

Survivors of St. Croix: limb loss and abnormal tail regeneration in *Anolis acutus* Hallowell, 1856

Nicole Stevens^{1,2,*}, Elizabeth J. Connor², Madison Thompson², Abigail Torres², and E. Griffin Nicholson^{1,2}

Observations of appendage loss or damage, such as that of tails, toes, or limbs, can provide insight into selective pressures exerted on vertebrate populations (Barr et al., 2020; Stroud et al., 2025). In lizards, caudal autotomy has evolved to distract predators and directly free the animal from capture (Vitt et al., 1977; Arnold, 1984). While the missing appendage generally regrows to mitigate long-term impacts to locomotion, abnormalities in the tail regeneration process sometimes occur and may have fitness costs (Caicedo-Martínez et al., 2022; Nunes, 2024). Limb and digit loss are also recorded in lizard populations and may result from predation attempts (Hudson, 1996) or intraspecific competition (Vervust et al., 2009). These losses may have adverse effects such as decreased clinging ability in arboreal lizard species (Bloch and Irschick, 2005).

Limb loss and subsequent healing of injuries have been documented in at least 58 lizard species (Stroud et al., 2025), and loss of digits has likely occurred in many others (Hudson, 1996). Many of the lizards in these cases remained agile even while missing an appendage (Stroud et al., 2025). Thus, not only are these morphological changes potential indicators of selective pressure, but the surprising fitness of these individuals may indicate variation in natural selection or that the lizards are performing compensatory behaviour to overcome detrimental impacts (Barr et al., 2020; Stroud et al., 2025). Adding to our understanding of the frequency and implications of these abnormalities and injuries in lizards, we report the first observations of abnormal tail regeneration, digit loss, and limb loss in the St. Croix Anole (*Anolis acutus*).

Anolis acutus is the only anole species in St. Croix, the largest of the U.S. Virgin Islands, and can be found from ground level to the high canopy (Ruibal and Philibosian, 1974b). It has not been assigned an ecomorph but is most closely related to trunk-crown ecomorph species (Losos, 2009). Up to 80 individuals can be found in a single tree, and there may be 2000–5600 lizards per hectare (Ruibal and Philibosian, 1974b). This high-density species has a small territory size, and frequent aggressive encounters are observed in both males and females (Ruibal and Philibosian, 1974a). Limited research has been published on *A. acutus* in recent years, but it has been noted that this species is insectivorous and consumes fruit (Stevens, 2024).

We collected individuals of *A. acutus* on St. Croix from 18 July–4 August 2025. We captured at least 30 individuals from each of our eight sites, four of which were on the main island. The other four sites were the offshore islands of St. Croix (Ruth Cay, Protestant Cay, Green Cay, and Buck Island). Most sites had little to no anthropogenic modification, but Protestant Cay has hotel grounds that cover much of the island and receives frequent visitors. Additionally, Altona Lagoon has a high volume of visitors, invasive plant species, and built structures.

Of the 249 captured *A. acutus*, 68 had regenerated tails (27.3%). One of these individuals, a male captured on Ruth Cay (17.6838°N, 64.7622°W; elevation 2 m) on 3 August 2025, had two areas of regeneration, indicating that it had autotomised and regrown its tail on at least two separate occasions (Table 1; Fig. 1G). When lizards autotomise their tails, the tail either splits off at a breakage plane in the vertebrae or splits between the vertebrae, and the regenerated section grows back as a cartilaginous rod (Bateman and Fleming, 2008). Therefore, subsequent breakages usually occur closer to the body where the vertebrae remain intact. However, it has been shown that, at least in some lizard taxa, a breakage in the cartilaginous regrowth section of the tail can still result in tail regeneration (Lozito and Tuan, 2017). This phenomenon was initially considered rare

¹ Ecology and Evolutionary Biology Program, Texas A&M University, College Station, Texas 77843-2258, USA.

² Department of Ecology and Conservation Biology, Texas A&M University, College Station, Texas 77843, USA.

* Corresponding author. E-mail: nstevens@tamu.edu

Table 1. Morphological abnormalities in *Anolis acutus* surveyed at various sites on St. Croix, U.S. Virgin Islands, and its offshore cays. Photos for each observation can be found in Fig. 1, with letters indicating the connection between images and associated data.

Photo	Observation	Date	Location	Human Impact	Sex	SVL (mm)	Weight (g)
A	Missing tip of 4 th digit on left front limb	29 Jul 2025	Protestant Cay	High	M	63	4.3
B	Missing entire 4 th digit on left front limb	29 Jul 2025	Protestant Cay	High	F	46	2.1
C	Missing tip of 4 th digit on left hind limb	4 Aug 2025	Green Cay	Low	M	63.5	5.5
D	Missing entire 4 th digit on left hind limb	30 Jul 2025	Sandy Point	Low	F	44	1.8
E	Additional growth on side of tail	28 July 2025	Protestant Cay	High	F	48	2.0
F	Missing entire left hind limb below knee	3 Aug 2025	Ruth Cay	Low	F	46.5	2.2
G	Two sections of measured tail regeneration (second section is re-regeneration)	3 Aug 2025	Ruth Cay	Low	M	61	5.5

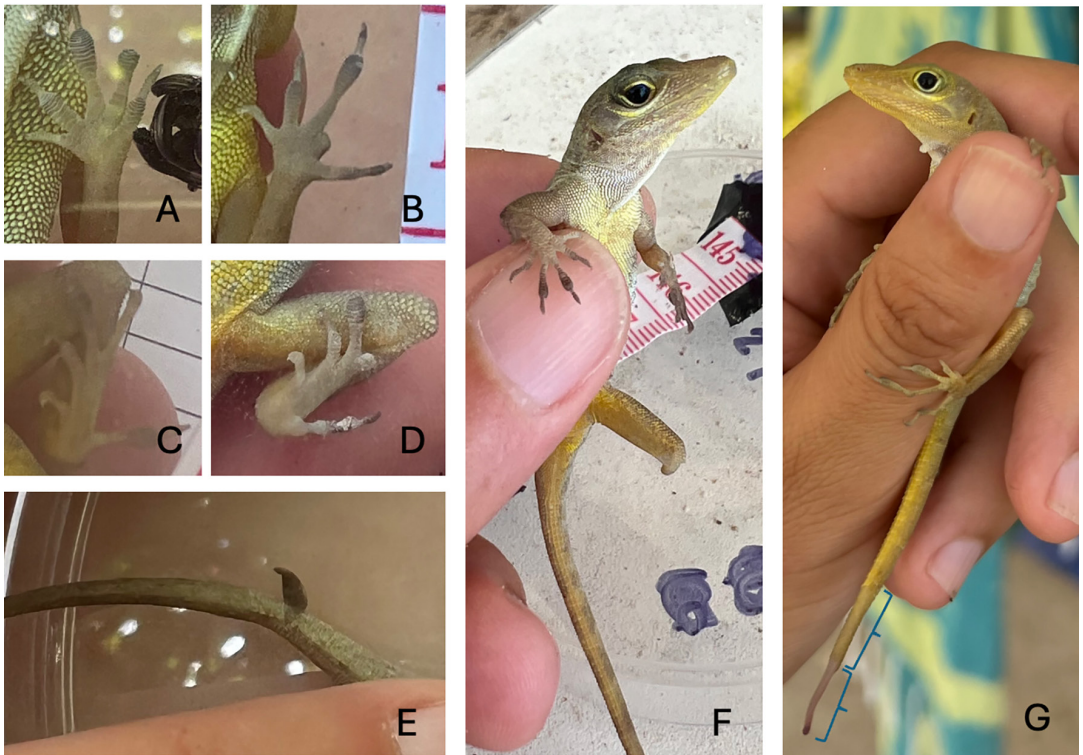


Figure 1. Observations of *Anolis acutus* with toe and limb injuries and aberrations in tail regeneration from St. Croix, U.S. Virgin Islands. (A) Male anole missing nail and tip of fourth digit on left front limb. (B) Female anole missing entire fourth digit on front limb. (C) Male and (D) female anoles missing at least entire toepad on fourth digit of left rear limb. (E) Additional growth on regenerated tail on female lizard. (F) Female anole missing entire left rear limb below the femur. (G) Male anole with two areas of tail regeneration (original regeneration and re-regeneration) marked in blue. Photos by Nicole Stevens.

but may not be as uncommon as initially thought. For example, in a study across three populations, 17.2% of King's Skinks (*Egernia kingii*) were found to have multiple areas of "re-regeneration" (Barr et al., 2019). Doubly regenerated tails have been recorded previously in Brown Anoles (*Anolis sagrei*) (Kamath, 2024a, b) but not yet in *A. acutus*. The ability to re-regenerate tails may help lizards better withstand predation or intra-specific aggression (Barr et al., 2019), both of which are common in *A. acutus*.

Another individual with tail regeneration, a female lizard captured on Protestant Cay (17.7497°N, 64.7030°W; sea level) on 28 July 2025, had an additional growth on the side of its tail (Table 1; Fig. 1E). The total tail length of this individual was 49 mm, with primary regrowth measuring 30.5 mm and the short fork measuring 3.5 mm. It appeared that the animal had a small injury that resulted in the short fork of additional regeneration. Thus, the abnormal tail regeneration was likely caused by incomplete caudal autotomy at this location. This observation of abnormal tail regeneration in *A. acutus* meets the definition of bifurcation, which is the most common type of caudal abnormality (Barr et al., 2020; Baum and Kaiser, 2024). *Anolis acutus* is now the 11th *Anolis* species to be recorded with abnormal tail regenerations (Baum and Kaiser, 2024) out of 435 total *Anolis* species (Uetz et al., 2025). While ecological impacts generally remain unknown, it has been suggested that abnormal tail regeneration may affect locomotion, intraspecific signalling and competition, and anti-predation behaviour (Barr et al., 2020).

Our observation of tail bifurcation was from our most anthropogenically modified site, Protestant Cay. The cause of this tail bifurcation appears to have been a predation attempt, since abnormal regeneration generally results from incomplete caudal autotomy or caudal wounds (Barr et al., 2020). Interestingly, the St. Croix Ground Lizard (*Pholidoscelis polops*), an endangered lizard found only on the offshore cays of St. Croix, also only had tail bifurcations observed on Protestant Cay (Angeli, 2012). The causes of these injuries were likely either from intraspecific conflict or predatory pressure. Invasive rats (*Rattus rattus*) may be found on Protestant Cay (Angeli, 2012) but were not trapped during recent surveys (Stevens, unpublished data). However, other predators, like birds, remain in the area. Predator inefficiency often results in incomplete caudal autotomy and caudal injuries that result in abnormal tail regeneration, as efficient predators would have consumed the entire animal (Schoener, 1979;

Bateman and Fleming, 2011; Winchell et al., 2019). Lizard behaviour may also affect predation efficiency as more obvious lizards are more susceptible to predators (Bateman and Fleming, 2011). Therefore, it is possible that the predators at Protestant Cay may be less efficient or lizards may be more obvious, but further research is needed to draw more detailed conclusions.

In addition to the lizards with abnormal tail regeneration, we also captured four anoles with toe damage or loss (Table 1; Fig. 1A–D). As we only measured morphology on the left side of the lizards, this is likely not an exhaustive list of all digit damage or loss from our captured lizards. However, these numbers do represent all animals that had damage to or had lost the fourth digit of either of the left limbs. Thus, our data represents the rate of these injuries across our sites. Our observations include two individuals (a male and a female) from Protestant Cay (17.7497°N, 64.7030°W; sea level) on 29 July 2025 (Fig. 1A, B). Both digit losses were of the fourth digit of the left front limb. We also recorded two observations of loss of the fourth digit of the rear left limb: a male on Green Cay (17.7649°N, 64.6664°W; elevation 4 m) on 4 August 2025 and a female at Sandy Point National Wildlife Refuge (17.6805°N, 64.8947°W; elevation 4 m) on 30 July 2025 (Table 1; Fig. 1C, D).

Additionally, we captured a female *A. acutus* on Ruth Cay (17.6838°N, 64.7622°W; elevation 2 m) on 3 May 2025 that was missing its entire left hindlimb below the knee (Table 1; Fig. 1F). This individual was found on top of a wooden table and sprinted away rapidly upon release. Therefore, despite its limb loss, this individual was quite agile and a proficient climber, which aligns with observations made by Stroud et al. (2025). All animals with toe or limb loss appeared in good physical condition and had body measurements consistent with other captured individuals (Stevens, unpublished data). The only individual with toe or limb loss that had a regenerated tail was the male from Green Cay (37 mm of the 79 mm total tail length was regenerated), and we found no relationship between toe/limb loss and tail loss in anoles from across our sites (Fisher's Exact Test, odds ratio = 1.69, $p = 1.0$).

Similar to our abnormal tail regeneration observation, we found that digit/limb damage and loss were higher in Protestant Cay (5.7% of anoles) than the mostly undisturbed sites of Green Cay, Ruth Cay, and Sandy Point ($3.3 \pm 0.1\%$ of anoles). However, at a broader comparison, we did not find a significant difference in limb injury frequencies amongst sites we categorized

as undisturbed ($n = 6$; median frequency = 1.6%) and disturbed ($n = 2$; median frequency = 2.9%; Mann-Whitney Test, $W = 4.5$, $p = 0.72$). Thus, though we were limited in scope with our number of disturbed sites, our observations resemble findings from a previous study on Puerto Rican Crested Anoles (*Anolis cristatellus*) that also found appendage damage and loss to be rare but higher in urban environments (Winchell et al., 2019).

We found only forelimb injuries in anoles from Protestant Cay and only hindlimb injuries from undisturbed sites. It is possible that forelimb injuries occur more frequently from intraspecific aggression and that hindlimb injuries generally result from predation attempts, though this is not always the case. If true, this difference between sites may reflect differences in selective pressures (Winchell et al. 2019). In contrast to our abnormal tail observation, this may suggest that *Anolis acutus* on Protestant Cay and other disturbed sites face less predation, while lizards at more natural sites have less intraspecific competition. This corroborates findings that urbanised sites have less evenly spaced resources, more competition, and higher predator exclusion (Winchell et al., 2019).

However, the difference in frequency of forelimb injuries was not significant when we compared only disturbed and undisturbed sites (Mann-Whitney Test, $W = 3$, $p = 0.15$). The difference in frequency of hindlimb injuries was also not significant (Mann-Whitney Test, $W = 9$, $p = 0.34$). Interestingly, we did not find any limb or toe injuries in any of the anoles from our sites ($n = 2$) that had some anthropogenic disturbance but not enough to be considered disturbed. This could possibly indicate intermediate disturbances decrease both predation and competition in these lizards, though additional data collection is warranted to adequately draw conclusions.

Natural selection is often expected to work against individuals with morphological abnormalities and injuries, and in many situations, it likely does (Stroud et al., 2025). However, many lizards that experience limb loss (53% of which are loss of the rear limb like our observation in *A. acutus*) remain fast and agile, posing interesting questions about the influence of natural selection (Stroud et al., 2025). Abnormalities may not affect individuals as much as predicted. Studies suggest that toe loss has minimal effects on running speed in terrestrial lizards (Borges-Landáez and Shine, 2003), and climbing species do not have significantly lower incidence of natural toe loss (Hudson, 1996). Similarly, many lizards with abnormal tail regenerations have been observed to be healthy individuals (Baum and

Kaiser, 2024). However, lizards may be adjusting behaviour to compensate for detrimental effects, or natural selection may not be acting on the abnormalities in an omnipresent way. Natural selection could be episodic or probabilistic (Stroud et al., 2025). Our new records of abnormal tail regeneration and limb and digit loss in *A. acutus* provide further context for the occurrence of these conditions in lizards and further indicate that the influence of abnormalities on fitness and natural selection should be explored.

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