



Tail Bifurcation in a Marine Iguana, *Amblyrhynchus cristatus* (Reptilia: Squamata: Iguanidae), from Isla Santa Cruz, Galápagos Islands

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Autotomy is an animal's ability to voluntarily amputate a specific body part, limb, or appendage (Bateman and Fleming 2009). Caudal or tail autotomy, considered an ancestral trait in most squamate families, is used frequently as a defensive strategy against predators (Bateman and Fleming 2009). Most lizards are able to regenerate amputated tails, and most species possess adaptations that both limit tissue damage in response to injury and initiate coordinated regenerative responses (Lozito and Tuan 2017). Lizards capable of tail autotomy possess caudal vertebrae with breakage planes, preformed areas of weakness that enable the tail to detach or self-amputate when external pressure is applied (Etheridge 1967). Regeneration is important following caudal autotomy (Clause and Capaldi 2006; Gilbert et al. 2013), as it ensures the cost of temporarily losing the tail will not affect the long-term health or mobility of the individual.

Research has demonstrated that some iguanids are able to autotomize their tails during early ontogeny but lose

that ability with age (e.g., *Iguana iguana*; Etheridge 1967). However, although present in many iguanids, fracture planes do not occur in Fijian Iguanas (*Brachylophus* spp.), Galápagos Land Iguanas (*Conolophus* spp.), the Lesser Antillean Iguana (*Iguana delicatissima*), and the Marine Iguana (*Amblyrhynchus cristatus*) (Pregill and Worthy 2003). A loss of fracture planes and an inability to autotomize the tail appears to be related to adaptations involving tail specializations that are critical to survival (Fleming et al. 2013). Losing a specialized tail could result in a loss of tail function and incapacitation until regeneration occurs, thus rendering autotomy more costly than beneficial (Arnold 1984).

Eleven subspecies of *A. cristatus* occur separately on thirteen islands in the Galápagos Archipelago (Miralles et al. 2017) and all were believed to be incapable of caudal autotomy. Tail regeneration and bifurcation was reported only recently in two individuals in the subspecies *A. cristatus cristatus* from Isla Fernandina and *A. cristatus hassi* from Isla Santa



Fig. 1. An adult Marine Iguana (*Amblyrhynchus cristatus*) with a bifurcated tail basking in close proximity to another adult on a dock in Puerto Ayora on Santa Cruz Island, Galápagos. Photograph © Cristina Arrivillaga.

Cruz (Barr et al. 2019). Herein we describe a third instance of tail regeneration and bifurcation, also in *A. cristatus hassi* from Isla Santa Cruz.

At 1000 h on 4 August 2019, CA observed approximately 30–40 Marine Iguanas basking on a dock in Puerto Ayora, Santa Cruz Island (0.7433°S, 90.3157°W), and noticed that one individual had a bifurcated tail (Fig. 1). That iguana appeared to be missing slightly more than half of its tail, which had begun regenerating as two distinct branches. Other than the broken tail, the lizard appeared to be healthy and exhibited no obvious signs of malnourishment. Although smaller than another adult in close proximity, the difference in size could be attributable to that individual being either a female or a subadult. Alternatively, because we do not know when the original injury occurred, a tail break during early ontogeny could have stunted growth by limiting the lizard's ability to swim and forage. Unfortunately, because we did not have permission to collect morphometric data, we were unable to confirm that individual's health, age, or sex.

Marine Iguanas forage underwater for algae and possess laterally compressed tails that do not differ substantially from those of terrestrial relatives but are crucial for swimming and diving (Dawson et al. 1977; Bedford and Christian 1996). Tails are thought to be indispensable for survival; however, the individual we encountered did not show obvious signs of malnourishment, leading us to assume that its broken tail had relatively little effect on its ability to survive. During El Niño events, the disappearance of high-quality algal food reserves has resulted in 90-percent declines in some populations of Marine Iguanas (Laurie 1990); so, some evidence

suggests that limited access to those resources can be fatal. This individual might have been able to survive by foraging on intertidal algae exposed during low tides (Shepherd and Hawkes 2005). Also, during times of food scarcity, Wikelski and Wrege (2000) indicated that iguanas expanded their diets by scavenging on the feces of sea lions and conspecifics, regurgitated material, and sea lion afterbirths, as well as by occasionally consuming land plants. Individuals disabled by broken tails, even if partially regenerated, might be forced to exploit a more opportunistic and unconventional diet.

Tail regeneration and abnormalities such as bifurcation have been described in many species of lizards, including iguanas (e.g., Spiny-tailed Iguanas, *Ctenosaura* spp.) that exhibit caudal autotomy (Hayes et al. 2012; Conzedy et al. 2013; Ariano-Sánchez and Gil 2016; Koleska et al. 2017). Malformations usually are associated with regeneration failures following injuries or incomplete tail breakage, as opposed to congenital malformations (Lynn 1950; Conzedy et al. 2013). As in other lizards, tail breakage in iguanids can be the result of intraspecific aggression due to crowding (Perez-Buitrago et al. 2010), sexual aggression during mating (Iverson et al. 2004), or failed predation attempts (Hayes et al. 2012).

We believe crowding and intraspecific competition are unlikely to be responsible for tail loss in *A. cristatus*. Despite considerable research on this topic (e.g., Eibl-Eibesfeldt 1966; Raunch 1988), tail loss and regeneration has only recently been described in this species. Marine Iguanas live in colonies of as many as 500 individuals (Trillmich 1979) and crowding (Fig. 2) is not only inevitable but apparently essential. During



Fig. 2. An agglomeration of Marine Iguanas (*Amblyrhynchus cristatus*) at Tortuga Bay, Santa Cruz Island. Photograph © Cristina Arrivillaga.

the day and especially at night, Marine Iguanas agglomerate in groups of as many as 50 individuals in order to conserve heat (Jackson 1993). Intraspecific aggression has been observed in egg-laying females and territorial males during the breeding season (Eibl-Eibesfeldt 1966; Rauch 1988), but territorial fights between males rarely result in injuries as they consist more of head thrusts than biting (Eibl-Eibesfeldt 1966). Females, however, are more aggressive when defending their nest sites and will frequently bite opponents (Eibl-Eibesfeldt 1966). Knapp (2000) demonstrated that female iguanids that defend nests have higher tail-breakage frequencies. That said, when possible, reproductively active female Marine Iguanas usually avoid fighting to conserve energy (Rauch 1988).

Considering their typical socially tolerant behavior, we believe that failed predation attempts are the primary reason for tail loss in *A. cristatus*. Prior to the arrival of humans in the archipelago, Marine Iguanas had only one natural predator, the Galápagos Hawk (*Buteo galapagoensis*), which probably colonized the Galápagos less than 300,000 years ago (Bollmer et al. 2006). However, hawks prey mostly on juveniles (Bollmer et al. 2006; Berger et al. 2007) and do not constitute a significant predatory threat to populations. In the last century or so, however, predation on Marine Iguanas likely has increased drastically owing to the human introduction of predators such as feral dogs, cats, rats, and pigs (Kuuk and Snell 1981; Cayot et al. 1994; Wikelski and Nelson 2004; Nelson et al. 2004).

The dock at Santa Cruz on which the senior author observed the *A. cristatus* with a bifurcated tail is a prime example of an urban coastal habitat utilized by this species. Santa Cruz has the highest human population of any island in the archipelago, and along with Isabela, has suffered the greatest human impact (Watson et al. 2010). Although feral cats have been reported on those islands, as well as on Floreana, San Cristóbal, and Baltra (Cayot et al. 1994), a considerable population of feral dogs on those islands is among the most visible sources of predation on the endemic fauna (Anonymous 1976; Kuuk and Snell 1981; Barnett and Rudd 1983). However, the greatest declines in populations of native vertebrates in the islands are attributed to invasive Black Rats (*Rattus rattus*) (Harris et al. 2006).

Hayes et al. (2012) demonstrated that tail-break and furcation frequencies are significantly higher in populations of West Indian Rock Iguanas (*Cyclura* sp.) that coexist with invasive rodents (i.e., *R. rattus*). They also concluded that failed predation attempts, rather than intraspecific aggression, were the primary cause of tail breaks. Injuries caused by rats typically cause irregular or incomplete tail breaks (Hayes et al. 2004), possibly due to rats gnawing on the tails of iguanas while they sleep at night. Such irregularities or incompletely broken tails are more likely to result in abnormal tail regeneration and furcation (Hayes et al. 2012; C. Knapp, pers. comm).

We suggest that the fact that Marine Iguanas with broken tails and furcation have been observed on anthropogenically threatened islands with high populations of invasive mammals is no coincidence. Prior to the introduction of non-native predators, Marine Iguanas experienced very low predation pressure for 5–15 myr and hence exhibit relatively little anti-predator behavior (Rödl et al. 2006; Berger et al. 2007). Nonetheless, Berger et al. (2007) proposed that, even with an absence of predators for several million years, *A. cristatus* could rapidly develop or possibly resurrect anti-predator defenses.

Adults previously observed with bite marks on their tails did not show any type of breakage or obvious regeneration; instead, open wounds apparently resulted in serious infections and even necrosis in large areas of their bodies that eventually caused their deaths (Berger 2006). This suggests that tail breakage in Marine Iguanas until recently has been an infrequent occurrence. As regeneration appears to be infrequent in *A. cristatus*, perhaps it is an adaptive trait that is expressed only under certain environmental conditions. Tail breakage in the Lesser Antillean Iguana (*Iguana delicatissima*), which (like *A. cristatus*) lacks caudal fracture planes, was first observed by Knapp et al. (2016) and tail regeneration and malformation by Koleska and Jablonski (2018). These similar observations tend to support the hypothesis of Barr et al. (2019), who proposed that the loss or lack of tail autotomy does not necessarily imply the disappearance of regenerative abilities. Consequently, if the regenerative ability of these iguanas has been dormant, the recent introduction of predators and the resultant increase in predation pressure might have triggered a reexpression of the trait. Because both *A. cristatus* and *I. delicatissima* have been subjected only relatively recently to novel predators such as rats, cats, and dogs (Powell 2004; Wikelski and Nelson 2004; Harris et al. 2006), we suggest that the recent reports of tail breakage and bifurcation are associated with increases in predation pressure.

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