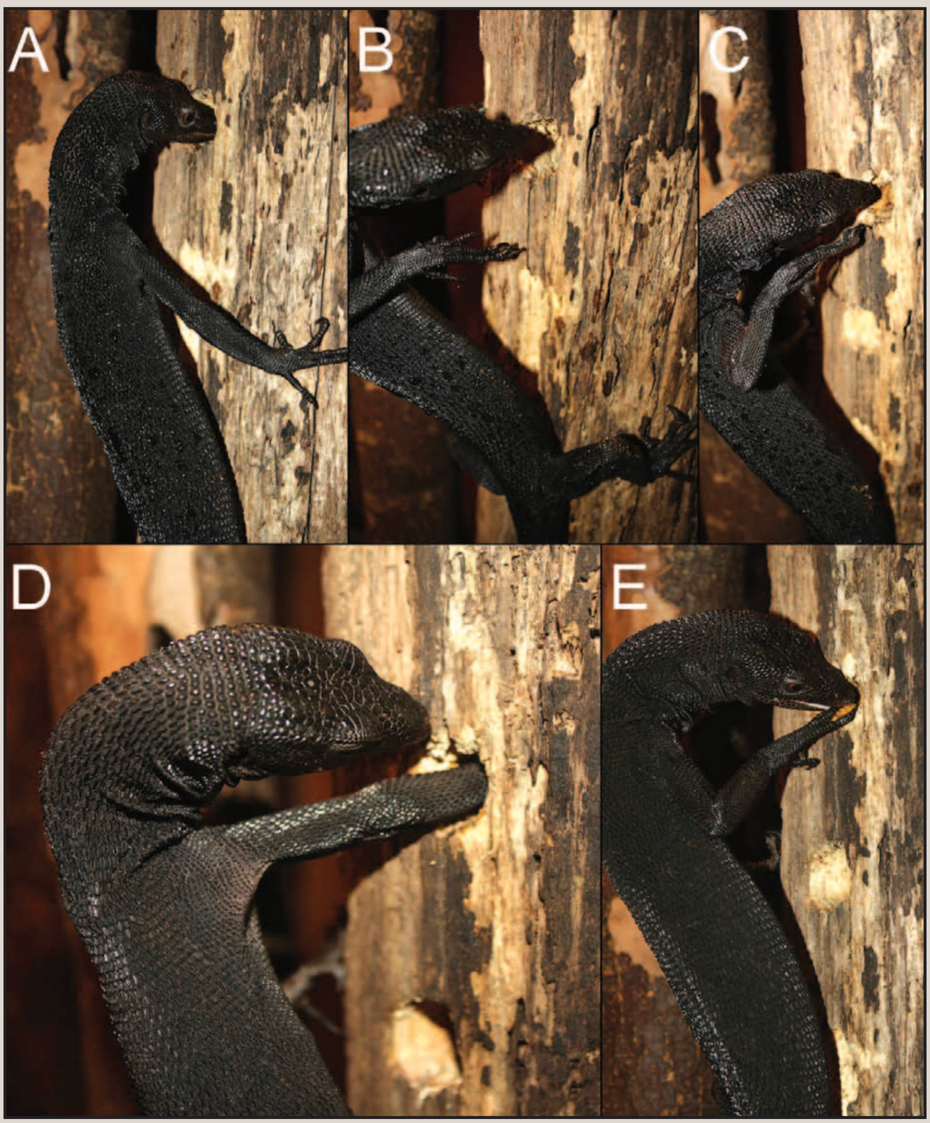

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Fig. 2. (left) Male *Varanus beccarii* using coordinated forelimb movements to extract a *Zophobas morio* larva from a hole in a vertically-oriented tree trunk. A) A tongue flick into the hole confirms the presence of prey; B) the monitor pulls its arm back; C) the digits are pulled together, rendering them and the forearm streamline for insertion into the hole; D) the forearm is inserted into the hole and jostled around to either flush out prey or snag prey with the claws; E) the forearm is retracted, pulling the prey out of the hole with the claws where it can then be seized with the jaws and swallowed.

Fig. 3. (above) Male *Varanus beccarii* using coordinated forelimb movements to extract prey from a hole in a horizontally-oriented tree limb.

PHOTO BY SAM SWEET

Fig. 4. Female *V. beccarii* using forearms to extract mouse parts from a hole in a diagonally-oriented tree limb.

monitor lizards (e.g., Eidenmüller 1993; Gaulke 1989; Sweet 2007). Similarly, skilled forelimb movements such as the ability to reach for and grasp food items are well-documented in a number of mammalian groups (Iwaniuk and Whishaw 2000), but few reptiles have the processing skills, motor coordination, and dexterity needed to perform such movements. As far as we can determine, this report is the first description of a reptile using coordinated forelimb movements to extract prey from narrow and otherwise inaccessible holes in trees. Often associated with primates (e.g., Erickson 1994), tree hole prey extraction provides further support for the idea that monitors share many biological similarities with mammals (e.g., Wood et al. 1977; see also Horn and Visser 1997; Sweet and Pianka 2007). Moreover, it specifically highlights the problem-solving abilities and behavioral complexity of *Varanus beccarii*, thereby supporting Greene's (2004) earlier statements regarding further behavioral specializations in the *V. prasinus* complex.

Is forelimb-assisted extractive foraging learned or genetically-fixed?—Given its apparent rarity among reptiles, the origin of this foraging behavior in *Varanus beccarii*– whether independently learned through insight, genetically-fixed, or some combination of the two, is of particular interest. Extracting food from embedded matrices often requires complex problem solving skills (Gibson 1986). Monitors do not typically rely on extractive foraging because most prey is captured out in the open by dashing forward and seizing it with the jaws. If successful, and if the prey is of sufficient size, it is immediately swallowed. However, in cases of embedded prey, the situation is complicated by the monitor's inability to use conventional prey capture techniques. Unable to insert its head into a narrow opening to seize a prey item, the monitor must devise an alternate capture strategy otherwise the feeding opportunity may be lost. Here, in the case of *V. beccarii*, a conscious decision derived through insight is made to abandon use of the jaws and switch to an alternate technique that utilizes a completely different set of motor skills. The ambidexterity of *V. beccarii* while performing this behavior also exemplifies keen insight given that switching usage between forelimbs represents a foresighted decision that will enable the monitor to reach deeper into a hole, thereby increasing its foraging effectiveness.

Unlike the decision-making component of this behavior, we suspect that the skilled forelimb movements used by *Varanus beccarii* to extract prey are instinctive, rather than individually learned through insight. Because all three *V. beccarii* tested in the present study used the same reaching forelimb movements and body positioning while performing the behavior, and were capable of using them in different experimental situations, the most parsimonious explanation for these consistencies is that the movements have a genetic basis. Alternately, if the limb movements were independently learned, we would expect to have seen some individual variation in body positioning and the performance of this behavior.

Based on these interpretations, we consider forelimb-assisted extractive foraging in *Varanus beccarii* to be a mutual interaction between insight learning and instinct, and therefore expect it to occur in wild populations. However, the ability to learn and successfully perform this behavior might vary from individual to individual since monitors differ greatly in their intellectual abilities (Lederer 1933, 1942). Loop (1976) demonstrated that monitors are gifted with excellent memories, and can remember trained, food-oriented procedures even after several weeks of latency. Therefore, once learned by an individual and added to its behavioral repertoire, extractive foraging is unlikely to be forgotten if it reliably produces feeding opportunities.

Requisites for use in the wild.—If forelimb-assisted extractive foraging is to be a useful strategy for *Varanus beccarii* in the wild, we contend that several conditions must be met. First, *V. beccarii* would have to be an arboreal forager that feeds on tree-dwelling prey, and second, it must forage in environments where both arboreal prey and tree holes are abundant and accessible.

Scientific observations on the natural history of *V. beccarii* in the Aru Islands, Indonesia are lacking despite frequent collection for the live reptile trade (Pernetta 2009), and all that has been published on its occurrence to date appears to have originated through second-hand sources. Bennett (1995, 1998) reported that *V. beccarii* occurs in mangrove swamps whereas Sprackland (2009) claims that it inhabits lowland wet forests and swamps. Like all other members of the *V. prasinus* complex, *V. beccarii* is indeed highly specialized morphologically for an arboreal lifestyle (Greene 1986, 2004), and behavioral observations of *V. beccarii* in captivity further suggest that it is a skilled tree-dweller (Hartdegen et al. 1999, 2000; Krebs, pers. comm; pers. obs.).

Dietary studies indicate that members of the *Varanus prasinus* complex feed predominantly on arboreal arthropods (Greene 1986; Irwin 1994). Though not recovered from the single *V. beccarii* stomach analyzed by Greene (1986), we suspect that the soft-bodied larvae of some wood-boring beetles and bark-dwelling caterpillars may make appropriate prey items for this particular foraging behavior in the wild. During experimental trials, soft-bodied prey such as neonatal mice and *Achroia grisella* larvae (but also more rigidly-bodied prey such as *Zophobas morio* larvae and *Nauphoeta cinerea*) were easily extracted from tree holes when impaled by the claws. The sharp foreclaws and reaching forearm movements of *V. beccarii* may also be useful for retrieving nocturnal geckos, tree frogs, and insects that seek refuge in tree holes and crevices by day.

When compared to other monitor lizards, members of the *Varanus prasinus* complex may possess the longest and slenderest forelimbs in relation to body size (compare drawings by Bellairs 1969). The long and slender forelimbs and elongated digits of *V. beccarii* clearly compliment tree hole extractive foraging well, and allow individuals to deeply penetrate narrow openings all the way up to the shoulder. This ability should enable *V. beccarii* to exploit an ecological niche that may not be utilized by many other predators within its range, and can potentially diversify the number of different prey items taken, maximizing the total number of foraging opportunities.

Comparisons of arboreal foraging in Varanus.—Limited observations on arboreal species in the field prevent a thorough analysis of tree hole foraging tactics used by monitors. However, field observations on the foraging habits of *Varanus glauerti* in northern Australia (Sweet 1999) enable direct comparisons between *V. beccarii* and this similar-sized arboreal species. Like *V. beccarii*, *V. glauerti* will also seek out hidden prey within holes and crevices in trees (Sweet 1999); however, the strategies employed by each to retrieve prey from narrow openings are markedly different. Once a prey item is discovered inside a tree hole that is too small to enter with the head, *V. glauerti* will attempt to widen the diameter of the opening by clawing at it margins until it is large enough for the head to enter, where the prey can then be seized with the jaws (Sweet 1999). Although captive *V. beccarii* will also enter holes to subdue prey if large enough for the head (pers. obs.), its use of the forelimbs to extract prey from smaller openings rather than attempting to widen them, distinguishes it behaviorally from *V. glauerti* as well as all other monitor lizards, as currently understood.

Forelimb-assisted prey extraction in additional taxa?—Given that several monitor species occur in forested environments and might have arboreal habits and diets similar to those of *Varanus beccarii*, it is possible that forelimb-assisted extractive foraging might be used by additional taxa. Given their relatedness, and the near-identical similarities in size, morphology, diet, and arboreality between *V. beccarii* and other members of the *V. prasinus* complex (Greene 1986; Sprackland 1991; Ziegler et al. 2007), we suspect that this behavior is also used by other members of the complex. Notably, Irwin (1996) reported seeing a wild *V. keithhornei,* sister taxon to *V. beccarii* (Ziegler et al. 2007), "on the ground scratching with its forefeet in a rotting log, obviously foraging for food." Whether this observation refers to the same prey extraction behavior reported here for *V. beccarii* is unclear; however, it necessitates the need for further investigation of forelimb-assisted extractive foraging in the *V. prasinus* complex.

It might seem obvious that the skilled forelimb movements described here for *Varanus beccarii* represent a specific behavioral adaptation for use in trees. However, we cannot rule out the possibility that this foraging behavior might also occur in terrestrial species. The ability to extract prey from rock crevices, tree stumps and felled trunks, burrows, and other narrow openings would benefit the foraging efficiency of terrestrial monitors. Indeed, some terrestrial species have developed unique and insightful methods of extracting prey from rock crevices and burrows using coordinated tail movements (Eidenmüller 1993; Gaulke 1989; Horn 1999). Use of the forelimbs in similar situations can be equally useful for extracting prey, and is perhaps more feasible from a developmental standpoint given that many species are known to use the forelimbs in various capacities while foraging (e.g., Auffenberg 1981, 1988, 1994; Blamires 2004) or handling and fragmenting prey (e.g., Auffenberg 1981; Hartdegen et al. 2000; Horn 1999; Kiehlmann 1999; Krebs 1979, 2007, pers. comm.; Stanner 2010).

Implications for future research.—Arboreal species offer unique opportunities for studying the insight and behavioral complexity of monitors, particularly because they inhabit complex, three-dimensional environments (Greene 2004) and may require more advanced processing skills and finer motor coordination than comparatively-sized terrestrial species. Studies on several mammalian groups have shown that brain sizes are positively correlated with arboreality (Budeau and Verts 1986; Eisenberg and Wilson 1981; Meier 1983). Because monitors vary considerably in habit from strictly terrestrial to largely arboreal, and share many ecological and physiological affinities with mammals (Wood et al. 1977; Horn and Visser 1997; Sweet and Pianka 2007), it is of interest whether selective pressures have favored a similar evolutionary trend in monitors. Surprisingly, the only direct study to compare relative brain sizes in monitors focused solely on the ecologically-dissimilar *Varanus salvator* complex and *V. glebopalma*, but did note distinct morphological differences between the two (Andres et al. 1999). Similar comparative studies on monitor brain sizes which sample a greater diversity of taxa can provide a framework for understanding the evolution of encephalization and intelligence within the genus.

Further investigations of skilled forelimb movements and extractive foraging in monitor lizards are planned. When applied to current phylogenies (Ast 2001; Fitch et al. 2006; Ziegler et al. 2007), confirmed usage of this behavior by additional taxa can allude to the evolution of skilled forelimb movements in monitor lizards, but more broadly in tetrapods as well (Iwaniuk and Whishaw 2000). Additionally, observations of forelimb-assisted extractive foraging in the field can yield important details about its usage and importance to wild monitor populations which cannot be inferred from captivity.

Finally, our observations have important implications for the management of *Varanus beccarii* in captivity. Given the importance of enrichment stimuli in the husbandry of monitor lizards (Burghardt et al. 2002; Manrod et al. 2008; Sunter 2008), replicating or modifying the drilled tree trunks described in this report and using them during feedings can provide a valuable source of behavioral enrichment for captive individuals. All specimens tested in the present study continue to show interest in the drilled tree trunks within their terraria, stopping to investigate holes and crevices as they are encountered through daily foraging activity. Such an apparatus can potentially increase activity, reduce boredom and stereotypic behaviors, and improve the overall quality of life for specimens of *V. beccarii* and possibly other members of the *V. prasinus* complex maintained in zoos and other captive situations.

We welcome correspondence and encourage feedback from zoos, researchers, and private keepers working with monitor lizards on the subjects of extractive foraging and skilled forelimb movements, as well as additional behavioral specializations in *Varanus*.

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