

# HUSBANDRY

# Green Iguanas (*Iguana iguana*) in Mixed-species Exhibits

Matthew Mo and Elouise Mo

Sydney, New South Wales, Australia (matthew.sk.mo@gmail.com)

ixed-species exhibits in zoological institutions have a Mlong history (Pawley 1971; Popp 1984), providing the operational benefits of maximizing space use and increasing holding capacity without changing space requirements (Veasey and Hammer 2010). Mixed-species exhibits also create more dynamic experiences for patrons and promote education of ecosystem values when taxa from similar natural environments are displayed together (Fig. 1). The integration of multiple taxa may also provide social and behavioral enrichment for exhibit animals (Clark and Melfi 2011; Daoudi et al. 2017). Nevertheless, zoological institutions planning mixed-species exhibits have obvious challenges that include avoiding potential aggression between species, whether accidental or associated with curiosity, territoriality, competition for food and water resources, and predatory behavior (Inglefield-Hatcher 2000; Kaandorp 2011). Aggression can result in physical injuries or physiological stress, both of which can contribute to mortality (Dorman and Bourne 2010). Another challenge involves developing feeding regimes to ensure that all exhibit animals receive adequate nutrition and that trace mineral and nutrient supplements are taken up by the intended species (Blount 1997; Kaandorp 2011). Disease transmission between animals in mixed-species exhibits also is well-documented (Lowenstine 1999; Probst et al. 2005; Lopez et al. 2016), requiring ongoing monitoring and preventative interventions. Possible hybridization is another factor that must be considered (Casares et al. 2011).

The family Iguanidae is a diverse group of medium-sized to large lizards that occur naturally in the Americas and the islands of Fiji (Alberts et al. 2004). The Green or Common Iguana (*Iguana iguana*) is one of the largest species (SVL to 29 cm with a tail length nearly three times greater) (Campos and Desbiez 2013). Green Iguanas exploit a range of habitat strata from arboreal perches to aquatic habitats. The species' adaptability corresponds with a wide natural range throughout the Neotropics and subsequent invasions of some West Indian islands, Florida, Hawaii, Fiji, Japan, Taiwan, Singapore, and Thailand (McKeown 1996; Krysko et al. 2007; Falcón et al. 2012; van den Burg et al. 2020; De Jesús Villanueva et al. 2021). The anthropogenic spread of the Green Iguana is largely associated with their popularity as pets (Knapp et al. 2020). Furthermore, they are also a popular exhibit species in zoological institutions.

Green Iguanas are almost entirely herbivorous, with documented animal prey, mostly of juveniles, limited to terrestrial snails (Townsend et al. 2005), insects (Hirth 1963), bird eggs (Schwartz and Henderson 1991), and carrion (Loftin and Tyson 1965; Krysko et al. 2007). Despite their large size, adult Green Iguanas have numerous natural predators; these include wild cats (Chinchilla 1997; Loc-Barragán 2017), mustelids such as Tayras (Galef et al. 1976; Barrio-Amorós and Ojeda 2015) and otters (Pereira et al. 2020), coatis (Greene et al. 1978), snakes (Rivas et al. 2007; Ribeiro Sanches et al. 2018), crocodilians (Platt et al. 2006; Balaguera-Reina et al. 2018), and raptors (Greene et al. 1978), including owls (Filipiak et al. 2012). Juvenile Green Iguanas are susceptible to an even broader range of predators that include other lizards (Burghardt et al. 1977), birds such as herons (Engeman et al. 2005), cuckoos (Guedes Coutinho et al. 2014), toucans, anis, flycatchers, and icterids (Rivas et al. 1998; Savage 2002), raccoons (Smith et al. 2006) and monkeys (Rivas et al. 1998).



**Fig. 1.** An immersive walk-through enclosure displaying Green Iguanas (*Iguana iguana*), other lizards, tortoises, and a range of passerines at the Antwerp Zoo, Belgium. Photograph by Kevin B.



**Fig. 2.** An indoor glass-fronted enclosure displaying Green Iguanas (*Iguana iguana*), marmosets, and tortoises at the De Zonnegloed Wild Animal Sanctuary, Belgium. Photograph by Kevin B.

Zoological institutions therefore require careful consideration when incorporating Green Iguanas in mixed-species exhibits (Figs. 2 & 3).

In this paper, we discuss combinations of taxa involving Green Iguanas in mixed-species exhibits based on our personal experiences and references in published literature.

### Reptiles (Class Reptilia)

**Order Squamata.**—Zoological institutions have combined Green Iguanas with numerous species of other lizards and snakes, which includes co-housing arrangements with other species of similar-sized iguanas. They have been successfully displayed with Rhinoceros Iguanas (*Cyclura cornuta*) in zoological institutions in Maryland, Florida, and Texas, USA (Murphy 1969), France, and Queensland, Australia. A zoological institution in Texas, USA, also held Andros Island Iguanas (*C. cychlura cychlura*), Exuma Island Iguanas (*C.* 



Fig. 3. An outdoor enclosure displaying Green Iguanas (*Iguana iguana*) with tortoises at the Hong Kong Zoological and Botanical Gardens. Photograph by Matthew Mo.

*cychlura figginsi*), Blue Iguanas (*C. lewisi*), and Cape Spinytailed Iguanas (*Ctenosaura hemilopha*) in the same exhibit with Green Iguanas (Murphy 1969). We also are aware of Green Iguanas combined with Black Spiny-tailed Iguanas (*C. similis*) in Belgium, Switzerland, and Mexico, and Cuban Rock Iguanas (*Cyclura nubila*) in France.

Zoological institutions in Europe have held Green Iguanas with basilisks (*Basiliscus* spp.) despite the fact that the latter are known predators of iguanas smaller than themselves (Burghardt et al. 1977). Specific examples include Green-crested Basilisks (*B. plumifrons*) in zoological institutions in Germany (Schwibbe and Ziegler 2002), Switzerland, Denmark, and The Netherlands; Common Basilisks (*B. basiliscus*) in Belgium; and Brown Basilisks (*B. vittatus*) in Switzerland. Presumably combining these species in captivity can be successful as long as the iguanas are of similar size or larger than the basilisks.



**Fig. 4.** A Green Iguana (*Iguana iguana*) and a Golden Tegu (*Tupinambis teguixin*) perched on a log in an indoor terrarium at Łódź Zoo, Poland. Photograph by Peter Kiedrzyński.



**Fig. 5.** A Green Iguana (*Iguana iguana*) and an African Spurred Tortoise (*Centrochelys sulcata*) converging near a heat lamp at the Berkenhof's Tropical Zoo, Kwadendamme, The Netherlands. Photograph by Maarten de Ruiter.

We know of two examples of adult Green Iguanas combined with monitor lizards (*Varanus* spp.). As in basilisks, to avoid predation, monitors in both cases were similar in size to the iguanas. A zoological institution in Scotland co-housed iguanas with the Bengal Monitor (*V. bengalensis*) and the aforementioned mixed-species exhibit in Texas also held an Asian Water Monitor (*V. salvator*), Lace Monitor (*V. varius*), and Nile Monitor (*V. niloticus*) (Murphy 1969). These mixed-species exhibits are of interest since large to medium-sized monitors are carnivorous and known to be opportunistic predators (Jessop et al. 2010; Karunarathna et al. 2017). Also, Green Iguana remains have been recovered in stomach contents of Nile Monitors in Florida (Mazzotti et al. 2020); however, whether they were taken as prey or carrion was not clear.

Two zoological institutions have held Green Iguanas with agamids, an indoor enclosure in the Philippines cohousing iguanas with Philippine Sailfin Lizards (*Hydrosaurus pustulatus*) and an outdoor walk-through aviary in The Netherlands co-housing iguanas with Chinese Water Dragons (*Physignathus cocincinus*).

Zoological institutions also have held Green Iguanas with three species of teiids, Argentine Black and White Tegus (*Salvator merianae*) in England, Golden Tegus (*Tupinambis teguixin*; Fig. 4) in Poland, and Northern Caiman Lizards (*Dracaena guianensis*) in an aquarium/terrarium in Idaho, USA.

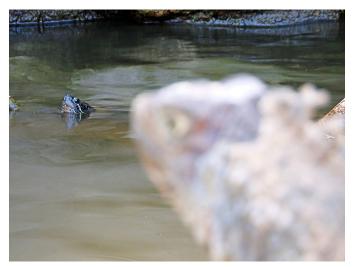
We are aware of only one zoological institution that combined Green Iguanas with chameleons. The aquarium in Idaho, mentioned above, also held Panther Chameleons (*Furcifer pardalis*). Thinner tree branches in the exhibit were only accessible to the chameleons, providing separation between species.

At least five zoological institutions have combined Green Iguanas with snakes. In all cases, the iguanas were adults. Three institutions in Ecuador, Italy, and Victoria, Australia, involved mature Boa Constrictors (*Boa constrictor*). Because the Boa Constrictor is a known predator of iguanas (Quick et al. 2005; Oliveira et al. 2015; Ribeiro Sanches et al. 2018), making sure that the snakes were continually well-fed was necessary to avoid iguanas becoming prey. We observed iguanas climbing on the snakes and walking up to the snakes' heads without any visible reactions by the snakes. Other examples of Green Iguanas co-housed with snakes involved a Red Sand Boa (*Eryx johnii*) in a zoological institution in Scotland and a pair of Burmese Pythons (*Python bivittatus*) in Indiana, USA.

Order Testudines.—Of the numerous examples of Green Iguanas exhibited with chelonians (Lonsdale and Klocek 1987; Sodaro 1999), the most commonly co-housed species is the Red-footed Tortoise (*Chelonoidis carbonarius*); examples include zoological institutions in Nebraska, Kansas, West Virginia, Florida, Texas, and Michigan, USA (Farmerie et al. 1999; Sodaro 1999; Grazian 2012), Hong Kong, Singapore, England, Wales, France, Belgium, and Germany (Schwibbe and Ziegler 2002), as well as a live exhibit in a Florida museum. Green Iguanas also are frequently held with Yellow-footed Tortoises (C. denticulatus), with examples in two zoological institutions in Florida, USA, as well as Taiwan, England, and Maryland, USA. Other tortoises combined with Green Iguanas include Asian Brown Tortoises (Manouria emys) in zoological institutions in Taiwan and Bali, Indonesia; African Spurred Tortoises (Centrochelys sulcata; Fig. 5) in Belgium and The Netherlands; Argentine Tortoises (Geochelone chilensis) in Florida, USA; Hermann's Tortoises (Testudo hermanni; Fig. 6) in Belgium and Germany (Schwibbe and Ziegler 2002); Russian Tortoises (Agrionemys horsfieldii) in Germany (Schwibbe and Ziegler 2002); and Aldabra Giant Tortoises (Aldabrachelys gigantea) in France. In many instances, iguanas and tortoises are observed congre-



**Fig. 6.** A Green Iguana (*Iguana iguana*) and a Hermann's Tortoise (*Testudo hermanni*) converging on a food bowl at the De Zonnegloed Wild Animal Sanctuary, Belgium. Photograph by Kevin B.



**Fig. 7.** A Red-eared Slider (*Trachemys scripta elegans*) in a pond under the watchful eye of an adult Green Iguana (*Iguana iguana*) at the Bali Zoo, Indonesia. Photograph by Matthew Mo.

gating near heat lamps and iguanas may bask on top of the carapaces of tortoises.

A number of freshwater turtle species have been used to inhabit the aquatic sections of terraria and walk-through enclosures that display Green Iguanas (Lonsdale and Klocek 1987). Likely the most frequently co-housed turtles are sliders (Trachemys spp.), including Red-eared Sliders (T. scripta elegans; Fig. 7) displayed with iguanas in an indoor aquarium in Sweden and outdoor enclosures in Germany, Hungary, Israel, and Bali, Indonesia; Yellow-bellied Sliders (T. scripta scripta) in Belgium and Denmark; and Ornate Sliders (T. ornata) displayed with iguanas in a Mexican zoological institution. Other combinations of Green Iguanas and freshwater turtles include Pig-nosed Turtles (Carettochelys insculpta) in an aquarium exhibit in Idaho, USA; Wood Turtles (Glyptemys insculpta) in an indoor enclosure in Pennsylvania, USA; Spotlegged Wood Turtles (Rhinoclemmys punctularia) in Florida, USA; Philippine Pond Turtles (Siebenrockiella leytensis) in the Philippines; Branderhorst's Snapping Turtles (Elseya branderhorstii) and Krefft's River Turtles (Emydura krefftii) in Florida, USA; Red-bellied Short-necked Turtles (Emydura subglobosa) and Yellow-spotted Amazon River Turtles (Podocnemis unifilis) in outdoor walk-through aviaries in Singapore; a Malaysian Giant Turtle (Orlitia borneensis) in an outdoor walk-through aviary in Bali, Indonesia; Florida Cooters (Pseudemys floridana) in outdoor enclosures in Germany and Israel; Scorpion Mud Turtles (Kinosternon scorpioides) in Italy; Florida Softshells (Apalone ferox) in France; and a Mata-mata (Chelus fimbriata) in Italy. Box turtles (Terrapene spp.) also have been co-housed with Green Iguanas in zoological institutions in Florida and Illinois, USA (Lonsdale and Klocek 1987) and England.

Order Crocodilia.--Mixed-species exhibits holding lizards with adult crocodilians are rare but we know of six zoological institutions that have undertaken this combination with Green Iguanas. In all these cases, the iguanas were adults. Small crocodilians such as Cuvier's Dwarf Caiman (Paleosuchus palpebrosus) have been co-housed with Green Iguanas in Illinois, USA (Lonsdale and Klocek 1987), Singapore, and The Netherlands, and the Smoothfronted Caiman (P. trigonatus) has been co-housed with Green Iguanas in Germany (Schwibbe and Ziegler 2002). The potential for iguanas sustaining injuries from dwarf caimans is probably mitigated by the animals being similar in size, as well as platforms and trees providing refugia inaccessible to caimans. However, Smooth-fronted Caimans in the German zoological institution were reported to have preyed on basilisks, acouchis, bats, and a bird that shared the exhibit (Schwibbe and Ziegler 2002), which demonstrates the alwayspossible risk of iguanas sustaining injuries from caimans.

Perhaps the most interesting combinations of Green Iguanas with crocodilians involve adult Morelet's Crocodiles (*Crocodylus moreletii*) in a zoological institution in Mexico



Fig. 8. An indoor enclosure shared by Green Iguanas (*Iguana iguana*) and American Alligators (*Alligator mississippiensis*), as well as other lizards and freshwater turtles, at the Antwerp Zoo, Belgium. Photograph by Kevin B.

and a subadult Spectacled Caiman (*Caiman crocodilus*) and subadult American Alligators (*Alligator mississippiensis*; Fig. 8) in Belgium. Although we are not aware of any evidence that dwarf caimans prey on adult Green Iguanas, dietary studies have certainly identified lizards of that size as prey of free-living Morelet's Crocodiles (Pérez-Higareda et al. 1989), Spectacled Caimans (Thorbjarnarson et al. 1993), and other medium-sized to large crocodilians (Platt et al. 2006; Balaguera-Reina et al. 2018). We can only assume that arboreal perches and elevated terrestrial areas are sufficient for minimizing the likelihood of crocodilians preying on iguanas; however, a risk presumably exists when iguanas descend to areas accessible to the crocodilians.

#### Amphibians (Class Amphibia)

**Order Anura.**—Anurans have been combined with Green Iguanas in at least two zoological institutions. In an aquarium in Maryland, USA, iguanas roam an indoor walk-through enclosure with Smooth-sided Toads (*Rhaebo guttatus*), and Rococo Toads (*Rhinella diptycha*) are co-housed with Green Iguanas in a zoological institution in Granby, Canada. Both toad species are large, with Smooth-sided Toads growing to lengths of 15 cm (Mueses-Cisneros et al. 2012) and Rococo Toads reaching lengths of 25 cm (Lavilla and Brusquetti 2018), and therefore less likely to be trampled by Green Iguanas.

**Order Urodela.**—We are only aware of one example of Green Iguanas combined with salamanders. An aquarium in Idaho, USA, co-housed Tiger Salamanders (*Ambystoma tigrinum*) with an assortment of lizards, including Green Iguanas.

# Mammals (Class Mammalia)

**Order Diprotodontia.**—We are aware of two examples of Green Iguanas combined with marsupials. A zoological insti-

tution in Singapore had Green Iguanas in an outdoor walkthrough aviary that also held Goodfellow's Tree Kangaroos (*Dendrolagus goodfellowi*). The other, a zoological institution in The Netherlands, displayed Green Iguanas with Ground Cuscuses (*Phalanger gymnotis*) and Sugar Gliders (*Petaurus breviceps*) in an outdoor walk-though aviary. In both cases, animals in the exhibits were provided ample space and interspecies encounters were rare.

Order Chiroptera.—Bats have been combined with Green Iguanas in at least six zoological institutions, all of which displayed animals in large walk-through enclosures. Iguanas and bats usually occupy different habitat strata, which, combined with the size of the enclosures, generally minimize contact between animals. A zoological institution in The Netherlands displayed colonies of two species of bats, Rodrigues Flying Foxes (Pteropus rodricensis) and Seba Short-tailed Bats (Carollia perspicillata), with a group of Green Iguanas in an indoor rainforest-themed dome. Seba Shorttailed Bats also have been co-housed with Green Iguanas in a zoological institution in Switzerland. Other megachiropteran bats combined with Green Iguanas include Indian Flying Foxes (P. giganteus) in a zoological institution in Massachusetts, USA, and Large Flying Foxes (P. vampyrus) in Singapore and Bali, Indonesia. The only other combination of Green Iguanas with a microchiropteran bat involved a colony of Long-tongued Nectar Bats (Glossophaga soricina) in a zoological institution in Germany (Schwibbe and Ziegler 2002).

**Order Primates.**—Tamarins and marmosets are frequently combined with Green Iguanas (Buchanan-Smith 2012). These small monkeys, ranging from 13 to 30 cm in body length, are naturally sympatric with Green Iguanas in Central and South America. In captivity, they sometimes display an inquisitiveness toward iguanas, riding or grooming them and even eating dead skin (Veasey and Hammer 2010). We found one report by Sodaro (1999) of a negative interaction during which tamarins were observed chewing on the crests of some iguanas and having their tails bitten in retaliation. Although no records document Green Iguanas preying on tamarins, some zoological institutions temporarily remove them from exhibits when tamarins have babies.

The most common combination between tamarins and Green Iguanas involved the Cotton-top Tamarin (Saguinus oedipus), which has been observed in zoological institutions in Ohio, Nebraska, Kansas, Michigan, Florida, New York, and West Virginia, USA (Farmerie et al. 1999; Sodaro 1999; Grazian 2012), Denmark, Spain, and Germany (Schwibbe and Ziegler 2002). These zoological institutions displayed the animals in a range of enclosure types, including indoor terraria and outdoor island-type enclosures. Other congeners held with Green Iguanas include Emperor Tamarins (S. imperator) in zoological institutions in England, Germany, and Kansas, USA (Sodaro 1999); Red-handed Tamarins (S. midas) in Belgium, Germany (Schwibbe and Ziegler 2002), Mexico, and Nebraska and California, USA (Sodaro 1999); Red-chested Moustached Tamarins (S. labiatus) in Sweden and The Netherlands; Pied Tamarins (S. bicolor) in Canada; and Saddleback Tamarins (S. fuscicollis) in New York, USA. In one example, keepers reported an adult Green Iguana being particularly aggressive toward humans but exceptionally tolerant of Red-handed Tamarins, allowing juveniles to pick off dead skin and swing on the iguana's toes (Schwibbe and Ziegler 2002).

Two species of lion tamarins have also been co-housed with Green Iguanas. The most frequent is the Golden Lion Tamarin (*Leontopithecus rosalia*), observed in mixed-species exhibits with iguanas in Florida, Indiana, Pennsylvania, and Maryland, USA (Farmerie et al. 1999), Germany, and Sweden. The enclosure in Maryland was a walk-through immersive exhibit in an indoor aquarium. The Goldenheaded Lion Tamarin (*L. chrysomelas*) has been combined with Green Iguanas in an outdoor meshed enclosure in Virginia, USA, and large indoor walk-through enclosures in Denmark and Hungary.

Western Pygmy Marmosets (*Cebuella pygmaea*; Fig. 9), the most frequent marmoset combined with Green Iguanas, were co-housed in zoological institutions in Florida



Fig. 9. Western Pygmy Marmosets (*Cebuella pygmaea*) investigating and climbing on top of adult Green Iguanas (*Iguana iguana*) at the Artis Amsterdam Royal Zoo, The Netherlands, and the Skansen Aquarium, Stockholm, Sweden. Photographs by J.A. Kok and Bosse Skansen-Akvariet.



**Fig. 10.** A Common Marmoset (*Callithrix jacchus*) grooming an adult Green Iguana (*Iguana iguana*) at the Duisburg Zoo, Germany. Photograph by Arjan Haverkamp.

and Nebraska, USA (Sodaro 1999), England, Denmark, Belgium, Germany, Sweden, and The Netherlands. Common Marmosets (*Callithrix jacchus*; Fig. 10) exhibited with Green Iguanas were observed in zoological institutions in England, Germany (Schwibbe and Ziegler 2002), Denmark, Belgium, and Indiana and Arkansas, USA. Other marmosets co-housed with Green Iguanas include Goeldi's Marmosets (*Callimico goeldii*) in Germany, Denmark, The Netherlands, and Florida, USA (Farmerie et al. 1999); White-fronted Marmosets (*Callithrix geoffroyi*) in Germany, The Netherlands, and Pennsylvania, USA; and Wied's Marmosets (*C. kuhlii*) in Massachusetts, USA. A number of these examples exhibited animals in large outdoor walk-through aviaries.

The White-faced Saki (*Pithecia pithecia*) was another monkey frequently combined with Green Iguanas and also sympatric with these lizards in the wild. These combinations were exhibited in a range of enclosures, including indoor spaces, island-type enclosures, and walk-through aviaries, in Pennsylvania, California, Arkansas, Nebraska, and Florida, USA (Sodaro 1999), Singapore, Denmark, Germany (Schwibbe and Ziegler 2002), and The Netherlands. Like tamarins and marmosets, sakis often are observed showing inquisitiveness toward iguanas.

Other monkeys combined with Green Iguanas include Common Squirrel Monkeys (*Saimiri sciureus*) in Florida, Texas, and Nebraska, USA (Sodaro 1999), and Russia; Azara's Night Monkeys (*Aotus azarae*) in Germany (Schwibbe and Ziegler 2002); Grey-handed Night Monkeys (*A. griseimembra*) in The Netherlands; Grey-legged Night Monkeys (*A. lemurinus*) in Denmark; Black Howler Monkeys (*Alouatta caraya*) in Pennsylvania and Nebraska, USA (Sodaro 1999); and Brown Woolly Monkeys (*Lagothrix lagotricha*) in Nebraska, USA (Sodaro 1999).



Fig. 11. An adult Green Iguana (*Iguana iguana*) co-housed with Ringtailed Lemurs (*Lemur catta*) at the Bali Zoo, Indonesia. Photograph by Matthew Mo.

Three zoological institutions have combined Green Iguanas with prosimians. An outdoor walk-through aviary in Singapore displayed iguanas with Black-and-white Ruffed Lemurs (*Varecia variegata*) and Ring-tailed Lemurs (*Lemur catta*; Fig. 11). Zoological institutions in The Netherlands and Bali, Indonesia, also have co-housed Green Iguanas with colonies of Ring-tailed Lemurs in outdoor walk-through aviaries.

We are aware of only one zoological institution that combined Green Iguanas with great apes. A zoological institution in Germany co-housed a Chimpanzee (*Pan troglodytes*) troop with a single Green Iguana, Cotton-top Tamarins, and a Green Basilisk (Schwibbe and Ziegler 2002). Chimpanzees can be dangerous to other animals, regularly displaying high levels of violent aggression (Pusey et al. 2008), even wounding conspecifics in the troop (Hosey et al. 2016). Schwibbe and Ziegler (2002) reported a Cotton-top Tamarin being killed in the exhibit in Germany, which corresponds with Chimpanzees hunting other primates in the wild (Newton-Fisher 2015). Although no reports document these omnivorous apes consuming reptiles (McGrew 2015), we deduce that Chimpanzees interacting roughly with iguanas could result in harm.

**Order Scandentia.**—We are aware of two examples of treeshrews combined with Green Iguanas, both in Europe. A zoological institution in Germany held Common Treeshrews (*Tupaia glis*) that often sunbathed on the backs of Green Iguanas (Schwibbe and Ziegler 2002), and a zoological institution in The Netherlands displayed Northern Treeshrews (*T. belangeri*) with Green Iguanas in an outdoor walk-though aviary.

**Order Rodentia.**—Fourteen species of rodents have been displayed in mixed-species exhibits alongside Green Iguanas. The most frequent of these combinations involved agoutis. The Brazilian Agouti (*Dasyprocta leporina*) has been co-housed with Green Iguanas in large outdoor enclosures in Florida, California, and Nebraska, USA (Sodaro 1999), as well as a smaller enclosure in West Virginia, USA, and an indoor walk-through enclosure in Denmark. The Crested Agouti (*D. cristata*) has been exhibited with Green Iguanas in an outdoor aviary attached to an indoor enclosure in California, USA (Sodaro 1999). This aviary was heavily planted to provide some visual separation between animals. The Central American Agouti (*D. punctata*) has been cohoused with Green Iguanas in a zoological institution in Texas, USA.

A similar species to agoutis, the Green Acouchi (*Myoprocta pratti*) has been combined with Green Iguanas by zoological institutions in Germany (Schwibbe and Ziegler 2002) and Connecticut and Kansas, USA (Sodaro 1999). Other caviomorphs combined with Green Iguanas include Capybaras (*Hydrochoerus hydrochaeris*) in zoological institutions in Illinois and Texas, USA; Patagonian Maras (*Dolichotis patagonum*) in indoor and outdoor spaces in Texas and Pennsylvania, USA; Guinea Pigs (*Cavia porcellus*) in Spain; Lowland Pacas (*Cuniculus paca*) in Beijing, China; Short-tailed Chinchillas (*Chinchilla chinchilla*) in Ohio, USA (Sodaro 1999); and North American Porcupines (*Erethizon dorsatum*) in Pennsylvania, USA.

Old World rodents co-housed with Green Iguanas include Indian Crested Porcupines (*Hystrix indica*) in a zoological institution in Massachusetts, USA; Malayan Porcupines (*H. brachyura*) in Java, Indonesia; and Prevost's Squirrels (*Callosciurus prevostii*) and Variable Squirrels (*C. finlaysonii*) in an outdoor walk-through aviary in Singapore.

**Order Artiodactyla.**—At least three mixed-species exhibits have combined Green Iguanas with even-toed ungulates. Lesser Mouse-deer (*Tragulus kanchil*) in zoological institutions in Singapore and Bali, Indonesia, roam outdoor walk-through aviaries with groups of iguanas, and a zoological institution in Florida, USA, co-housed Green Iguanas with Southern Pudus (*Pudu puda*).

**Order Perissodactyla.**—We are aware of only one mixed-species exhibit displaying Green Iguanas with an odd-toed ungulate. In a zoological institute in Nebraska, USA, various taxa, including Green Iguanas and Lesser Brazilian Tapirs (*Tapirus terrestris*), co-exist in an outdoor island-type enclosure (Sodaro 1999).

**Order Sirenia.**—The only case of which we are aware of Green Iguanas combined with sirenians is in a zoological institution in Denmark that houses West Indian Manatees (*Trichechus manatus*) in a naturalistic pool that is part of a large indoor walk-through enclosure. The manatees and iguanas potentially come into contact when iguanas swim in the pool; however, this probably occurs rarely since the iguanas have substantial arboreal and terrestrial space in the exhibit.



Fig. 12. A large outdoor aviary shared by a Green Iguana (*Iguana iguana*), a Linnaeus's Two-toed Sloth (*Choloepus didactylus*), and a flock of Sun Conures (*Aratinga solstitialis*). Photograph courtesy of Wild Florida Airboats and Gator Park.

Order Pilosa.—Two-toed sloths are the most frequent pilosans combined with Green Iguanas. Linnaeus's Twotoed Sloths (Choloepus didactylus; Fig. 12) are co-housed with Green Iguanas in zoological institutions in England, Germany (Schwibbe and Ziegler 2002), Denmark, The Netherlands, Israel, Russia, China, Singapore, and Pennsylvania, Florida, Texas, and Maryland, USA. The exhibits in Singapore and The Netherlands are large outdoor walk-through aviaries that display sloths and iguanas with a range of other mammalian, avian, and reptilian taxa. Hoffman's Two-toed Sloths (C. hoffmanni) have shared large outdoor enclosures with Green Iguanas in California (Sodaro 1999) and Florida, USA (Farmerie et al. 1999), and have also been kept with iguanas in smaller enclosures by zoological institutions in Massachusetts, West Virginia, and New York, USA (Farmerie et al. 1999). A further pilosan, the Southern Tamandua (Tamandua tetradactyla) has been co-housed with Green Iguanas in zoological institutions in Germany (Schwibbe and Ziegler 2002) and Nebraska, USA (Sodaro 1999).

# Birds (Class Aves)

**Order Tinamiformes.**—We are aware of only one zoological institution that combined tinamous with Green Iguanas. The Elegant-crested Tinamou (*Eudromia elegans*) shares a densely planted outdoor aviary attached to an indoor enclosure with Green Iguanas in California, USA (Sodaro 1999).

**Order Anseriformes.**—Zoological institutions have combined a varied range of waterfowl with Green Iguanas; these include larger species such as the Black Swan (*Cygnus atratus*) and Mute Swan (*C. olor*), both featured in a mixedspecies walk-through aviary in Mexico and the latter in an outdoor enclosure in Ohio, USA. Zoological institutions also have held Crested Screamers (*Chauna torquata*) with Green Iguanas in an outdoor island-type enclosure in Nebraska, USA (Sodaro 1999) and an indoor walk-through enclosure in Denmark.

Smaller waterfowl co-housed with Green Iguanas include Blue-winged Teal (*Anas discors*) in a large indoor walkthrough enclosure in Switzerland; Sunda Teal (*A. gibberifrons*) in an outdoor walk-through aviary in Bali, Indonesia; Laysan Teal (*A. laysanensis*) in Florida, USA (Farmerie et al. 1999); Northern Mallards (*A. platyrhynchos*) in an outdoor walk-through aviary in Mexico; Indian Whistling Ducks (*Dendrocygna arborea*) in an indoor walk-through enclosure in Denmark; and White-faced Whistling Ducks (*D. viduata*) in an outdoor enclosure in Texas, USA.

Many mixed-species exhibits combine multiple species of smaller waterfowl with Green Iguanas; examples include Green Iguanas that shared an outdoor island-type enclosure in Nebraska, USA, with Ringed Teal (*Callonetta leucophrys*) and White-faced Whistling Ducks (Sodaro 1999), and with Spotted Whistling Ducks (*Dendrocygna guttata*), Carolina Ducks (*Aix sponsa*), White-winged Wood Ducks (*Asarcornis scutulata*) and Baer's Pochards (*Aythya baeri*) in an outdoor walk-through aviary in Singapore. Two zoological institutions in The Netherlands have also displayed Green Iguanas with Ringed Teal in walk-through aviaries.

**Order Galliformes.**—At least three species of pheasants have been combined with Green Iguanas. The Great Argus (*Argusianus argus*) and Malayan Peacock-pheasant (*Polyplectron malacense*) share an outdoor walk-through aviary with Green Iguanas in a zoological institution in Singapore. The combination involving the Great Argus also has been used by a zoological institution in The Netherlands. Golden Pheasants (*Chrysolophus pictus*) have been co-housed with Green Iguanas in an indoor walk-through enclosure in The Netherlands and an outdoor walk-through aviary in a zoological institution in Mexico. Other gallinaceous birds combined with Green Iguanas in zoological institutions include Crested Partridges (*Rollulus rouloul*) in an indoor walk-through enclosure in The Netherlands, and Great Curassows (*Crax rubra*) in an indoor walk-through enclosure in Switzerland.

**Order Phoenicopteriformes.**—We are aware of two zoological institutions combining Green Iguanas with flamingos, a flock of Greater Flamingos (*Phoenicopterus roseus*; Fig. 13) was displayed in an indoor enclosure in Russia, and a flock of Lesser Flamingos (*Phoeniconaias minor*) in an outdoor enclosure in Singapore.

Order Columbiformes.—At least five zoological institutions have combined pigeons and doves with Green Iguanas. A large outdoor walk-through aviary in Singapore held a small group of Green Iguanas with Zebra Doves (Geopelia striata), Nicobar Pigeons (Caloenas nicobarica), Green Imperial Pigeons (Ducula aenea), Pied Imperial Pigeons (D. bicolor), Pinon's Imperial Pigeons (D. pinon), Peruvian Pigeons (Patagioenas oenops), Bruce's Green Pigeons (Treron waalia), and Western Crowned Pigeons (Goura cristata). Similarly, an indoor walk-through enclosure in Switzerland held Green Iguanas with Blue Ground-doves (Claravis pretiosa), Common Ground-doves (Columbina passerina), Caribbean Doves (Leptotila jamaicensis), White-fronted Doves (L. verreauxi), and White-winged Doves (Zenaida asiatica). A zoological institution in Massachusetts, USA, co-housed Green Iguanas with Victoria Crowned Pigeons (G. victoria); a zoological institution in Texas, USA, co-housed Green Iguanas with Peruvian Pigeons; and a zoological institution in Bali, Indonesia, held Green Iguanas with a Common Emerald Dove (Chalcophaps indica) in an outdoor walk-through aviary.

**Order Musophagoformes.**—Two zoological institutions in Mexico and Massachusetts, USA, combined turacos (family Musophagidae) with Green Iguanas.



Fig. 13. An indoor enclosure combining Green Iguanas (*Iguana iguana*) with Greater Flamingos (*Phoenicopterus roseus*), other waterbirds, and fishes, such as Basa (*Pangasius bocourti*) at the Crocus City Oceanarium, Russia. Photographs by Max Blake.

**Order Cuculiformes.**—We are aware of only one zoological institution that combined Green Iguanas with cuckoos; a mixed-species aviary in Florida, USA, co-housed Guira Cuckoos (*Guira guira*) with iguanas.

**Order Caprimulgiformes.**—Only one zoological institution of which we are aware combined Green Iguanas with frogmouths; these were Tawny Frogmouths (*Podargus strigoides*) in a mixed-species aviary in Massachusetts, USA.

**Order Gruiformes.**—Green Iguanas have been combined with a variety of gruiforms, including larger species such as crowned cranes (*Balearica* sp.), displayed together in an outdoor walk-through aviary in Mexico, and Grey-winged Trumpeters (*Psophia crepitans*) in zoological institutions in Germany (Schwibbe and Ziegler 2002) and New York, USA (Farmerie et al. 1999). Small and medium-sized gruiforms combined with Green Iguanas include Lewin's Rails (*Rallus pectoralis*) in a zoological institution in Florida, USA (Farmerie et al. 1999); Grey-necked Wood Rails (*Aramides cajaneus*) in Switzerland and Florida, USA; Giant Wood Rails (*A. ypecaha*) in Spain; and Gray-headed Swamphens (*Porphyrio poliocephalus*) in Russia.

**Order Charadriiformes.**—Three zoological institutions have combined Green Iguanas with waders, which include American Avocets (*Recurvirostra americana*) and lapwings (*Vanellus* sp.) in an outdoor island-type enclosure in Nebraska, USA (Sodaro 1999); Inca Terns (*Larosterna inca*) in a mixed-species aviary in Texas, USA; and Wattled Jacanas (*Jacana jacana*; Fig. 14) in a large indoor walk-through enclosure in Denmark. Furthermore, buttonquails (family Turnicidae) have been co-housed with juvenile iguanas in a zoological institution in Indiana, USA.

Order Eurypygiformes.—Two zoological institutions have displayed Sunbitterns (*Eurypyga helias*) with Green



**Fig. 14.** A Wattled Jacana (*Jacana jacana*) comes face to face with a Green Iguana (*Iguana iguana*) at the Randers Regnskov Tropical Zoo, Denmark. Photograph courtesy of euro-t-guide.com

Iguanas, an indoor walk-through enclosure in Denmark and an aviary in New York, USA (Farmerie et al. 1999).

**Order Suliformes.**—A zoological institution in Mexico has the only exhibit we know of that combined cormorants (family Phalacrocoracidae) with Green Iguanas. These animals were displayed together in an outdoor walk-through aviary.

**Order Pelecaniformes.**—Waterbirds such as Scarlet Ibises (*Eudocimus ruber*) and Roseate Spoonbills (*Platalea ajaja*) have been combined with Green Iguanas in an indoor glass-fronted enclosure in Russia. The former species also was co-housed in outdoor aviaries in Bermuda and Texas, USA, and the latter in an indoor walk-through enclosure in Switzerland.

Some waterbirds such as herons are known predators of juvenile Green Iguanas (Engeman et al. 2005); however, zoological institutions have successfully co-housed adult Green Iguanas with herons such as the Black-crowned Night Heron (*Nycticorax nycticorax*) in a large indoor walk-through enclosure in Denmark, the Green-backed Heron (*Butorides striata*) in an indoor walk-through enclosure in Switzerland, and the Boat-billed Heron (*Cochlearius cochlearius*) in an outdoor enclosure in Florida, USA. Similarly, adult Green Iguanas were displayed with pelicans (*Pelecanus* sp.) in an outdoor walk-through aviary in Mexico.

**Order Cathartiformes.**—At least two zoological institutions have combined diurnal raptors with Green Iguanas. An indoor walk-through enclosure in Denmark displayed iguanas with Turkey Vultures (*Cathartes aura*), and a South American-themed aviary in Texas, USA, kept iguanas with King Vultures (*Sarcoramphus papa*). Although records exist of King Vultures killing animals and consuming large iguanas (Greene et al. 1978; Ferguson-Lees and Christie 2001), this species is predominantly a carrion eater (Houston 1984; Mallon et al. 2013) and presumably able to be co-housed with other animals provided the birds are well-fed.

**Order Strigiformes.**—We are aware of one zoological institution in South America that co-housed Green Iguanas with Burrowing Owls (*Athene cunicularia*). This mixed-species exhibit represents the sympatry of these species observed in the wild (McKie et al. 2005). Burrowing Owls are known predators of juvenile Green Iguanas (McKie et al. 2005) but co-housing them with adult iguanas is not considered a risk.

**Order Bucerotiformes.**—We are aware of only one zoological institution that combined Green Iguanas with hoopoes; these were Green Wood Hoopoes (*Phoeniculus purpureus*) in an indoor walk-through enclosure in Belgium.

**Order Coraciiformes.**—Two zoological institutions have combined Green Iguanas with motmots, Blue-crowned Motmots (*Momotus coeruliceps*) in mixed-species aviaries in Switzerland and Florida, USA. We are aware of only one zoological institution combining Green Iguanas with kingfishers; these were Laughing Kookaburras (*Dacelo novaeguineae*) in an indoor enclosure in Minnesota, USA.



Fig. 15. A group of Green Iguanas (*Iguana iguana*) sharing an aviary with a Channel-billed Toucan (*Ramphastos vitellinus*) at the Santa Ana Zoo, California (USA). Photograph by Luis Miguel Bugallo Sánchez.

**Order Piciformes.**—A number of zoological institutions have combined Green Iguanas with toucans. Examples of which we are aware include Channel-billed Toucans (*Ramphastos vitellinus*; Fig. 15) in a heavily planted outdoor aviary attached to an indoor enclosure in California, USA (Sodaro 1999) and an outdoor walk-through aviary in Singapore; Toco Toucans (*R. toco*) in walk-through aviaries in Singapore and Denmark; Keel-billed Toucans (*R. sulfuratus*) in Florida, USA (Farmerie et al. 1999); Emerald Toucanets (*Aulacorhynchus prasinus*) in Kansas (Sodaro 1999) and New York, USA (Farmerie et al. 1999); and aracaris (*Pteroglossus* sp.) in The Netherlands. Although toucans are known predators of juvenile Green Iguanas (Savage 2002), they evidently are no threat to adults.

**Order Psittaciformes.**—A range of parrots have been combined with Green Iguanas, including smaller species

such as the Cockatiel (*Nymphicus hollandicus*), which are cohoused with iguanas in a zoological institution in Indonesia. Zoological institutions also have co-housed larger parrots with Green Iguanas, including an outdoor walk-through aviary in Mexico that displays Blue and Yellow Macaws (*Ara ararauna*), Scarlet Macaws (*A. macao*), Military Macaws (*A. militaris*), and Sulphur-crested Cockatoos (*Cacatua galerita*) with a group of iguanas. Combinations of Scarlet Macaws with Green Iguanas also are present in zoological institutions in Denmark and West Virginia, USA, and Blue and Yellow Macaws have also been co-housed with Green Iguanas in a zoological institution in Denmark.

Mixed-species exhibits combining medium-sized parrots with Green Iguanas are mostly outdoor walk-through aviaries. These species include: Yellow-crowned Amazons (*Amazona* ochrocephala) in zoological institutions in Florida, USA (Farmerie et al. 1999) and Mexico; Yellow-headed Amazons (*A. oratrix*) in Texas and Florida, USA (Farmerie et al. 1999); Yellow-shouldered Amazons (*A. barbadensis*) in Spain; Sun Conures (*Aratinga solstitialis*; Fig. 12) in Florida and Texas, USA, and Singapore; Golden Conures (*Guaruba guarouba*) in Florida, USA; Rose-fronted Conures (*Pyrrhura picta roseifrons*) in Denmark; Burrowing Parrots (*Cyanoliseus patagonus*) in Mexico and Texas, USA; Eclectus Parrots (*Eclectus roratus*; Fig. 16) in Mexico and Singapore; Black-capped Lories (*Lorius lory*) in Bali, Indonesia; and Red Lories (*Eos bornea*) in Singapore and Bali, Indonesia.

**Order Passeriformes.**—A number of zoological institutions have combined Green Iguanas with passerines, particularly in large walk-through exhibits that afford substantial space for diverse assortments of birds. An outdoor aviary in Bali, Indonesia, displayed a group of Green Iguanas with Black-naped Orioles (*Oriolus chinensis*), a Greater Bird-of-Paradise (*Paradisaea apoda*), Helmeted Friarbirds (*Philemon buceroides*), Bali Mynahs (*Leucopsar rothschildi*), and White-



Fig. 16. A Green Iguana (*Iguana iguana*) sharing a wooden platform in a large outdoor aviary with Eclectus Parrots (*Eclectus roratus*) at the Singapore Zoo. Photographs by Pancy Siam.

necked Mynas (Streptocitta albicollis). Similarly, an indoor walk-through enclosure in Switzerland houses Green Iguanas with passerines such as Green Jays (Cyanocorax yncas), Tropical Mockingbirds (Mimus gilvus), and Northern Cardinals (Cardinalis cardinalis). A zoological institution in Florida, USA, also has held Green Jays and Yellow-rumped Caciques (Cacicus cela) in an aviary with Green Iguanas. Other passerines combined with Green Iguanas include Chinese Hwameis (Garrulax canorus) in an outdoor walk-through aviary in Singapore; Red-cowled Cardinals (Paroaria dominicana) in an indoor walk-through enclosure in Denmark; Silver-beaked Tanagers (Ramphocelus carbo) in Florida, USA; Purple Glossy Starlings (Lamprotornis purpureus) in Massachusetts, USA; Black-throated Magpie Jays (Calocitta colliei) in Texas, USA; Red-billed Leiothrixs (Leiothrix lutea) in Belgium; Madagascar Fodies (Foudia madagascariensis) in Belgium; and Gouldian Finches (Chloebia gouldiae) in Belgium and The Netherlands. Some passerines have been recorded preying on Green Iguana hatchlings (Rivas et al. 1998); however, they are no danger to adults.

# Cartilaginous Fishes (Class Chondrichthyes)

**Order Mykiobatiformes.**—We are aware of only one zoological institution that has combined Green Iguanas with cartilaginous fishes; these were Ocellate River Stingrays (*Potamotrygon motoro*) that inhabit a pond in an outdoor walk-through aviary in Singapore. The stingray barbs were removed to keep other animals in the exhibit safe. The large size of the enclosure also minimized regular contact between stingrays and other animals.

# Ray-finned Fishes (Cass Actinopterygii)

**Order Cypriniformes.**—Carp (family Cyprinidae), especially Koi (*Cyprinus rubrofuscus*), frequently inhabit ponds in enclosures displaying Green Iguanas and other animals (Lonsdale and Klocek 1987).

**Order Characiformes.**—Three characiforms have been combined with Green Iguanas, Pacu (*Myleus pacu*) in zoological institutions in Russia and Denmark, Red-bellied Piranhas (*Pygocentrus nattereri*) in France and Argentina, and Tetras (*Hyphessobrycon anisitsi*) in England. While piranhas are reputed to be voracious predators, studies of Red-bellied Piranhas have found their diet comprised primarily of other fishes, arthropods, molluscs, other invertebrates, and vegetation (Nico and Taphorn 1988; Winemiller 1989; Winemiller and Kelso-Winemiller 1993), and that vertebrate prey are typically carrion (Pauly 1994). They appear to be safely cohoused with iguanas provided they are sufficiently fed.

**Order Siluriformes.**—At least three zoological institutions have combined catfish with Green Iguanas. The aquatic strata of an exhibit in Russia were inhabited by Barred Catfish (*Pseudoplatystoma fasciatum*), Common Plecos (*Hypostomus*) *plecostomus*), Four-lined Pimelodus (*Pimelodus blochii*), Red-tailed Catfish (*Phractocephalus hemilopterus*), and Basa (*Pangasius bocourti*; Fig. 13). A zoological institution in The Netherlands also co-housed the latter two species with Green Iguanas. Furthermore, Upside-down Catfish (*Synodontis nigriventris*) and bristle-nosed catfishes (*Ancistrus* spp.) inhabit the aquatic section of a Green Iguana enclosure in a zoological institution in England.

Order Cyprinodontiformes.—Two species of toothcarps have been combined with Green Iguanas, both cases in Europe. These were Butterfly Goodeids (*Ameca splendens*) in a zoological institution in England and Guppies (*Poecilia reticulata*) in a large indoor walk-through enclosure in Denmark.

**Order Cichliformes.**—At least three zoological institutions have combined Green Iguanas with cichlids, an unidentified species in an aquarium in Italy, Freshwater Angelfish (*Pterophyllum scalare*) in a terrarium in England, and Red Oscars (*Astronotus ocellatus*) in a large indoor walk-through enclosure in Denmark.

**Order Beloniformes.**—Green Iguanas have been combined with needlefishes (*Xenentodon* spp.) in a zoological institution in Illinois, USA (Lonsdale and Klocek 1987).

**Order Osteoglossiformes.**—A large pool in an indoor walk-through enclosure in Denmark was inhabited by adult Silver Arowanas (*Osteoglossum bicirrhosum*).

# Gastropods (Glass Gastropoda)

**Order Cycloneritida.**—We are only aware of one example of Green Iguanas combined with gastropods. A zoological institute in England housed Zebra Nerite Snails (*Neritina turrita*), an aquatic gastropod, in an indoor glass-fronted enclosure with Green Iguanas. This might appear to be a risk for the snails as Townsend et al. (2005) noted Green Iguanas feeding on terrestrial snails. However, invertebrate prey is rarely taken by iguanas, and we expect that well-fed iguanas are unlikely to consume aquatic snails.

# Malacostracans (Class Malacostraca)

**Order Decapoda.**—We are aware of only one example of Green Iguanas combined with crustaceans. A colony of Red Cherry Shrimp (*Neocaridina davidi*), a popular ornamental shrimp bred in aquaria (Viau et al. 2020), inhabit the aquatic section of a Green Iguana enclosure in a zoological institution in England. These shrimp typically scatter when iguanas enter the water but will settle on the iguanas when they are submerged.

# Discussion

In the past few decades, zoological institutions have increasingly leveraged mixed-species exhibits for public education potential and enhanced patron experiences (Dorman and Bourne 2010). Immersive exhibits, which surround patrons in artificial habitats displaying combinations of taxa (Fig. 17), are particularly appealing for patrons (Ross and Gillespie 2009). This paper, although not an exhaustive review, highlights the broad range of animal taxa that zoological institutions have co-housed with Green Iguanas, accounting for species from eight taxonomic classes and 44 orders. Because of its compatibility with so many other animals, the Green Iguana is an ideal candidate for mixed-species and immersive exhibits, especially considering the existing abundance of this lizard in captive collections throughout the world (De Jesús Villanueva et al. 2021). Although some literature records document invertebrate prey taken by Green Iguanas (Hirth 1963; Townsend et al. 2005), the species' largely herbivorous diet allows for combining them with taxa such as toads, tamarins, treeshrews, and small birds that would not be suitable for other medium-sized to large lizards such as monitors and teiids.

Zoological institutions designing mixed-species exhibits that account for factors associated with combinations of various taxa have reduced probabilities of encountering problems. Enclosure size is a key factor determining the extent that animals can distance themselves from each other and avoid other species if necessary (Thomas and Maruska 1996). Outdoor enclosures are generally more spacious than indoor enclosures (Veasey and Hammer 2010); however, zoological parks in cooler climatic zones often require reptiles to be housed indoors to ensure adequate heating. Features other than size, such as branches, logs, vegetation, rock structures, and elevated platforms, also facilitate separation between animals and, in some cases, render parts of some enclosures inaccessible to certain species. They can also provide visual barriers between animals, contributing to a reduced likelihood of aggression and stress (Veasey and Hammer 2010). Studies of animals in stratified exhibits have shown that different species may habitually use different spaces, thus minimizing interspecies contact (Dalton and Buchanan-Smith 2005). Potential aggression can also be minimized by separating species in their own quarters during after-hours periods (Sodaro 1999).

Nevertheless, we found some combinations that are quite daring. Mixed-species exhibits that combined Green Iguanas with animals that would naturally prey on even adult iguanas were of particular interest. Notable examples were large snakes (Ribeiro Sanches et al. 2018), crocodilians (Pérez-Higareda et al. 1989; Thorbjarnarson et al. 1993), and vultures (Ferguson-Lees and Christie 2001). These animals are presumably managed with feeding schedules designed to maintain a continuously low demand for other food in order to minimize the likelihood of iguanas becoming prey. Enclosure features were generally utilized in these exhibits, providing iguanas with different strata for reprieve or to escape. Similarly, we found examples where iguanas were cohoused with animals that could otherwise harm them. For example, the Chimpanzees kept with iguanas in Germany were recorded to have killed other animals in the exhibit (Schwibbe and Ziegler 2002) and even play behavior could potentially result in iguana deaths.

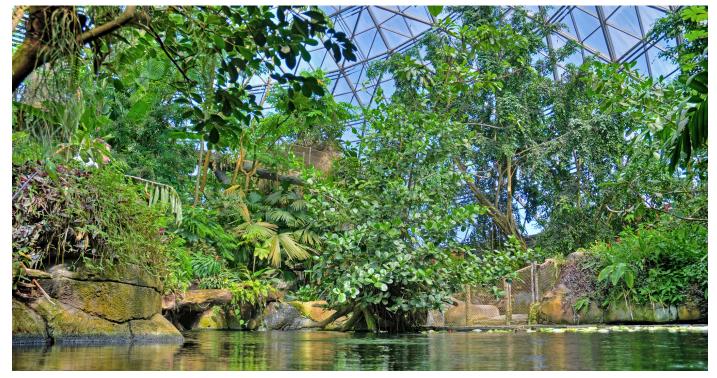


Fig. 17. A large immersive walk-through enclosure featuring stratified viewing for patrons, including below-water, ground level, elevated rock platforms, and treetop walkways, at the Randers Regnskov Tropical Zoo, Denmark. Photograph by Per Erik Sviland.

Adult Green Iguanas have also been co-housed with animals that may prey on them as juveniles, such as basilisks (Burghardt et al. 1977), monitors (Mazzotti et al. 2020), herons (Engeman et al. 2005), owls (McKie et al. 2005), kookaburras (Blomberg and Shine 2000), and toucans (Savage 2002). This demonstrates the importance of zoological institutions assessing animal size ratios when planning mixedspecies exhibits. We note that most zoological institutions regulate breeding or remove egg clutches from reproducing animals; however, this may not be possible for large extensively stratified enclosures such as rainforest-themed walkthrough exhibits (Fig. 17). In these cases, iguanas may produce offspring that are at some risk of predation.

Monkeys were notably common mammals to combine with Green Iguanas. Although some species are recorded predators of lizards (e.g., Rivas et al. 1998), monkeys we observed in these mixed-species exhibits were either omnivorous with prey limited to smaller animals and/or bird eggs, such as tamarins and marmosets (Nickle and Heymann 1996; Raboy and Dietz 2004), sakis (Norconk and Conklin-Brittain 2004), squirrel monkeys (Pinheiro et al. 2013), night monkeys (Montilla et al. 2021), and woolly monkeys (Fiore 2003), or entirely herbivorous, such as howler monkeys (Prates and Bicca-Marques 2008).

### Acknowledgements

We thank Arjan Haverkamp, Bosse Skansen-Akvariet, J.A. Kok, Kevin B., Luis Miguel Bugallo Sánchez, Maarten de Ruiter, Max Blake, Pancy Siam, Per Erik Sviland, Peter Kiedrzyński, and Wild Florida Airboats and Gator Park for permission to use their photographs.

#### Literature Cited

- Alberts, A.C., R.L. Carter, W.K. Hayes, and E.P. Martins (eds.). 2004. *Iguanas: Biology and Conservation*. University of California Press, Berkeley and Los Angeles, California, USA.
- Balaguera-Reina, S.A., M. Venegas-Anaya, V. Beltrán-López, A. Cristancho, and L.D. Densmore. 2018. Food habits and ontogenetic dietary partitioning of American Crocodiles in a tropical Pacific Island in Central America. *Ecosphere* 9: e02393. https://doi.org/10.1002/ecs2.2393.
- Barrio-Amorós, C. and R.A. Ojeda. 2015. Iguana iguana. Predation by Tayras (Eira barbara). Mesoamerican Herpetology 2: 112–114.
- Blomberg, S. and R. Shine. 2000. Size-based predation by kookaburras (*Dacelo novaeguineae*) on lizards (*Eulamprus tympanum*: Scincidae): what determines prey vulnerability? *Behavioral Ecology and Sociobiology* 48: 484–489. https://doi.org/10.1007/s002650000260.
- Blount, J.D. 1997. Design and management of a mixed-species 'African Plains' exhibit: large ungulates, small carnivores and 'dangerous' rodents. *International Zoo News* 44: 389–396.
- Buchanan-Smith, H.M. 2012. Mixed-species exhibition of Neotropical primates: analysis of species combination success. *International Zoo Yearbook* 46: 150– 163. https://doi.org/10.1111/j.1748-1090.2011.00151.x.
- Burghardt, G.M., H.W. Greene, and A.S. Rand. 1977. Social behavior in hatchling Green Iguanas: life at a reptile rookery. *Science* 195: 689–691. https://doi. org/10.1126/science.195.4279.689.
- Campos, Z. and A.L.J. Desbiez. 2013. Structure of size and reproduction of Green Iguanas (*Iguana iguana*) in the Brazilian Pantanal. *Reptiles & Amphibians* 20: 75–78. https://doi.org/10.17161/randa.v20i2.13941.

- Casares, M., J. Recuero, and G. Fernández-Hoyo. 2011. Talapoin monkeys *Miopithecus* spp. in European zoos: status and management in mixed-species exhibits. *International Zoo Yearbook* 45: 226–236. https://doi.org/10.1111/ j.1748-1090.2010.00119.x.
- Chinchilla, F.A. 1997. La dieta del Jaguar (*Panthera onca*), el Puma (*Felis concolor*) y el Manigordo (*Felis pardalis*) (Carnivora: Felidae) en el Parque Nacional Corcovado, Costa Rica. *Revista de Biología Tropical* 45: 1223–1229.
- Clark, F.E. and V.A. Melfi. 2011. Environmental enrichment for a mixedspecies nocturnal mammal exhibit. *Zoo Biology* 31: 397–413. https://doi. org/10.1002/zoo.20380.
- Dalton, R. and H.M. Buchanan-Smith. 2005. A mixed-species exhibit for Goeldi's Monkeys and Pygmy Marmosets *Callimico goeldii* and *Callithrix pygmaea* at Edinburgh Zoo. *International Zoo Yearbook* 39: 176–184. https://doi. org/10.1111/j.1748-1090.2005.tb00017.x.
- Daoudi, S., G. Badihi, and H.M. Buchanan-Smith. 2017. Is mixed-species living cognitively enriching? Enclosure use and welfare in two captive groups of Tufted Capuchins (*Sapajus apella*) and Squirrel Monkeys (*Saimiri sciureus*). Animal Behavior and Cognition 4: 72–90. https://doi.org/10.12966/ abc.06.02.2017.
- De Jesús Villanueva, C.N., W. Falcón, X. Velez-Zuazo, R. Papa, and C.L. Malone. 2021. Origin of the Green Iguana (*Iguana iguana*) invasion in the greater Caribbean region and Fiji. *Biological Invasions* 23: 2591–2610. https://doi. org/10.1007/s10530-021-02524-5.
- Dorman, N. and D.C. Bourne. 2010. Canids and ursids in mixed-species exhibits. *International Zoo Yearbook* 44: 75–86. https://doi.org/10.1111/j.1748-1090.2009.00108.x.
- Engeman, R.M., E.M. Sweet, and H.T. Smith. 2005. *Iguana iguana* (Green Iguana). Predation. *Herpetological Review* 36: 320.
- Falcón, W., J.D. Ackerman, and C.C. Daehler. 2012. March of the Green Iguana: non-native distribution and predicted geographic range of *Iguana iguana* in the Greater Caribbean Region. *Reptiles & Amphibians* 19: 150–160. https:// doi.org/10.17161/randa.v19i3.14532.
- Farmerie, M., D. Neiffer, and K. Vacco. 1999. Enrichment and operant conditioning of callitrichids, pp. 64–89. In: V. Sodaro and N. Saunders (eds.), *Callitrichid Husbandry Manual*. Neotropical Primate Taxon Advisory Group, Chicago, Illinois, USA.
- Ferguson-Lees, J. and D.A. Christie. 2001. *Raptors of the World*. Houghton Mifflin Company, Boston, Massachusetts, USA.
- Filipiak, D., G. Geisler, and C. Wappl, C. 2012. Iguana iguana (Green Iguana). Predation. Herpetological Review 43: 487–488.
- Fiore, A.D. 2003. Ranging behavior and foraging ecology of Lowland Woolly Monkeys (*Lagothrix lagotricha poeppigii*) in Yasuní National Park, Ecuador. *American Journal of Primatology* 59: 47–66. https://doi.org/10.1002/ajp.10065.
- Galef, B.G., R.A. Mittermeier, and R.C. Bailey. 1976. Predation by the Tayra (*Eira barbara*). Journal of Mammalogy 57: 760–761. https://doi. org/10.2307/1379450.
- Grazian, D. 2012. Where the wild things aren't: exhibiting nature in American zoos. *Sociological Quarterly* 53: 546–565.
- Greene, H.W., G.M. Burghardt, B.A. Dugan, and A.S. Rand. 1978. Predation and defensive behavior of Green Iguanas (Reptilia, Lacertilia, Iguanidae). *Journal* of *Herpetology* 12: 169–176. https://doi.org/10.2307/1563404.
- Guedes Coutinho, A., K. Sivino Serra, L.G. Sales Junior, and D. Cassiano Lima. 2014. Predation of Green Iguana (*Iguana iguana*) by Guira Cuckoo (*Guira guira*) in northeastern Brazil. *Revista Brasileira de Ornitologia* 22: 305–306. https://doi.org/10.1007/BF03544267.
- Hirth, H.F. 1963. Some aspects of the natural history of *Iguana iguana* on a tropical strand. *Ecology* 44: 613–615. https://doi.org/10.2307/1932553.
- Hosey, G., V. Melfi, I. Formella, S.J. Ward, M. Tokarski, D. Brunger, S. Brice, and S.P. Hill. 2016. Is wounding aggression in zoo-housed Chimpanzees and Ring-tailed Lemurs related to zoo visitor numbers? *Zoo Biology* 35: 205–209. https://doi.org/10.1002/zoo.21277.
- Houston, D.C. 1984. Does the King Vulture Sarcorhamphus papa use a sense of smell to locate food? *Ibis* 126: 67–69. https://doi.org/10.1111/j.1474-919X.1984.tb03665.x.
- Inglefield-Hatcher, S. 2000. Bird compatibility in mixed-species free-flight aviaries: a study of species aggression in North American zoos. *Proceedings of the Association of Zoos and Aquariums Annual Conference* 2000: 35–44.
- Jessop, T., J. Urlus, T. Lockwood, and G. Gillespie. 2010. Preying possum: assess-

ment of the diet of Lace Monitors (*Varanus varius*) from coastal forests in southeastern Victoria. *Biawak* 4: 59-63.

- Kaandorp, J. 2012. Veterinary challenges of mixed species exhibits, pp. 24–31. In: R.E. Miller and M. Fowler (eds.), *Fowler's Zoo and Wild Animal Medicine*. Elsevier, Saint Louis, Missouri, USA. https://doi.org/10.1016/B978-1-4377-1986-4.00004-4.
- Karunarathna, S., T. Surasinghe, D. Dissanayake, M. Botejue, D. Gabadage, and M. Madawala. 2017. Dietary habits and the predators of the Bengal Monitor *Varanus bengalensis* in Sri Lanka. *Biawak* 11: 28–39.
- Knapp, C.R., T.D. Grant, S.A. Pasachnik, B. Angin, E. Boman, J. Brisbane, S.D. Buckner, J.E. Haakonsson, P.S. Harlow, F. Mukhida, N. Thomas-Moko, M.P. van denBurg, and J.A. Wasilewski. 2020. The global need to address threats from invasive alien iguanas. *Animal Conservation*: online early. https:// doi.org/10.1111/acv.12660.
- Krysko, K.L., K.M. Enge, E.M. Donlan, J.C. Seitz, and E.A. Golden. 2007. Distribution, natural history, and impacts of the introduced Green Iguana (*Iguana iguana*) in Florida. *Iguana* 14: 142–151. https://doi.org/10.17161/ randa.v14i3.
- Lavilla, E.O. and F. Brusquetti. 2018. On the identity of *Bufo diptychus* Cope, 1862 (Anura: Bufonidae). *Zootaxa* 4442: 161–170. https://doi.org/10.11646/ zootaxa.4442.1.9.
- Loc-Barragán, J.A. 2017. Iguana iguana. Predation. Mesoamerican Herpetology 4: 929–930.
- Loftin, H. and E. Tyson. 1965. Iguanas as carrion eaters. *Copeia* 1965: 515. https:// doi.org/10.2307/1441007.
- Lonsdale, D.D. and R. Klocek. 1987. The coral reef exhibit at the John G. Shedd Aquarium. *International Zoo Yearbook* 26: 9–18. https://doi. org/10.1111/j.1748-1090.1987.tb03127.x.
- Lopez, K.M., G.J. Fleming, and N.D. Mylniczenko. 2016. A serologic and polymerase chain reaction survey of equine herpesvirus in Burchell's Zebras (*Equus quagga*), Hartmann's Mountain Zebras (*Equus zebra hartmannae*) and Thomson's Gazelles (*Eudorcas thomsonii*) in a mixed species savannah exhibit. Journal of Zoo and Wildlife Medicine 47: 1013–1018. https://doi. org/10.1638/2013-0297.1.
- Lowenstine, L.J. 1999. Health problems in mixed-species exhibits, pp. 26–29. In: M.E. Fowler and R.E. Miller (eds.), *Zoo and Wild Animal Medicine: Current Therapy*. 4th edition. W.B. Saunders, Philadelphia, Pennsylvania, USA.
- Mallon, J.M., K. Swing, and D. Mosquera. 2013. Neotropical vulture scavenging succession at a Capybara carcass in eastern Ecuador. *Ornitología Neotropical* 24: 475–480.
- Mazzotti, F.J., J.H. Nestler, J.M. Cole, C. Closius, W.H. Kern, M.R. Rochford, E. Suarez, R. Brubaker, S.G. Platt, T. Rainwater, and J.K. Ketterlin. 2020. Diet of Nile Monitors (*Varanus niloticus*) removed from Palm Beach and Broward Counties, Florida, USA. *Journal of Herpetology* 54: 189–195. https:// doi.org/10.1670/18-115.
- McGrew, W.C. 2015. Why don't Chimpanzees eat monitor lizards? African Primates 10: 41-52.
- McKeown, S. 1996. A Field Guide to Amphibians and Reptiles in the Hawaiian Islands. Diamond Head Publishing, Los Osos, California, USA.
- McKie, A.C., J.E. Hammond, H.T. Smith, and W.E. Meshaka. 2005. Invasive Green Iguana interactions in a Burrowing Owl colony in Florida. *Florida Field Naturalist* 33: 125–127.
- Montilla, S.O., A.M. Mopán-Chilito, L.N.S. Murcia, J.D.M. Triana, O.M.C. Ruiz, J. Montoya-Cepeda, D.A. Gutierrez-Barreto, J.A. Holguín-Vivas, C.J. Agámez, L.J. Pérez-Grisales, M. Cruz-Moncada, N.J. Corredor-Durango, E.A.C. Díaz, A.H. Cardona-Cardona, E. Franco-Pérez, A.M. Rivera-Ospina, and A. Link. 2021. Activity patterns, diet and home range of night monkeys (*Aotus griseimembra* and *Aotus lemurinus*) in tropical lowland and mountain forests of Central Colombia. *International Journal of Primatology* 42: 130– 153. https://doi.org/10.1007/s10764-020-00192-1.
- Mueses-Cisneros, J.J., D.F. Cisneros-Heredia, and R.W. McDiarmid. 2012. A new Amazonian species of *Rhaebo* (Anura: Bufonidae) with comments on *Rhaebo* glaberrimus (Günther, 1869) and *Rhaebo guttatus* (Schneider, 1799). Zootaxa 3447: 22–40. https://doi.org/10.11646/zootaxa.3447.1.2.
- Murphy, J.B. 1969. Notes on iguanids and varanids in a mixed exhibit at Dallas Zoo. *International Zoo Yearbook* 9: 39-41. https://doi. org/10.1111/j.1748-1090.1969.tb02602.x.
- Newton-Fisher, N.E. 2015. The hunting behavior and carnivory of wild Chimpanzees, pp. 1661–1691. In: W. Henke and I. Tattersall (eds.),

Handbook of Paleoanthropology. Springer, Heidelberg, Germany. https://doi.org/10.1007/978-3-642-39979-4\_42.

- Nickle, D.A. and E.W. Heymann. 1996. Predation on Orthoptera and other orders of insects by tamarin monkeys, *Saguinus mystax mystax* and *Saguinus fuscicollis nigrifons* (Primates: Callitrichidae), in north-eastern Peru. *Journal of Zoology London* 239: 799–819. https://doi.org/10.1111/j.1469-7998.1996. tb05479.x.
- Nico, L.G. and D.C. Taphorn. 1988. Food habits of piranhas in the low llanos of Venezuela. *Biotropica* 20: 311–321. https://doi.org/10.2307/2388321.
- Norconk, M.A. and N.L. Conklin-Brittain. 2004. Variation on frugivory: the diet of Venezuelan White-Faced Sakis. *International Journal of Primatology* 25: 1–26. https://doi.org/10.1023/B:IJOP.0000014642.68751.ed.
- Oliveira, J.M., V.L.A. Souza, and S.A.A. Morato. 2015. *Boa constrictor* (Common Boa) feeds on and regurgitates alive a lizard *Iguana iguana* (Green Iguana). *Herpetological Bulletin* 133: 33.
- Pauly, D. 1994. Quantitative analysis of published data on the growth, metabolism, food consumption, and related features of the Red-bellied Piranha, *Serrasalmus nattereri* (Characidae), pp. 423–437. In: E.K. Balon, M.N. Bruton, and D.L.G. Noakes (eds.), *Women in Ichthyology: An Anthology in Honour of ET, Ro and Genie.* Springer, Dordrecht, The Netherlands. https:// doi.org/10.1007/978-94-011-0199-8\_30.
- Pawley, R. 1971. Mixed species exhibits in the reptile building at Brookfield Zoo, Chicago. *International Zoo Yearbook* 11: 220–224. https://doi. org/10.1111/j.1748-1090.1971.tb01911.x.
- Pereira, K.D.L., J.V. Teixeira, E.M.J.N. Silva, and M.V. Ribeiro. 2020. Predation attempted on *Iguana iguana* (Squamata, Iguanidae) by *Lontra longicaudis* (Carnivora, Mustelidae) in the state of Tocantins, Brazil. *Herpetology Notes* 13: 491–493.
- Pérez-Higareda, G., A. Rangel-Rangel, H. Smith, and D. Chiszar. 1989. Comments on the food and feeding habits of Morelet's Crocodile. *Copeia* 1989: 1039– 1041. https://doi.org/10.2307/1445994.
- Pinheiro, T., S.F. Ferrari, and M.A. Lopes. 2013. Activity budget, diet, and use of space by two groups of Squirrel Monkeys (*Saimiri sciureus*) in eastern Amazonia. *Primates* 54: 301–308. https://doi.org/10.1007/s10329-013-0351-9.
- Platt, S.G., T.R. Rainwater, A.G. Finger, J.B. Thorbjarnarson, T.A. Anderson, and S.T. McMurry. 2006. Food habits, ontogenetic dietary partitioning and observations of foraging behaviour of Morelet's Crocodile (*Crocodylus moreletii*) in northern Belize. *Herpetological Journal* 16: 281–290.
- Popp, J.W. 1984. Interspecific aggression in mixed ungulate species exhibits. Zoo Biology 3: 211–219. https://doi.org/10.1002/zoo.1430030304.
- Prates, H.M. and J.C. Bicca-Marques. 2008. Age-sex analysis of activity budget, diet, and positional behavior in *Alouatta caraya* in an orchard forest. *International Journal of Primatology* 29: 703–715. https://doi.org/10.1007/ s10764-008-9257-6.
- Probst, C., H. Hofer, S. Speck, and K. Frölich. 2005. Epidemiology of selected infectious diseases in zoo ungulates: single species versus mixed species exhibits, pp. 29–31. In: W. Graffam, D. Hellinga, M. Maslanka, and A. Ward (eds.), *Proceedings of the Sixth Conference on Zoo and Wildlife Nutrition*. AZA Nutrition Advisory Group, Omaha, Nebraska, USA.
- Pusey, A., C. Murray, W. Wallauer, M. Wilson, E. Wroblewski, and J. Goodall. 2008. Severe aggression among female *Pan troglodytes schweinfurthii* at Gombe National Park, Tanzania. *International Journal of Primatology* 29: 949–973. https://doi.org/10.1007/s10764-008-9281-6.
- Quick, J.S., H.K. Reinert, R. Eric, and R.A. Odum. 2005. Recent occurrence and dietary habits of Boa Constrictor on Aruba, Dutch West Indies. *Journal of Herpetology* 39: 304–307. https://doi.org/10.1670/45-04N.
- Raboy, B.E. and J.M. Dietz. 2004. Diet, foraging, and use of space in wild Goldenheaded Lion Tamarins. *American Journal of Primatology* 63: 1–15. https://doi. org/10.1002/ajp.20032.
- Ribeiro Sanches, P., F.P. Santos, C.S. Gama, and C.E. Costa-Campos. 2018. Predation on *Iguana iguana* (Squamata: Iguanidae) by Boa Constrictor (Squamata: Boidae) in a fluvial island in the Amazonas River, Brazil, including a list of saurophagy events with Boa Constrictor as predator. *Cuadernos de Herpetología* 32: 129–132. https://doi.org/10.31017/CdH.2018.(2018-002).
- Rivas, J.A., C. Ramon Molina, and T. Manuel Vila. 1998. *Iguana iguana* (Green Iguana). Juvenile predation. *Herpetological Review* 29: 238–239.
- Rivas, J.A., M.C. Muñoz, J.B. Thorbjarnarson, G.M. Burghardt, W. Holmstrom, and P.P. Calle. 2007. Natural history of the Green Anaconda (*Eunectes murinus*) in the Venezuelan Llanos, pp. 129–138. In: R.W. Henderson and R.

Powell (eds.), *Biology of the Boas and Pythons*. Eagle Mountain Publishing, Eagle Mountain, Utah, USA.

- Ross, S.R. and K.L. Gillespie. 2009. Influences on visitor behavior at a modern immersive zoo exhibit. *Zoo Biology* 28: 462–472. https://doi.org/10.1002/ zoo.20220.
- Savage, J.M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna Between Two Continents, Between Two Seas. University of Chicago Press, Chicago, Illinois, USA.
- Schwartz, A. and R.W. Henderson. 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions and Natural History. University of Florida Press, Gainesville, Florida, USA.
- Schwibbe, M. and T. Ziegler. 2002. Mixed Species Exhibits in German Zoological Parks (Part 1): Special References on Primates. German Primate Center, Göttingen, Germany.
- Smith, H.T., W.E. Meshaka, R.M. Engeman, S.M. Crossett, M.E. Foley, and G. Bush. 2006. Raccoon predation as a potential limiting factor in the success of the Green Iguana in southern Florida. *Journal of Kansas Herpetology* 20: 7–8.
- Sodaro, V. 1999. Housing and exhibiting mixed species of neotropical primates, pp. 7–34. In: V. Sodaro and N. Saunders (eds.), *Callitrichid Husbandry Manual*. Neotropical Primate Taxon Advisory Group, Chicago, Illinois, USA.
- Thomas, W.D. and E.J. Maruska. 1996. Mixed-species exhibits with mammals, pp. 204–211. In: D.G. Kleiman, M.E. Allen, K.V. Thompson, and S. Lumpkin (eds.), Wild Mammals in Captivity: Principles and Techniques. University of Chicago Press, Chicago, Illinois, USA.

- Thorbjarnarson, J.B. 1993. Diet of the Spectacled Caiman (*Caiman crocodilus*) in the central Venezuelan llanos. *Herpetologica* 49: 108–117.
- Townsend, J.H., J. Slapcinsky, K.L. Krysko, E.M. Donlan, and E.A. Golden. 2005. Predation of a tree snail *Drymaeus multilineatus* (Gastropoda: Bulimulidae) by *Iguana iguana* (Reptilia: Iguanidae) on Key Biscayne, Florida. *Southeastern Naturalist* 4: 361–364. https://doi.org/10.1656/1528-7092(2005)004[0361:POATSD]2.0.CO;2.
- van den Burg, M.P., S.M. Van Belleghem, and C.N. De Jesús Villanueva. 2020. The continuing march of Common Green Iguanas: arrival on mainland Asia. *Journal for Nature Conservation* 57: 125888. https://doi.org/10.1016/j. jnc.2020.125888.
- Veasey, J. and G. Hammer. 2010. Managing captive mammals in mixed-species communities, pp. 151–161. In: D.G. Kleiman, K.V. Thompson, and C.K. Baer (eds.), Wild Mammals in Captivity: Principles and Techniques for Zoo Management. Second edition. University of Chicago Press, Chicago, Illinois, USA.
- Viau, V.E., J.G. Pérez, A.L. Tomas, P.A. Fracas, F.B. Veira, I. Vatnick, and L.S.L. Greco. 2020. Breeding and life cycle of the ornamental freshwater shrimp *Neocaridina davidi* in a biofilm-based culture system. *Aquaculture Research* 51: 3847–3864. https://doi.org/10.1111/are.14733.
- Winemiller, K.O. 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. *Environmental Biology of Fishes* 26: 177–199. https://doi.org/10.1007/BF00004815.
- Winemiller, K.O. and L.C. Kelso-Winemiller. 1993. Predatory response of piranhas to alternative prey. *National Geographic Research and Exploration* 9: 344–357.