

***Iguana iguana* Linnaeus 1758**

Common Green Iguana

Brian C. Bock

Instituto de Biología, Universidad de Antioquia, Medellín, Colombia

Status:

IUCN Not Assessed, likely to be Least Concern. CITES Appendix II.

Taxonomy:

The Common Green Iguana (*Iguana iguana*) belongs to a monophyletic clade of large-bodied, primarily herbivorous lizards. Some authors recognized this clade as a family (Iguanidae), while others prefer to restrict it to the subfamily level (Iguaninae). Regardless, the phylogenetic relationships within this clade have not been completely resolved (Sites *et al.* 1996, Malone *et al.* 2000, Wiens and Hollingsworth 2000, Hollingsworth 2004). However, it is clear that the center of origin of this species group was Mesoamerica, probably in xeric habitat. Iverson (1982) argued that the evolution of partitions in the colon, and the associated symbiosis with nematodes, bacteria, and protozoans, was a key adaptation in the ancestral iguana that permitted the transition from an omnivorous diet to a completely herbivorous diet. Other adaptations associated with herbivory, such as large body size and the presence of extra-renal (nasal) glands for eliminating salts, also helped iguanas in their capacity to colonize oceanic islands. One genus of iguanas is endemic to islands of the Caribbean (*Cyclura*), two genera are endemic to the Galápagos Islands (*Conolophus* and *Amblyrhynchus*), and another genus has colonized and evolved in the islands of Fiji and Tonga (*Brachylophus*).

The genus *Iguana* is comprised of two species (Lazell 1973, Conrad and Norell 2010, Valette *et al.* 2013), the widely distributed *I. iguana* (described here) and *I. delicatissima*, restricted to the Lesser Antilles. Populations of *I. iguana* exhibit morphological variation that has led to the description of two subspecies (*I. i. iguana* and *I. i. rhinolopha*), neither of them currently recognized (Lazell 1973). The first genetic study of populations of *I. iguana* found no evidence of a marked distinction between Central and South American populations (Bock and McCracken 1988), but recently analyses employing more variable molecular markers (Malone and Davis 2004, Stephen 2006, Stephen *et al.* 2013) have suggested a South

American origin for the genus (presumably after having colonized South America from Mesoamerica), with several later invasions of the Caribbean and Central America. These same molecular data also suggest the existence of two or more morphologically cryptic species within the taxon known currently as *I. iguana*.

Description:

The Common Green Iguana may vary in body size from 7.7 cm snout-to-vent length (SVL) in neonates to more than 50 cm SVL in adult males, with a total length including the tail of almost 2 m. There is an ontogenetic change in coloration, with neonates normally a brilliant green color (although there are populations in xeric habitats where they may have a more brownish tone) with an aquamarine bar over the anterior limbs and dark pigmentation on the eyelids. Juveniles are a light-green color and adults are a dark green; adult males take on an orange hue in the reproductive season. Both sexes possess an enlarged sub-tympanic scale and a green dewlap that is extended when an individual is basking or interacting with a conspecific. There is a row of thin, enlarged vertebral scales that extend along the dorsum from the neck to the anterior portion of the tail. The tail is long and robust, with wide black bands (on non-regenerated portions). They possess robust limbs with long claws on the toes.

Adult iguanas are usually sexually dimorphic with males being larger, but not always (Bakhuis 1982). Males also are relatively larger than females of the same SVL in head dimensions, length of the dorsal crest scales, and size of the femoral pores (Müller 1968, Fitch and Henderson 1977, Rodda 1991). There is no outward evidence of sexual dimorphism in neonates or juveniles although they may be successfully sexed by close inspection of cloacal morphology (Rivas and Avila 1996).

It is normally possible to assign individuals to different age classes during the first two years of life, but high variability in growth rate beyond age two eventually eliminates distinguishing size differences among cohorts (but see Müller 1972, Fitch and Henderson 1977).

Distribution (ITWG 2011):

Iguana iguana occurs from northern México in Sinaloa and Veracruz south through Central America and the northeast of South America to Paraguay and southeastern Brazil. It also occurs naturally on numerous islands, including Cozumel, Utila, Roatán, Guanaja, Corn

Islands, Providencia, San Andrés, Aruba, Trinidad, Tobago and other islands of the Lesser Antilles. It also has been introduced in Anguilla, Antigua, Bahamas, Barbuda, British Virgin Islands, Canary Islands, Cayman Islands, Fiji, Guadeloupe, Marie Galante, Martinique, Puerto Rico, Saint-Martin/Sint Maarten, U.S. Virgin Islands, and the United States of America (Florida and Hawaii).

Habitat and Ecology:

The basic biology of *I. iguana* has been studied in many portions of its wide range of distribution (México: Casas Andreu and Valenzuela López 1984, Alvarado *et al.* 1995; Honduras: Klein 1982; Costa Rica: Hirth 1963, Fitch and Henderson 1977, van Devender 1982; Panamá: Rand 1968a; Colombia: Müller 1968, 1972; Harris 1982; Muñoz *et al.* 2003; Venezuela: Rodda 1990, 1992; Rodda and Grajal 1990; Curaçao: Bakhuis 1982, van Marken Lichtenbelt and Albers 1993; Brazil: Ferreira *et al.* 2002, Campos and Desbiez 2013). Those studies, and other more specific ones, form the basis of the following review of *I. iguana* ecology.

Habitat – In contrast to the majority of iguana species, the Common Green Iguana has colonized humid tropical rainforests and can be exclusively arboreal, descending to the ground principally for nesting. However, in this habitat, iguanas never venture far from the edge of continuous forests, occupying the margins of rivers, lakes, or natural or artificial clearings. The first study of dispersal in Green Iguanas employing radio-telemetry (Montgomery *et al.* 1973) reported post-nesting females that migrated three km into continuous forest, but apparently the effort to visually confirm the daily locations of these individuals was a methodological procedure that affected the normal behavior of these animals (M. Sundquist, pers. comm.). Subsequent studies on movements in continuous forest habitats using telemetry have invariably documented that iguanas restrict their movements to the forest edge (Bock *et al.* 1989, Rand *et al.* 1989, Morales *et al.* 2007, Escobar *et al.* 2010).

Iguana iguana inhabits other types of habitat than tropical rainforest, including dry forest, gallery forest, savannahs with few trees, and even xeric islands with exclusively shrub vegetation. They normally sleep in available vegetation, but occasionally, in some populations individuals have been observed sleeping in tunnels they have constructed in the ground (Rodda and Burghardt 1985).

Maximum elevation records for the species include 800 m in Michoacán, México, and 1000 m in Colombia (Etheridge 1982), although in Colombia it is common to find individuals occurring at higher elevations (presumably released pets). However, successful reproduction has not been reported for elevations exceeding 1000 m, with the exception of events where females nested in a compost pile at the Santa Fe Zoo in Medellín (G. Valencia, pers. comm.).

Diet – Herbivory in the Common Green Iguana has been studied primarily from an ecophysiological point of view (Rand 1978; Iverson 1982; McBee and McBee 1982; van Devender 1982; Troyer 1984a, 1984b, 1984c; Govender *et al.* 2012), rather than from an ecological perspective (Benítez-Malvido *et al.* 2003). *Iguana iguana* is one of the few generalist herbivores of tropical forest canopies (Rand 1978), but even so, there is evidence they prefer to feed on certain plant species, not necessarily the most abundant (Rand *et al.* 1990, van Marken Lichtenbelt 1993, Lara-López and González-Romero 2002, Gómez *et al.* 2006, Campos *et al.* 2014). Consumption of snails and insects that occur on vegetation is probably incidental (Hirth 1963, Townsend *et al.* 2005). Consumption of dead animal flesh (Loftin and Tyson 1965, Arendt 1986, Anderson and Enge 2012) and feces of conspecifics (Troyer 1984c) or other species (Campos *et al.* 2011) also has been documented; this behavior may be related to the maintenance of an intestinal microbial fauna for fermentation of plant matter. Thermoregulation in juveniles and adults apparently also is tightly related to digestive processes (Wilhoft 1958; McGinnis and Brown 1966; Müller 1972; van Marken Lichtenbelt *et al.* 1993, 1997).

Behavior – In contrast to most lizard species, neonates of the Common Green Iguana are notoriously social, emerging from the nest in groups that disperse together to suitable juvenile habitat (low bushes), and they maintain these social groups for at least the first year of life (Burghardt 1977; Burghardt *et al.* 1977; Drummond and Burghardt 1982, 1983; Mora 1991). Experimental studies have shown that neonates are capable of recognizing relatives within social groups (Werner *et al.* 1987) and there is evidence that juvenile males act altruistically towards juvenile females (Rivas and Levín 2004).

Larger iguanas perch in higher vegetation (Hirth 1963, Henderson 1974), establishing home ranges that range from 0.11 to 0.96 ha in size (Dugan 1982a, Rand *et al.* 1989, Morales *et al.* 2007). They normally do not descend from the vegetation except to move between habitat

patches or to escape predators (Greene *et al.* 1978). The social system of *I. iguana* has been studied under both natural conditions and in captivity (Dugan 1982a, 1982b; Pratt *et al.* 1992; Rodda 1992; Phillips *et al.* 1993; Phillips 1995). Adults are territorial, maintaining considerable overlap between male and female territories. During the mating season, dominant males reduce the size of their territories to much smaller portions where they are able to produce conspicuous displays and exclude subordinate males from the area, guaranteeing them exclusive access to the reproductive females present. However, subordinate males occasionally steal copulations (Dugan 1982a), although the incidence of multiple paternity in iguana nests has not yet been evaluated (see below).

Iguanas interact among themselves using visual signals (Hazlett 1980, Dugan 1982b, Pratt *et al.* 1992, Phillips 1995), chemical secretions produced by their femoral glands (Burghardt *et al.* 1986; Weldon *et al.* 1990; Alberts *et al.* 1992a, 1992b, 1993; Alberts 1993; Alberts and Werner 1993; Alberts *et al.* 1994), and via direct physical fights among members of the same sex. Males apparently are only capable of copulating once a day, producing a competition among females during the reproductive season for access to dominant males, in addition to the normal male-male competition for access to females (Rodda 1992). Females also compete amongst themselves for access to partially completed nest burrows, at least in areas where they nest in aggregation (Rand 1968a; Rand and Rand 1976, 1978; Dugan *et al.* 1981; Haller and Rodriguez 2005).

Reproduction – In areas where it has been documented, the phenology of the Common Green Iguana reproductive cycle is correlated tightly to the tropical wet and dry seasons. Males establish reproductive territories at the beginning of the dry season and females oviposit during a restricted period in the middle of this season, so that eggs begin hatching near the onset of the rainy season, a time when new leaves are abundant and easier for neonates to digest (Hirth 1963; Rand 1968a; Müller 1968, 1972; Fitch and Henderson 1977; Harris 1982; Klein 1982; van Devender 1982; Casas Andreu and Valenzuela López 1984; Muñoz *et al.* 2003; van Marken Lichtenbelt 1993). Because the climate varies seasonally between hemispheres, there is a clinal variation in the dates of mating, nesting, and hatching across the range of the species (Rand and Greene 1982).

The first studies of *I. iguana* egg incubation (Licht and Moberly 1965; Rand 1968b, 1972) argued that they had very narrow tolerances in terms of the temperature and humidity

required for successful hatching, consistent with the fact that females construct deep burrows to maintain stable microclimatic conditions and nest exclusively in soils that receive direct sunlight. However, later studies have shown that the tolerance ranges for iguana eggs are less constrained (Bock *et al.* 1998), although temperature and humidity conditions that incubating eggs experience do have important effects on characteristics of the neonates (Werner 1988, Phillips *et al.* 1990, Packard *et al.* 1992).

In some populations, female iguanas may migrate up to three km to find sites with appropriate characteristics, where they nest in aggregation (Rand 1968a; Bock *et al.* 1985, 1989; Rodda 1990; Rodda and Grajal 1990; Morales *et al.* 2007). Females migrate by walking or swimming to find beaches, clearings, or islands with the appropriate micro-climatic conditions. On small islands, nests experience lower predation rates (Rand and Robinson 1969, Drummond 1983).

At communal nesting sites, the first females to arrive each nesting season construct simple burrows that are not exceedingly deep (20-30 cm), filling them with soil after ovipositing. A female may remain guarding the entrance to the burrow for several days after nesting before returning to her territory (Rand 1968a, Alvarez del Toro 1972). Gravid females that arrive at the site later may take advantage of already finished nests by re-opening the burrow, often digging into the existing clutch, but they always extend the burrow further before ovipositing. In this way, a complex burrow system of inter-connected tunnels may develop each nesting season, with females that arrive at the end of the season sometimes nesting at depths of up to one meter and emerging several meters from where they disappeared underground (Rand and Dugan 1980, 1983).

The first females to nest in a reproductive season are more vulnerable to predation in the shallow burrows and it is more likely that their clutches will be disturbed by subsequently nesting females. On the other hand, clutches of the last females to nest are more vulnerable to mortality due to flooding associated with the beginning of the rainy season (Bock *et al.* 1989). This stabilizing selection may explain the evolution of such a restricted reproductive cycle synchronized to rainfall seasonality (Weiwandt 1982, Bock *et al.* 1989), which is not a typical pattern in tropical lizard species.

Demography – There is a significant relationship between female body size and clutch size, with clutch sizes ranging from nine to 71 eggs (Rand 1984, Alvarado *et al.* 1995). In the majority of Common Green Iguana populations that have been examined, mean clutch size is near 35 eggs (Hirth 1963, Müller 1972, Klein 1982, Casas Andreu and Valenzuela López 1984, Rand 1984, but see Bakuis 1982, Muñoz *et al.* 2003). To date, only one nest per female in only one annual nesting season has been documented, although Rand and Greene (1982) speculated that some populations of *I. iguana* near the equator, where there are two well-defined dry seasons each year, might exhibit two reproductive seasons each year, with some females nesting in both.

Iguana nests are depredated by snakes (Mora 1987) and terrestrial mammals (Rand and Robinson 1969). Rand and Dugan (1980), working in three sites in Panama, documented egg mortality rates not related to predation of between 5% and 56%, although the exact cause of mortality was not determined. Some of the dead eggs were found isolated in the tunnels of the burrow system, rather than together in a nest chamber. Presumably, these eggs were separated when a nesting female dug into a previously oviposited clutch. Nesting females also sometimes displace eggs onto the surface while they are excavating, where the eggs are consumed by vultures or desiccate (Rand 1968, Sexton 1975, Rand and Dugan 1980).

Juvenile iguanas are preyed upon by crocodiles, caiman, and fish while swimming during their dispersal away from the nesting sites, and by other large lizards (e.g., *Basiliscus*), snakes, birds, and mammals when in their terrestrial habitat (van Devender 1982, Rivas *et al.* 1998, Knapp and Abarca 2009, Ribeiro-D 2010, Wehrle and Guzman 2012). Adults are vulnerable to attacks by snakes, raptors, owls, and a variety of mammals (Swanson 1950, Greene *et al.* 1978, Bessier *et al.* 2010). Adult females also are vulnerable to attack by crocodiles and caiman while swimming during migration to and from nesting sites and while they are excavating nest burrows (Dugan *et al.* 1981, Bock and Rand 1989, Platt *et al.* 2010).

Several studies have employed mark-recapture techniques with juvenile *I. iguana* to document developmental growth rates. There is considerable variation in growth rates among individuals and populations (Burghardt 2004). In populations studied to date, juveniles grow on average between 0.22 and 0.58 mm/day (Henderson 1974, Müller 1968, Harris 1982, van Devender 1982, Burghardt and Rand 1985), with greater growth rates in individuals that remain in social groups instead of living solitarily (Burghardt and Rand 1985).

Extrapolations of these growth rates indicate that females may attain the minimum size of sexual maturity during their third year, which is consistent with studies in captivity, although apparently males become sexually mature at much smaller sizes (Pratt *et al.* 1994).

In natural populations, early studies reported declines in the recapture rates of juveniles in a cohort during the course of their first year of life (Henderson 1974, Harris 1982, van Devender 1982, Burghardt and Rand 1985). Although these studies describe low rates of “survivorship”, this parameter is technically the recovery rate. Studies are needed that rigorously separate the effects of mortality, emigration, and a lack of detection of individuals present, which together combine to produce the observed recovery rate (Mazerolle *et al.* 2007). Quantification of the true detectability of individuals in studies of this type is important, given it has been shown that the probability of capturing an iguana decreases after it has been captured a first time (Rodda *et al.* 1988). An alternative is to estimate survivorship with individuals that are monitored by radio-telemetry, such as in the study by Knapp and Abarca (2009), who estimated that only half of the neonate iguanas to emerge survive the first month of life, consistent with the impression of many mark-recapture studies that most hatchlings fail to survive their first year.

The only mark-recapture study of adult Common Green Iguanas was a five-year monitoring of females at a communal nesting site in Panama (Rand and Bock 1992). Most females were recaptured each year re-nesting in the same site until their eventual disappearance, and very few females (four individuals) were recaptured in alternative nesting sites in different years (Bock *et al.* 1985). This nesting site fidelity implies that the majority of females that did not return in a subsequent year probably died (up to 60% of all nesting females each year). Females that returned had grown very little (6.8 mm SVL/year on average), suggesting that females invest in growth until they begin reproducing, and then invest all available energy into reproduction (up to 15% of their annual energy budget, van Marken Lichtenbelt *et al.* 1993).

One surprise in the Rand and Bock (1992) study was the variability in body sizes of females nesting for the first time (between 295 mm SVL and 425 mm SVL). Also, Zug and Rand (1987) analyzed marks of arrested bone growth in cut toes from females of the same study population, in an attempt to estimate their ages. They estimated that these first-nesting females were between two and eight years of age. There was no evidence of a trade-off

between the two parameters (there were young, small females and old, large females nesting for the first time, but there also were young, large females and old, small females nesting for the first time as well). Given the implications of this body size variation in terms of female fecundity over their reproductive life spans (Rand 1984), such marked variation presumably has its origin in environmental factors, such as differences in the quality of food items available in the territories of the females, and/or in the complexity and efficiency of their intestinal microbial fauna to digest plant cell walls. Natural selection would rapidly eliminate whatever genetic component that contributes to this body size variation, given it is such an important fitness component.

Given the conservation problems that the Common Green Iguana faces, and the conservation problem it represents where it has been introduced outside of its natural distribution (see below), it is surprising there is not more information available on densities of iguanas in natural or introduced populations. Henderson (1974) used the Lincoln-Peterson index with mark-recapture data and estimated a density of 41 juveniles/ha in Belize. Based upon the capture of all individuals inhabiting a 13.5 ha island, Dugan (1982) estimated a density of 36-50 adult iguanas/ha. Rodda (1992) conducted censuses of gallery forest and estimated 55-364 iguanas/ha (including juveniles but not hatchlings) in three sites in the llanos of Venezuela. Muñoz *et al.* (2003) used line transects (and measured the distances of each iguana from the transect to correct the density estimates based upon estimates of iguana detectability) in two sites in the Mompox Depression of Colombia, and estimated 1.2-3.7 iguanas/ha. Finally, two studies have estimated the densities of iguanas in introduced populations: Smith *et al.* (2007) calculated a density of 6.27 iguanas/ha based on the number of iguanas captured each year in a small (131.5 ha) nature reserve and López-Torres *et al.* (2011) counted iguanas while walking transects in two areas along the coast of Puerto Rico, documenting densities of 119-223 iguanas/ha. Obviously, a standardized method to estimate densities should be developed to facilitate comparisons among studies (Arce-Nazario and Carlo 2012).

Threats:

The Common Green Iguana has been consumed by humans since pre-colonial times (Cooke *et al.* 2007), but the exploitation rates in many areas are no longer sustainable (Fitch and Henderson 1977, Fitch *et al.* 1982). The meat and eggs of iguanas are protein sources for many human communities, and are also prized for their alleged medicinal or aphrodisiacal

properties (Stephen *et al.* 2011). The use of iguana hides for producing leather is also common. Iguanas are especially vulnerable to overharvest because adults are conspicuous during the mating season, females are easy to capture while nesting, and because in many areas these times of vulnerability coincide with the Catholic Lent period, stimulating consumption of iguanas because they have “white meat”. Müller (1972) mentioned a sex ratio skew among adult iguanas in northern Colombia in favor of males, presumably because of a harvest directed towards females at the nesting sites.

The international market in juvenile *I. iguana* as pets is enormous, and even though the majority of these individuals come from iguana farms, it is likely these businesses supplement their stocks with individuals from natural populations (Stephen *et al.* 2011). It is estimated that the legal international trade in juvenile iguanas as pets from 2001 and 2008 was approximately 4.5 million individuals (Stephen *et al.* 2011). The magnitude of the illegal iguana pet trade is more difficult to document.

Conservation Measures:

In addition to commercial iguana farms, there are multiple projects within the range of the Common Green Iguana where they are raised in captivity as part of a conservation strategy (“head-starting”). One of the most well known of these projects is Fundación Pro Iguana Verde, initially under the administration of the Smithsonian Tropical Research Institute in Panama (Werner 1987, 1991). The idea was to develop economic strategies to make land use more sustainable (Werner and Miller 1984, Miller 1987) by permitting rural peoples to raise iguanas for food and wild release. Several communities participated in trial releases as part of this project, where juveniles were reared until attaining harvestable sizes, offering an additional source of protein to participating families without requiring the removal of individuals from natural populations (Cohn 1989). A similar project is currently functioning in Costa Rica, where they also operate an ecotourism attraction, conduct environmental education, and continue releasing head-started iguanas in natural habitats (Escobar *et al.* 2010).

In addition, there are dozens of other projects that raise iguanas for conservation strategies in Central America, almost all supported by local governments and NGOs (Stephen *et al.* 2011). However, recent analyses have concluded that these projects are not economically viable, and their impact on the natural populations has been minimal (Eilers *et al.* 2002,

Stephen *et al.* 2011). These projects may play an important environmental education role, but apparently the repopulation efforts have not been very effective, and there is no evidence that they are helping to reduce the harvest levels in natural populations where they operate.

Ironically, despite the problems many Green Iguana populations face due to overharvest throughout its natural range of distribution, the species is also considered an important invasive species, often becoming an ecological problem where it has been introduced (Engeman *et al.* 2005; Smith *et al.* 2006, 2007; Meshaka *et al.* 2007; Garcia-Quijano *et al.* 2011; López-Torres *et al.* 2011; Falcón *et al.* 2013; Pasachnik *et al.* 2012). In many cases, this has required actions attempting to eliminate them, or reduce their densities, and thereby mitigate their impact on humans and the local native flora and/or fauna.

Current Research and Needs:

With such a widespread species, any attempt to summarize current research is destined to be incomplete and soon out of date. However, recent work on Common Green Iguana genetics warrants mention. Investigators primarily interested in the Lesser Antillean Iguana (*I. delicatissima*) have developed microsatellite loci (Valette *et al.* 2013) and analysis of these and other genetic markers are being used to investigate hybridization between *I. iguana* and *I. delicatissima*. Genetic markers are also being employed to extend the work published recently by Stephen *et al.* (2013) and further document the phylogeography of *I. iguana* in Panama and northern South America. Finally, genetic markers are being employed to infer the geographic origin of introduced populations of *I. iguana* and to inspect for levels of multiple paternity within Green Iguana clutches.

As mentioned above, there is a need for standardization of methods employed in demographic research on Common Green Iguana populations to facilitate comparisons among studies (Arce-Nazario and Carlo 2012). For example, using software packages that attempt to address the issue of detectability in monitoring projects (Mazerolle *et al.* 2007), such as Program MARK (White and Burnham 1999) or Program Distance (Thomas *et al.* 2010), is preferable to merely estimating relative abundances. Finally, methods need to be developed to eliminate introduced *I. iguana* populations, or at least to reduce their densities and limit their potential for spreading.

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