Adult Marine Iguana (*Amblyrhynchus cristatus*) from San Cristobal Island in the Galápagos Archipelago. *Photograph by Colette Adams.*

Conservation of Galápagos Marine Iguanas (*Amblyrhynchus cristatus*)

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Photographs by Martin Wikelski except where indicated.

Abstract.—Galápagos Marine Iguanas are highly abundant along many of the archipelago's shorelines. Total estimated population size varies between 37,000 and 280,000 individuals. Marine Iguanas have evolved in the absence of major predators, and their populations are regulated by cyclically recurring famine (El Niño) and feast (La Niña) events. Population declines are strongly density-dependent: the higher the population density, the higher the mortalities during El Niños (from 10–90%). Recovery after El Niños is rapid, as females compensate by reproducing younger and laying more eggs. Marine Iguana morphology differs between islands. Seven subspecies have been proposed, although only three major clades can be distinguished genetically. Twelve populations (approximately 74% of all Marine Iguanas) still live in pristine environments, whereas five populations (26% of all Marine Iguanas) suffer from anthropogenic influences. Major conservation problems arise from introduced predators (cats, dogs, rats, and pigs) and from combinations of natural events (El Niño) and anthropogenic disasters such as oil spills. The most recent oil spill in 2001 killed 62% of all Marine Iguanas on Santa Fe Island. Management requirements for the future include: (i) investigating population trends in Western Isabela and San Cristobal islands, (ii) investigating whether harbor areas are population sinks because of environmental contaminants, (iii) establishing a recovery program for oil-contaminated iguanas, especially their reinoculation with hindgut microsymbionts, and (iv) developing husbandry techniques and establishing a captive propagation program as a population backup plan (Marine Iguanas have not been bred in captivity).

Key Words: Marine Iguanas, *Amblyrhynchus cristatus*, South America, Galápagos Archipelago, Conservation, Oil Spill, Feral Predators

Introduction

When the Galápagos' most famous visitor, Charles Darwin, arrived on the rocky lava shores, he likened the islands to the entrance of Hell. He found myriads of "dirty black" Marine Iguanas (Darwin 1883). Young Charles found them "hideous in appearance, sluggish, stupid, and ugly." Nevertheless, like every modern visitor, he was fascinated by their sociality and their marine foraging style — Marine Iguanas are the only lizards known to feed exclusively on algae. Marine Iguanas live in dense clusters of up to 8,000 animals per kilometer of coastline. However, iguana colonies are distributed very patchily, and tend to occur only along the southwestern shores of the islands.

Amazingly, little has changed for Marine Iguanas on the uninhabited islands since Darwin's visit more than 170 years ago. However, although Marine Iguanas still occur in healthy population densities on the uninhabited islands, they face potentially serious threats on several inhabited islands.

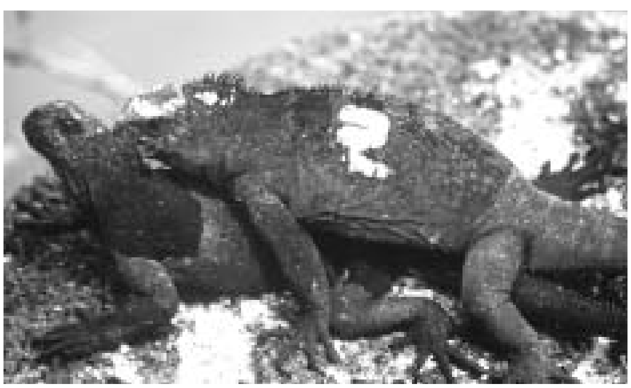
Marine Iguana Natural History

Marine Iguanas are endemic to the Galápagos Archipelago, which belongs to the Republic of Ecuador. They feed exclusively on marine algae in the rocky intertidal zone (Darwin 1883, Carpenter 1966, Trillmich and Trillmich 1986, Wikelski et al. 1993, Wikelski and Hau 1995, Drent et al. 1999). Marine Iguanas possess an internal biological clock that is synchronized to the tides. This clock cues them to walk to the intertidal zone every day at low tide, when the algae are exposed (Wikelski and

Male Marine Iguana on Seymour Norte Island eating Saltwort (*Batis maritima*) on land. Some individuals supplement their food with land plants.

Marine Iguanas in the intertidal zone on Genovesa Island during the low tide, grazing on green algae (mostly *Ulva* sp.). This population is the smallest in body size and males with body mass as little as 500 g are seen diving.

Two sneaker male Marine Iguanas on Genovesa Island attempt to forcefully copulate with a female outside of a territory (on sand). The territorial male (right) left his territory and interrupted the copulation attempt.



A satellite male Marine Iguana forcefully approaches a female to attempt copulation.

Hau 1995). The largest iguanas of each island population also dive for algae (2–30 m depth; Buttemer and Dawson 1993). On Genovesa, males with body mass >500 g are seen diving, whereas on Fernandina usually only males >3500 g dive for food (Wikelski and Trillmich 1994). A few individuals supplement their food with land plants, in particular on Seymour Norte Island. Only highly salty land plants are ingested (primarily Saltwort, *Batis maritima*, but also other coastal succulents such as *Sesuvium portulacastrum*), presumably because Marine Iguanas possess very specialized hindgut micro-symbionts that help them digest their food and effectively break up cell walls (Mackie et al. 2003).

Marine Iguanas reproduce once a year during a month-long mating season. The precise timing of the mating season coincides with the highest abundance and best quality of food (Rubenstein and Wikelski, in preparation). Because the nutrient-rich upwelling from the Cromwell current affects all islands in the archipelago differently, mating seasons occur at different times (e.g., December on Santa Fe and Genovesa, January on Santa Cruz, February/March on Española). During the mating season, males defend small territories that contain no resources other than the males themselves, which prompted the description of the mating system as a lek, or mating arena (Trillmich 1983, Wikelski et al. 1996). Male Marine Iguanas use three different mating strategies. The largest males defend territories and court females using a slow, stereotyped head-bob courtship behavior. Male mating success is highly skewed and depends on body size, condition, and display rate (Wikelski et al. 1996, 2001). Male territories are generally clustered, but single territories also occur. Satellite males are smaller than territorial males and roam around territories, attempting to (forcibly) mate with females. "Sneaker" males are the smallest males, physically indistinguishable from females. Sneakers try to copulate with females "in secret" on territories of large males (Wikelski and Bäurle 1996). These three mating tactics appear to be partially regulated by plasma levels of testosterone, and can be manipulated by hormone administration (Wikelski et al., submitted).

Receptive females generally copulate only once after they have selected a specific male, which they do after long periods of mate choice. Mate choice is apparently costly for Marine Iguanas, as indicated by mass loss of females that visit many males, compared to those that visit only a few males or mate in low-density areas (Wikelski et al. 2001). Females leave the mating area shortly after copulation to lay one to six eggs in deep burrows in sandy areas. Eggs incubate for three months (Laurie 1990; Laurie and Brown 1990a, 1990b). Some females guard their nests for a few days after egg-laying, mostly to defend against other females that try to dig at the same spot. The entire clutch amounts to about 20–28% of a female's body mass. Both males and females typically reproduce every other year, replenishing their energy reserves in the year they do not reproduce. However, during periods of food abundance, females may reproduce annually (Laurie 1990).

Marine Iguanas have only one natural predator, the Galápagos Hawk (*Buteo galapagoensis*), which is generally unable to prey on healthy adults. However, hawks can capture weakened adult iguanas, such as starving individuals or females exhausted by nesting. They also can learn to capture juveniles or hatchlings close to the shoreline (Boersma 1983; personal observation, Santa Fe Island).

Natural Population Regulation via El Niño Events

Unpredictably recurring El Niño events can dramatically reduce the abundance and diversity of marine algae — Marine Iguanas' only food source — and can cause mass starvation (Laurie and Brown 1990b). During El Niño events, the cold, nutrient-rich upwelling ceases and warm water from the Gulf of Panama flows toward the Galápagos. The normal food algae (red *Gelidium* and

Centroseras species or green *Ulva* species) disappear when water temperatures become too high and are replaced by brown algae. However, brown algae are not as easily digested by the Marine Iguanas' hindgut bacteria, and they may also be toxic. The result is widespread starvation of Marine Iguanas throughout the archipelago. Individual animals are affected differently — the largest animals starve first (Wikelski and Trillmich 1997, Wikelski et al. 1997), presumably because they have the highest absolute calorie requirements. Therefore, natural selection favors smaller animals during food shortages. Interestingly, Marine Iguanas can shrink their body size during El Niño events and survive such conditions better (Wikelski and Thom 2000). How such shrinkage is achieved physiologically or whether and to what degree bone loss is involved is not clear.

Marine Iguana populations can crash dramatically. During the El Niño of 1997–1998, about 90% of all Marine Iguanas on Seymour Norte Island disappeared, thus reducing population size on this island to less than 150 individuals (Wikelski and Wrege 2000, Romero and Wikelski 2001). A similar situation occurred on Genovesa Island in 1991–1994, reducing the total population size from about 15,000 to approximately 900 individuals. However, Marine Iguanas have survived such dramatic natural selection events throughout their evolutionary history and apparently adjust to such situations. As soon as nutritious red and green algae reappear after an El Niño ceases, individuals face plentiful intertidal and subtidal foraging grounds. Iguanas quickly replenish their fat reserves and return to good body condition. They reproduce more frequently (every year), at a younger age (mostly females), and lay larger clutches (e.g., three instead of two eggs). The "rules" by which Marine Iguanas determine whether to breed and how many eggs to lay are still unclear.

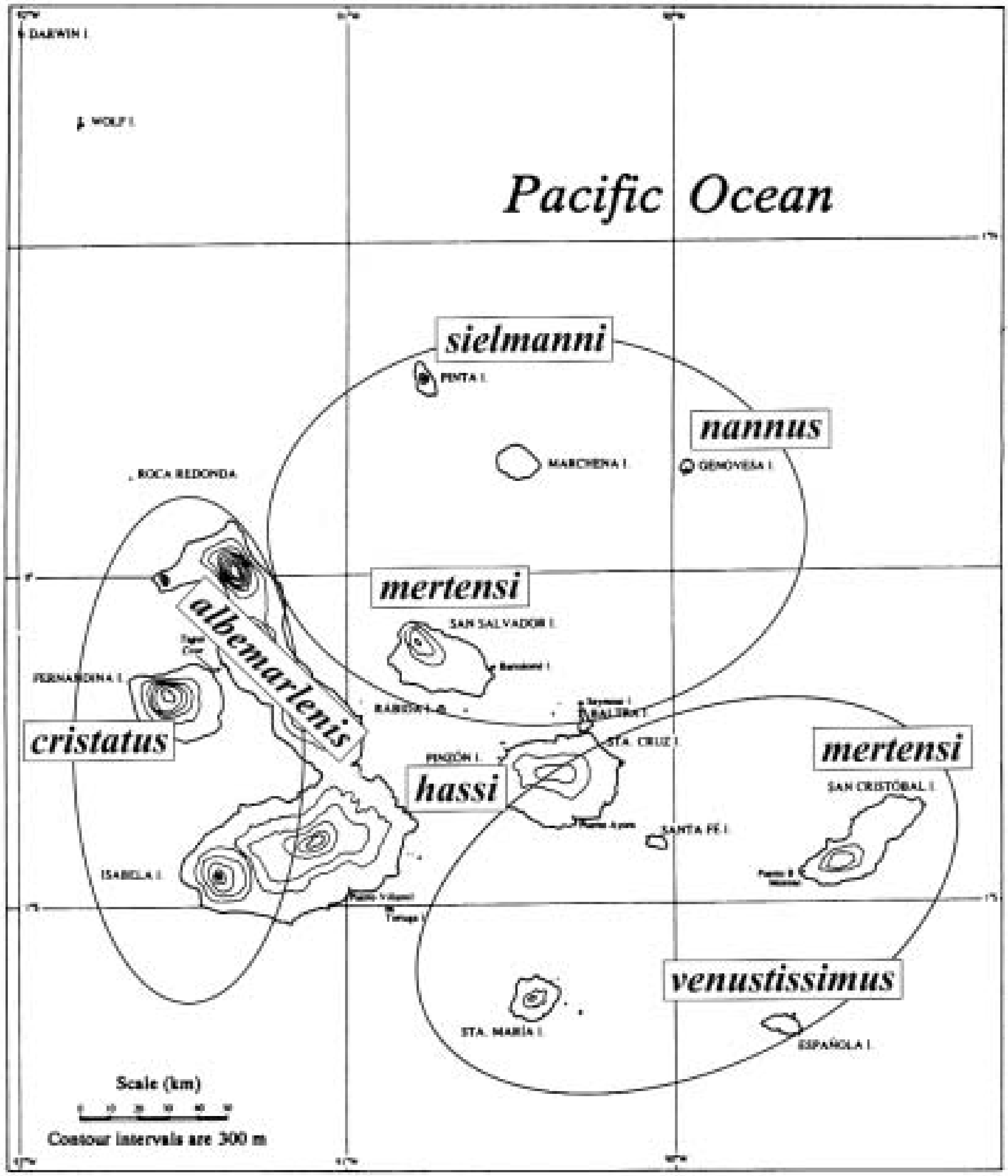
These adaptations allow Marine Iguanas to increase their numbers after dramatic population declines, such that mortality rates of 30–50% after an El Niño event can be compensated within four years. Even after enormously strong population declines (90%), Marine Iguanas congregate along the shoreline in small groups to reproduce (Wikelski et al. 1996). This gregariousness helps them to find each other after dramatic population declines that could otherwise cause individuals to scatter along the long lava shores of the islands.

Island Populations and Threats

Early naturalists discovered that not all Marine Iguana populations are alike (Fig. 1). For example, iguanas on Genovesa only grow up to a maximum of 900 g (subspecies: *A. c. nanus*, "the small ones"). Animals on Española are the most brilliant, at least during the mating season, when they display a bright red and green coloration (*A. c. venustissimus*). Fernandina iguanas have especially elaborate spines (*A. c. cristatus* subspecies). Although these populations differ very obviously on the phenotypic level, genetic dis-

Table 1. Rough estimate of Marine Iguana population sizes on the Galápagos Archipelago. Data are based on our own surveys, accounts by Galápagos guides, and data by Andrew Laurie (unpublished report to the Darwin Foundation, 1981). Minimum numbers indicate estimates for total island numbers after a strong El Niño famine. Maximum numbers indicate total numbers after several years of La Niña (cold, nutrient-rich) conditions. Maximum density estimates relate iguana numbers to the total size of the island. Please note that these are only very rough estimates.

ISLAND	SUBSPECIES	MINIMUM NUMBER	MAXIMUM NUMBER	MAXIMUM DENSITY (n/km^2)	THREATS
Fernandina	*cristatus*	15,000	120,000	187	Oil spill
Isabela	*albemarlensis*	5,000	40,000	9	Oil spill, dogs, cats, rats, pigs
Santa Fe		3,000	16,000	667	Oil spill
Floreana		2,000	16,000	92	Oil spill, cats, rats, pigs
Santa Cruz	*hassi*	2,000	13,000	13	Oil spill, dogs, cats, rats, pigs
Española	*venustissimus*	1,700	21,000	350	Oil spill
Genovesa	*nanus*	900	15,000	1071	Oil spill
Marchena		1,000	10,000	77	Oil spill
Pinta	*sielmanni*	800	6,000	100	Oil spill
Santiago	*mertensi*	450	4,000	7	Oil spill, cats, rats
Wolf		400	1,500	1154	Oil spill
Darwin		200	800	727	Oil spill
Pinzon		200	900	50	Oil spill
Rabida		200	2,000	408	Oil spill
Seymour Norte		100	1,500	789	Oil spill
San Cristobal		50	400	1	Oil spill, cats, rats, pigs
Remaining islands		2,000	10,000	NA	Oil spill
TOTAL		**~37,000**	**~280,000**		



Schematic map of the Galápagos Archipelago and the different subspecies of Marine Iguanas as described by Eibl-Eibesfeldt (1962; inset subspecies names). Superimposed (ovals) are the three genetically similar clades, based on nuclear and mitochondrial genetic analysis (Rassmann et al. 1997). Genetic and morphological information is not entirely compatible, indicated, for example, by the fact that the *Amblyrhynchus cristatus mertensi* subspecies is found in two genetically distinct clades (on San Cristobal and Santiago islands).

tinction of "subspecies" is less clear (Fig. 1; Rassmann 1997, Rassmann et al. 1997). Marine Iguanas reached the Galápagos archipelago as early as 10–15 million years ago. They presumably arrived by "leap-frogging" across now-sunken islands that are only detectable as sea mounts between the present-day Galápagos Islands and the South American mainland. From those early Galápagos Islands, Marine Iguanas dispersed to the present islands and split into northwestern, central, and southeastern clades.

Interestingly, the northwestern clade includes both the largest (on southwestern Isabela) but also fairly small iguanas (on Pinta), indicating that strong selection on body size is present, although not apparent in the genetic markers that were investigated (Rassmann et al. 1997). These distinct inter-island differences obviously indicate that all island populations should be conserved, although no immediate threat exists to most island populations. However, even the most pristine populations may suffer immediately and heavily from environmental disasters such as an oil spill, even if the contamination levels are very minor (Wikelski et al., in preparation; Charles Darwin Research Station, unpublished report on the January 2001 oil spill). On Santa Fe, approximately 60% of the entire Marine Iguana population disappeared as a consequence of low-level oiling when

Galápagos Hawk killing a hatchling Marine Iguana on Santa Fe Island.

the oil tanker "Jessica" ran ashore on nearby San Cristobal Island and spilled about 750,000 gallons of diesel and bunker oil. Consequently, oil contamination could pose a serious threat to all populations of Galápagos Marine Iguanas, even those that live far from human settlements and would otherwise be considered pristine. As to the specific mechanism of mortality, we suggest that hindgut endosymbionts are highly susceptible to oil in their digestive substrate. Marine Iguanas need these bacteria to digest algae fully, a process that can take up to two weeks. These specialized and highly effective gut bacteria probably suffered heavily due to the oil spill, which in turn caused failed digestion and widespread starvation among Marine Iguanas.

On at least five islands, Marine Iguana populations also are heavily impacted by human-introduced predators (Cayot et al. 1994). The most important predators are feral cats, dogs, rats, and pigs. We are currently uncertain whether those Marine Iguana populations already affected are jeopardized to an extent that their long-term survival is in question. Some populations on certain parts of western Isabela Island appear to be in immediate danger of extinction. During several research expeditions, we only found adult iguanas and very few young or hatchlings, indicating almost no recruitment, at least not along the shoreline of the main island. Nevertheless, some hatchlings and yearlings were seen on small offshore islets. A similar situation applies to Marine Iguanas on San Cristobal Island, where only several hundred iguanas survive. Thus, we would classify these populations as highly endangered, and recommend that immediate action be taken.

Management Needs for the Future

Four major problems exist for Marine Iguana populations, and we recommend the following conservation-related research projects to determine the causes of the threats and to elaborate possible solutions:

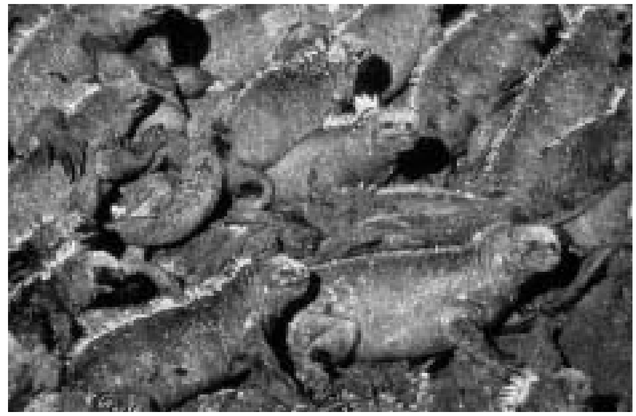
(i) We need to study population trends and identify threats to Marine Iguanas at sites where iguanas show no apparent recruitment. Those sites include western Isabela and San Cristobal Islands as mentioned above. We presently do not know where and when reproduction occurs, which predators are preventing recruitment of hatchlings, and to what degree big mammalian predators are responsible for the observed lack of recruitment. The most desirable conservation project would be to habituate feral cats to the presence of a researcher and follow them along their daily activities (H. Snell, personal communication). Such data would reveal the dangers that feral cats pose to Marine Iguanas and would allow us to study the impact of these fierce predators on other endangered coastal species. Dog predation could be a problem on other islands like San Cristobal, and this also needs further investigation (Kruuk and Snell 1981).

(ii) The second important project is to study the impact of human habitation and low-level environmental contamination on Marine Iguanas. We are particularly concerned about oil residues from boats around human settlements (e.g., the towns of Puerto Ayora on Santa Cruz Island and Villamil on Isabela Island). We currently do not know if areas around human settlements should be considered population sinks for Marine Iguanas or whether such areas still produce sufficient recruits to be considered viable populations. Based on the current information about the effects of a low-level oil spill in 2001, Marine Iguanas in oil-impacted areas conceivably will suffer long-term effects. Furthermore, our own observations in and around Puerto Ayora (the main harbor town on Santa Cruz Island) suggest that many of the hatchlings that pass through the town after hatching disappear from the harbor area, and may die due to human (or feral animal) actions. A long-term mark/recapture program could resolve such questions.

(iii) A third area of high interest for the management of Marine Iguanas is the planning and establishment of a program for rehabilitation of Marine Iguanas. This would include indi-

Adult female Marine Iguana from Genovesa Island; this single egg was laid about two hours prior to taking this picture.

Comparing two Marine Iguanas on Santa Fe Island showing how much individual iguanas can shrink. The iguana on the left could shrink in body length to the size of the individual on the right during an El Niño.



Bachelor male Marine Iguanas from Fernandina Island. Note the elaborate spines that are very prominent in this population of large individuals. On Fernandina, diving males usually exceed 3500 g.

viduals that suffered low levels of environmental contamination. Hindgut microbes probably die during anthropogenic disasters such as oil spills, and Marine Iguanas subsequently starve. Such a situation is comparable to what happens to other vertebrates when endogenous gut symbionts are eliminated, for example, by chemical contamination or antibiotic medication. In such situations, the gut fauna can be reinoculated using pills containing spores of endogenous gut symbionts. The horizontal transfer of gut symbionts from unaffected to affected individuals also is possible in Marine Iguanas. Thus, once we have established how many and what kind of hindgut endosymbionts Marine Iguanas possess, and how such symbionts work, researchers presumably could collect gut material from healthy individuals and treat suffering individuals.

(iv) The fourth and potentially most difficult research activity for the conservation of Marine Iguanas would be to try to breed animals in captivity. Astonishingly, this has never been attempted, and we are unsure whether it is even possible. The challenges for holding and breeding Marine Iguanas in captivity are manifold. First, Marine Iguanas have very specific dietary requirements. Only certain types of seaweed are preferred and eaten — as soon as the natural algae composition changes, we find dramatic mortality rates in the wild. Second, although early naturalists removed several Marine Iguanas from the Galápagos Islands and brought them into zoos, none of those iguanas ever tried to reproduce. Nevertheless, several Marine Iguanas were maintained for more than ten years. Marine Iguanas have a different breeding system than most other iguanids, and a fairly large colony may be required in order to stimulate mating activities. At the same time, we do not know how hatchling Marine Iguanas survive their first months, how they acquire their endogenous hindgut microsymbionts, and how they become recruited into the population. Marine Iguanas are the only Galápagos animal about which we are uncertain whether they can be kept and bred in captivity, should such a need arise. We would like to remind the reader critical of any effort to remove individuals from the wild that a combination of a strong El Niño event and even small-scale anthropogenic disasters (like a low-level environmental contamination) could effectively wipe out an entire island population. If our aim is to conserve each island population of Marine Iguanas because of their distinctive differences, we should seriously consider developing the husbandry practices necessary to rear Marine Iguanas in a captive setting.

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Dead Marine Iguana on Fernandina Island during the 1998–99 El Niño period. The likely cause of death was starvation.

Martin Wikelski holding a large male Marine Iguana on western Isabela Island.

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