REPTILES & AMPHIBIANS

Current Status and Natural History of the Critically Endangered Variable Harlequin Toad (*Atelopus varius*) in Costa Rica

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Abstract.—The Variable Harlequin Toad (*Atelopus varius*) has suffered extensive declines in Panama and Costa Rica. Of 169 previously documented populations, only seven are known to survive. Herein we review the status of the surviving populations of this species in Costa Rica, describing the results of random visits to five of the seven surviving populations during the last six years, novel information on the natural history of three of these, and the results of a monitoring program of one continuous year on one of them. We identify three distinct morphs that might be the only survivors of what once was a wide array of phenotypic color patterns.

Resumen.—El sapo arlequín variable (*Atelopus varius*) ha sufrido una grave disminución de sus poblaciones en Panamá y Costa Rica. Revisamos aquí las poblaciones sobrevivientes de esta especie en Costa Rica. De 169 poblaciones conocidas, actualmente sólo se conocen siete supervivientes. Se han realizado visitas casuales a cinco de las siete poblaciones supervivientes durante los últimos seis años, y se ofrece información novedosa sobre la historia natural en tres de ellas y un programa de monitoreo en una de ellas. También se definen tres morfos distintos y posiblemente sean los únicos supervivientes de una amplia gama de coloraciones fenotípicas de la especie en el país.

Of the 96 known species of Neotropical anurans in the genus *Atelopus* (Frost 2021), a search of the IUCN Red List of Threatened Species (https://www.iucnredlist.org/search/list?query=Atelopus&searchType=species) listed two as extinct and 78 as critically endangered or endangered, making this by far the most threatened genus of anurans in the Neotropics (La Marca et al. 2005). Of the four Costa Rican species of *Atelopus* (Savage 2002; Savage and Bolaños 2009; Köhler 2011), the high-elevation Chiriqui Harlequin Toad (*A. chiriquiensis*) and Pass Stubfoot Toad (*A. senex*) are listed as extinct (EX), the higher-elevation Chirripó Harlequin Toad (*A. chirripoensis*) as data deficient (DD), and the low- to mid-elevation Variable Harlequin Toad (*A. varius*) as critically endangered (CR) on the IUCN Red List of Threatened Species (IUCN SSC Amphibian Specialist Group 2020a, 2020b, 2020c IUCN SSC Amphibian Specialist Group and NatureServe 2020). *Atelopus chirripoensis* is known from a single specimen collected in Fila Norte, near Chirripó, Costa Rica in 1980, and has not been seen since (Savage and Bolaños 2009). *Atelopus chiriquiensis*, restricted to Costa Rica and western Panama, has not been observed in Costa Rica since 1996 (Lips et al. 2010; IUCN SSC Amphibian Specialist Group 2020b), and records from Panama date to the late 1990s

Fig. 1. A pair of harlequin toads (*Atelopus* sp.) in amplexus along the Río Lagarto at Monteverde, Costa Rica. That population is now considered extinct. Treated as *A. varius* by Martha Crump and collaborators during their studies, the population is currently thought to be more closely related to *A. senex* (Ramírez et al. 2020). Photograph by Martha Crump.

(Lewis et al. 2019). *Atelopus senex*, a Costa Rican endemic, has not been found since 1986 (Bolaños et al. 2008).

The most widely distributed species, *A. varius*, originally occurred from northwestern Costa Rica to western Panama (Savage 1972, 2002; IUCN SSC Amphibian Specialist Group 2020c). In Costa Rica, it was an abundant element of the lowland and mid-elevation forests throughout the cordilleras of the Pacific and Caribbean versants from 16 to 2,000 m (Savage 1972, 2002). Over 100 populations of *A. varius* were known from Costa Rica (IUCN SSC Amphibian Specialist Group 2020c), but in the 1980s and early 1990s populations began to decline dramatically, including those in well-known localities such as Monteverde (Pounds and Crump 1994; Fig. 1). The Variable Harlequin Toad became a poster child of these declines, which affected mostly stream-breeding species including those in pristine and protected habitats that have been linked to climate change (Pounds et al. 1999), and which were attributed largely to the emergence of chytridiomycosis (Lips et al. 2006). By 1996, *A. varius* was considered extirpated in Costa Rica (IUCN SSC Amphibian Specialist Group 2020c).

A glimmer of hope occurred in 2004 when a population of *A. varius* was discovered in the Pacific lowlands at Fila Chonta, about 12 km NE of Parrita, Puntarenas (Ryan et al. 2005). Surveys in 2005, however, yielded no additional populations (Ryan et al. 2005). Then, in 2008, González-Maya et al. (2013) reported the rediscovery of a breeding population of *A. varius* at a private property in Zona Protectora Las Tablas near San Vito de Coto Brus, Puntarenas, at an elevation of 1,300 m. Previous surveys conducted from 2002 to 2004 in the same area, however, failed to detect this species (Santos-Barrera et al. 2008). Solano-Cascante et al. (2013) reported finding a single individual of *A. varius* near Buenos Aires, Puntarenas, at an elevation of 840 m. Barrio-Amorós and Abarca (2016) reported a surviving population near Uvita, Puntarenas, which is described in detail below. Lastly, Jiménez-Monge et al. (2019) conducted a preliminary survey of another population close to San Isidro del General, San José Province.

Atelopus varius was present and abundant until the early eighties in the Central Valley and in some valleys extending toward the Caribbean side of the country (Savage 2002). The only detailed published information for *A. varius* stems from Monteverde, where its distribution and population dynamics were documented for several years (Pounds and Crump 1987, 1994; Crump and Pounds 1989), and most of the information about the species has been extrapolated from this single population (Savage 2002).

A total of 751 *A. varius* were recorded in one year on a 200-m transect along the Río Lagarto (Pounds and Crump 1987). The numbers of *A. varius* along the Río Lagarto appeared to be stable until the late 1980s; however, surveys conducted between 1990 and 1992 did not detect a single toad (Pounds and Crump 1994). Since then, no more sightings of the species have been recorded in the vicinity of Monteverde, perhaps one of the most extensively surveyed tropical sites in Costa Rica. However, the harlequin toads from Monteverde recently have been shown to represent a distinct, undescribed species of *Atelopus* that is more closely related to *A. senex* than to *A. varius* (Ramírez et al. 2020).

Puschendorf (2003) recorded the first *A. varius* infected with the pathogen *Batrachochytrium dendrobatidis* (= *Bd*) from San Ramón (Alajuela Province) in 1986, and the second from Rivas de Pérez Zeledón (San Jose Province) in 1992. Lips and Papendick (2003) reported an outbreak of *Bd* in areas close to known populations of A. varius that also affected multiple species of anurans. In Panama, Hertz et al. (2012) reported finding four individuals of *A. varius* at Cerro Negro, Provincia de Veraguas; none appeared to be sick, and a histological examination failed to find evidence of *Bd*. Subsequently, Pérez et al. (2014) found *A. varius* persisting at multiple sites in western Panama where *Bd* was enzootic. Lewis et al. (2019) presented information on *Bd*-free captive populations of *A. varius*.

Of the 169 localities recorded in the University of Costa Rica database, only seven are known to survive. Herein we report the current status of extant populations of *Atelopus varius* in Costa Rica. We evaluate the sizes, conditions, natural history, and habitat of three extant populations and comment on the other four. We also describe and compare dorsal color patterns among extant populations.

Methods

Study sites.—Population A (Fig. 2) is located on private land in the general area of Uvita de Osa, Puntarenas Province, at elevations of 350–480 m asl in the Fila Brunqueña (Fig. 3). A 780-m long transect was divided into four sections to facilitate recognition of individuals in each section. Section 1 was 225 m long and covered by primary rainforest; section 2 was 140 m in length and included a mudslide (possibly from 2015) and a 30-m long streambed that is dry during the dry season (January–April); section 3 was 265 m long and entirely within primary rainforest; and section 4, 150 m in length, included steep, narrow sections and recent small mudslides. We visited the site once each month (except October) from May 2017 to May 2018 plus an additional eleven visits before and after the monitoring year, conducting two-person surveys during one or two 8–10 hour days, sometimes staying overnight to run nocturnal transects, for a total of 213 person-hours. CBA spent 69 hours searching for other remaining populations in 18 other valleys with similar characteristics in Uvita, San Josecito, Dominical, Ojochal, and Palmar Norte without finding any other population.

Populations B1 and C1 were described by González-Maya et al. (2013) and Jiménez-Monge et al. (2019), respectively.

Population B2 (Fig. 2) was described by Solano-Cascante et al. (2014). CBA invested 73 hours in 2017, 2019, and

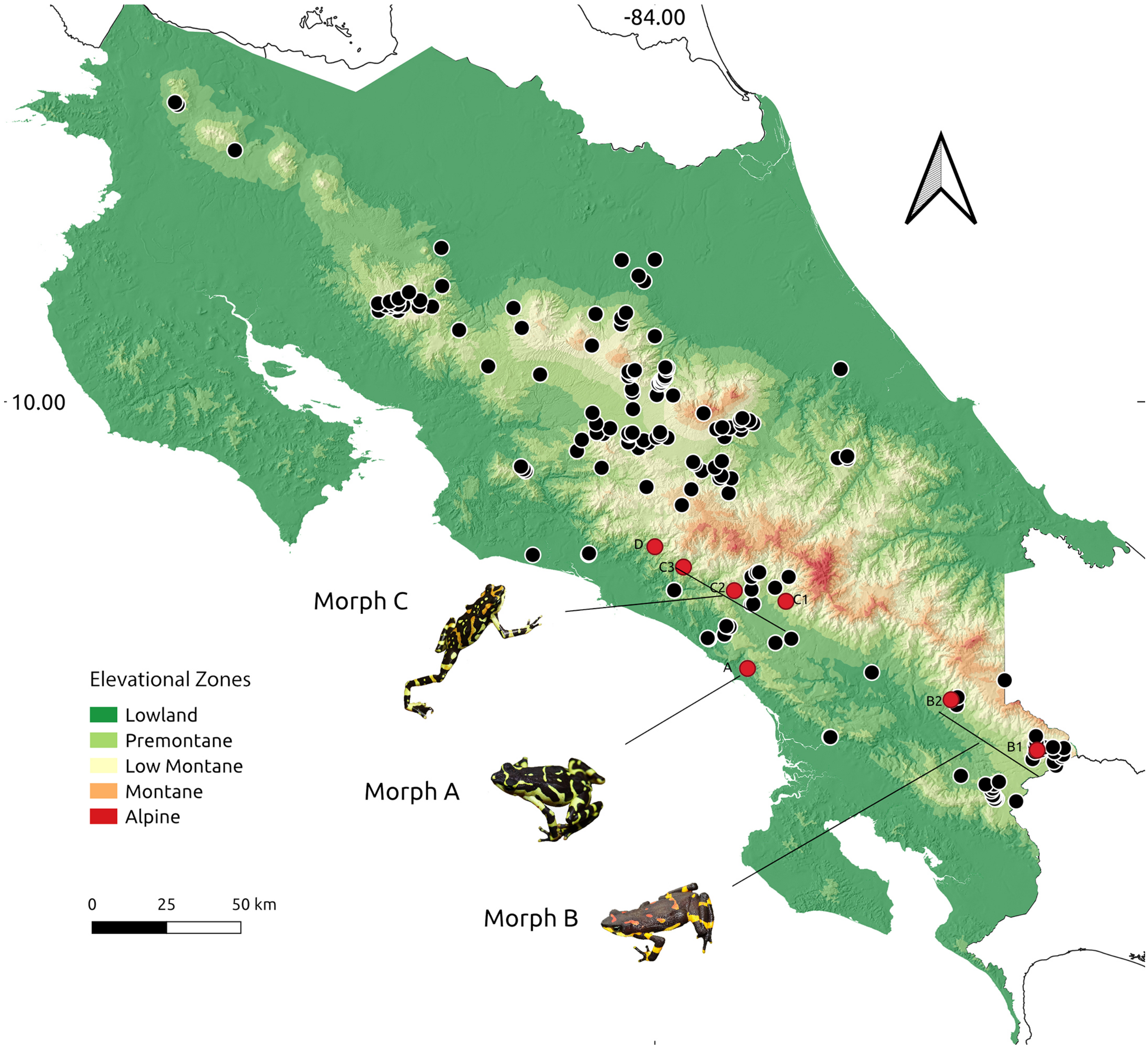

Fig. 2. Map of Costa Rica showing 169 historical and seven extant localities where Variable Harlequin Toads (*Atelopus varius*) have been recorded (some dots represent more than one record). To determine the historical distribution of the species, we downloaded data from the GBIF (Global Biodiversity Information Facility) and the herpetology collection of the Museo de Zoología of the Universidad de Costa Rica. Three color/pattern morphs survive in Costa Rica: Morph A in the southwestern versant of the Cordillera Brunqueña, morph B in the southwestermost part of the country, and morph C in the southwestern versant of the Cordillera Talamanca. Map generated by G. Chaves; photographs by C. Barrio-Amorós.

2021 surveying the main river and four tributary streams within very humid premontane tropical forest at elevations of 810–1,086 m asl. The main river is 5–10 m wide and 30–130 cm deep, and has a streambed with many large rocks.

Access to Population C2 (Fig. 2) is only through private property that the owners, aware of its importance, are carefully conserving. The swiftly flowing main river is 4–8 m wide with a rocky boulder-strewn streambed surrounded by primary riparian vegetation at elevations of 1,050–1,180 m asl. The only location where we observed harlequin toads during five visits totaling 44 person-hours was along a narrow, 2–4 m-wide tributary with several low waterfalls and mossy walls under a dense canopy. Upstream from the site, a dirt road crosses both the river and the smaller stream and essentially delimits well conserved primary forest along the water courses from various crops of bananas, coffee, and sugar cane. The patch of well conserved forest extends no farther than 1.3 km, and this population likely is the most threatened of those surveyed.

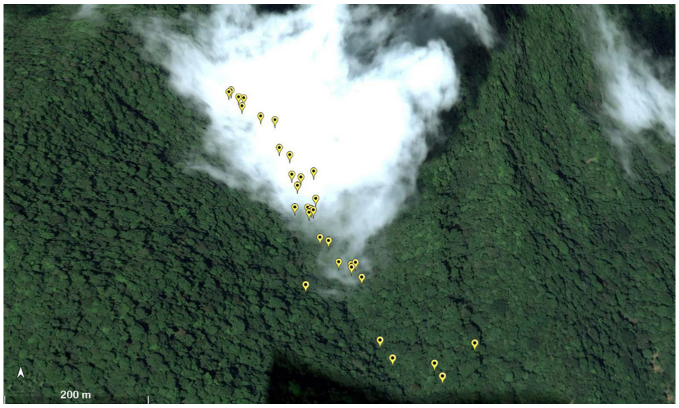

Fig. 3. Google Earth© image showing locations of 50 sightings of Variable Harlequin Toads (*Atelopus varius*) in population A. As many as six individuals are indicated by some dots.

Population C3 is associated with the largest river at any sampled site. The main area, with an elevation of 670 m asl, was within primary rainforest. The river was 8–15 m wide and had a number of deep pools. Parts of the river was with shaded deep canyons bordered by high, wet walls— ideal habitat for *A. varius*; however, other extensive areas receiving direct sun were not suitable.

Population D is in the lowlands of the northwestern piedmont of the Cordillera de Talamanca. No surveys have been conducted at this site and a description of the area is unavailable.

Data collection.—We used visual-encounter methods while walking up- and then downstream. When an individual was located, we recorded coordinates and temperature of water and air. CBA photographed its dorsum in order to generate a collection of labeled individual images for each locality. We categorized each individual according to the four dorsal pattern groups (Chaves et al., in prep.; Fig. 2). We then recorded sex and measured snout-vent length (SVL) with a ruler, in most cases holding the ruler in proximity to the toad without touching it. We consistently applied appropriate bioprotocols (Phillott et al. 2010) and, if handling was necessary, we used a different pair of nitrile gloves for each animal. Individuals seen during the day were not counted as recaptures when they also were found sleeping at night. Recaptures were confirmed by checking each individual's unique dorsal pattern.

Results

Color morphs of extant populations.—**Morph A (**Fig. 4) is a bicolored morph characterized by a pale to vivid yellow ground color with a dorsal pattern of black blotches, inverted and sometimes interrupted chevrons, and spotting; a few individuals had irregular red-orange dorsal markings on the yellow ground color (Fig. 4G); the upper arm is yellow, followed by a long black band connecting the upper and lower arm with a yellow spot on the elbow; the lower arm bears another black band that extends from above to the lower portion of the wrist; the upper portion of the hand is yellow and the fingers are mostly black with varying amounts of yellow; the black banding on the thighs and legs is more evenly dispersed, although the bands often are irregular in shape and contain yellow spotting; undersides are mainly white, with or without isolated black or brown spots of varying sizes; undersides of the hands, feet, vent, and posteroventral portion of the thighs orange in males, cream in females; the iris is greenish yellow. This morph currently occurs only in one population near Uvita in the Cordillera Brunca; historically, it also is known to have occurred in a population near Palmar Norte.

Morph B (Fig. 5) is a tricolored morph characterized by a dark brown to black dorsal ground color with irregular or symmetrical spots or wide stripes that form open or closed orange to red chevrons; the upper two-thirds of the flanks are dark to black, the lower third is yellow, usually extending from the tip of the snout through the upper lip (sometimes broken by a black spot under the eye) to the groin; many types of intrusions on the dark upper flanks include large yellow to orange spots or yellow undulations; arms and legs are black with yellow to orange bands of various widths; hands are usually yellow but fingers are black with yellow tips; the throat, chest, and belly are white, becoming grayish or with orange small stippling turning the lower belly dirty orange, with or without irregular black spots; undersides of the arms and legs are black with narrow yellow to orange bands or totally yellowish becoming more orange around the vent; palms and soles are vivid orange to reddish; the iris is greenish. This morph is present along a straight line of at least 35 km in the southwestern versant of the Cordillera de Talamanca in Costa Rica (not known from Panama) from the Cotón and Java Rivers to around 25 km east of Buenos Aires (the limits are not clear). Two populations are known and monitored, but additional streams between the two known sites could harbor additional populations.

Morph C (Fig. 6) is a tricolored morph characterized by a black or very dark brown dorsal ground color with a variable number (almost none to many) of small yellow rounded to irregular spots, and larger, elongated red-orange spots, giving the appearance of morph B marked with little yellow spots; the flanks are black or yellow with greater or lesser number of yellow/orange or black spots or stripes, respectively; the limbs are black with yellow narrow bands, with or without smaller orange spots; the throat and chest are white (sometimes with one or a few small black spots), becoming yellowish toward the back, with black spots in unique patterns; the vent, soles, and palms are orange; the iris is greenish. This is the most widely distributed morph, with about 38 km between the most widely separated localities; it also occurs in the southwestern (Pacific) versant of the Cordillera de Talamanca.

Fig. 4. Variants of Variable Harlequin Toad (*Atelopus varius*) Morph A in Population A: Adult males (A–D, F) and adult females (E, G–H); note the irregular red-orange dorsal marks on the yellow ground color (F–G) and the wounds (red arrow) probably attributable to *Bd* (H). Photographs by C. Barrio-Amorós.

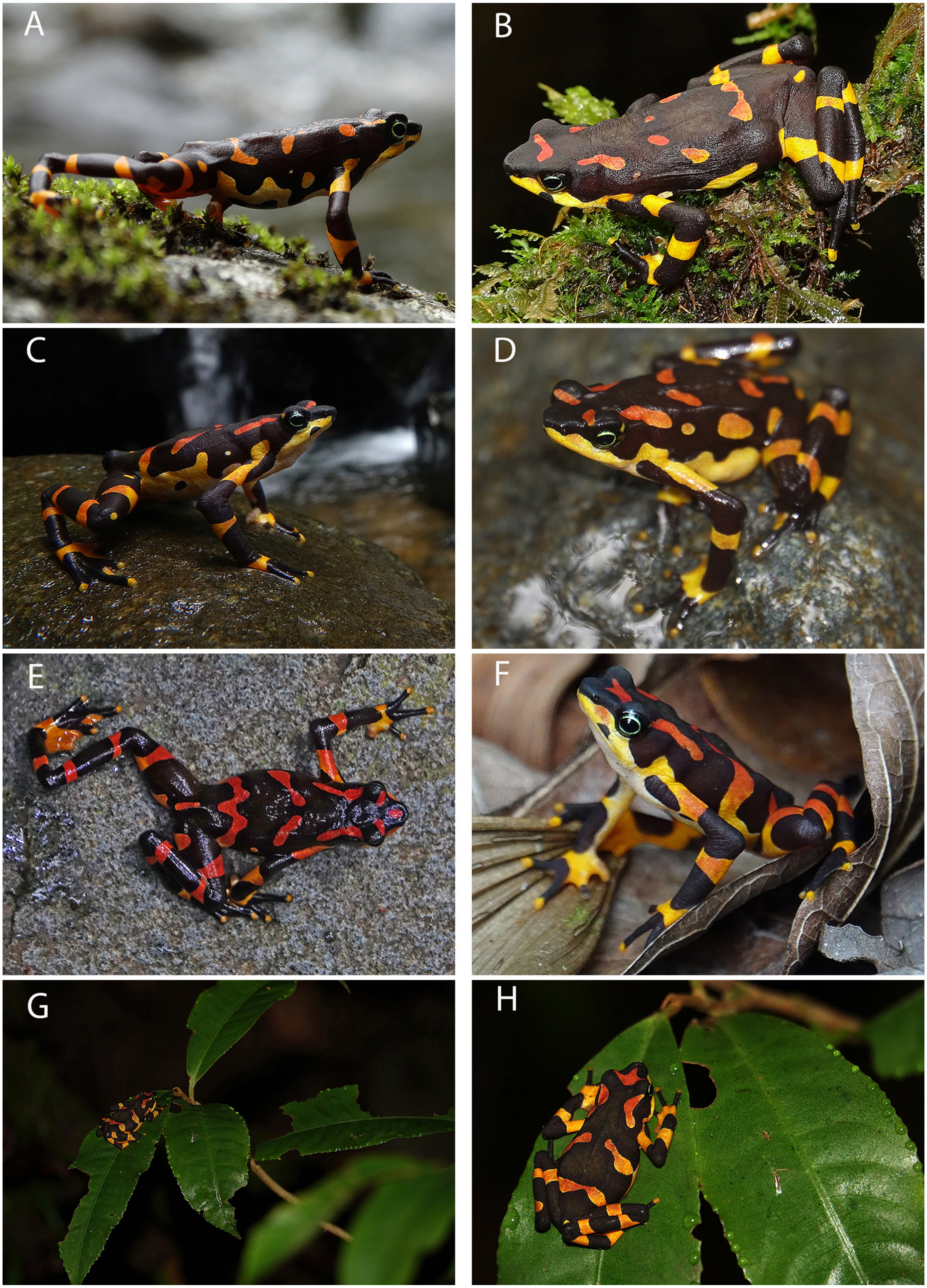

Fig. 5. Variants of Variable Harlequin Toad (*Atelopus varius*) Morph B: An adult male in population B1 (A), adult males in population B2 (B–F), and adult male sleeping on leaves at night (G–H). Photographs by C. Barrio-Amorós.

Fig. 6. Variants of Variable Harlequin Toad (*Atelopus varius*) Morph C: An adult male in population C1 (A), adult males in population C2 (B–G), and an apparent adult male in population C3. Photographs by C. Barrio-Amorós (A–G) and Edwin Mora (H).

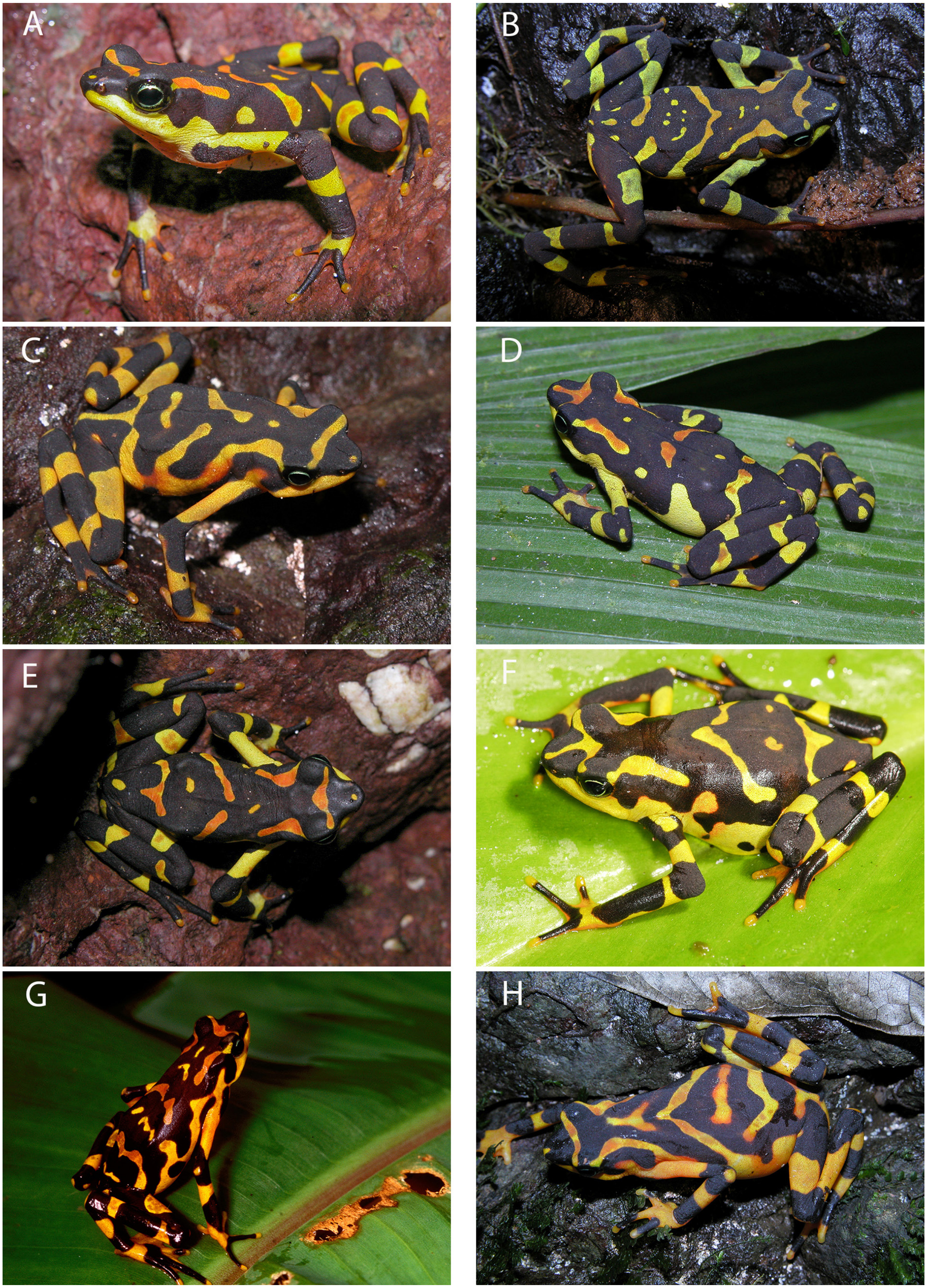

Fig. 7. Variants of Variable Harlequin Toad (*Atelopus varius*) Morph D: A-G, Adult males (A–G) and an adult female (H). Photographs by Twan Leenders (A–F & H) and R. Puschendorf (G).

Whether morph C is distinct and separated geographically from morph B or if morph C is merely a derivative of morph B with a profusion of yellow spots is unclear. Three populations are known to date, but more might occur in similar habitats in the same general area.

Morph D (Fig. 7) from Fila Chonta (Parrita) is quite variable. Few published photographs of the Parrita population (Fig. 7D) exist (IUCN SSC Amphibian Specialist Group 2020c; Leenders 2016). In collaboration with T. Leenders, who visited the population on several occasions, we have noted that some individuals look very similar to Morph A (Figs 7C & F) and some like morph B (Figs. 7A & E), whereas others look like morph C (Figs. 7B & G). The Parrita population is in the lowlands (around 325–395 m asl) along a 150-m long sector of a stream, but this site is separated from the Cordillera Brunqueña and more closely connected to the foothills of the Cordillera de Talamanca. Its bio- and phylogeographic limits should be tested. This population was monitored on several occasions in 2005–2007 by T. Leenders, who counted a total of 31 individuals.

Status of extant populations.—Of the seven known remaining populations of *Atelopus varius* in Costa Rica, CBA visited all except population D in 2015–2021. Population D, which is within a private reserve, is closed to visitors and the owners are not open to collaboration. CBA encountered the species in five of the visited sites, failing to detect toads only in population C3; however, three animals were photographed by local residents (Fig. 6H; Henry Parra, pers. comm.).

Population A was discovered in June 2015 by CBA and subsequently has been visited intermittently. Barrio-Amorós and Abarca (2016) recorded nine live individuals and one dead toad (Fig. 8) during the first visit. The dead toad tested positive for *Bd*, whereas one living individual tested negative. An almost complete year of monitoring of this population was completed during 2017–2018.

The creek is rugged (38% incline), with many waterfalls 4–15 m high and splash zones. Along the transect, the stream width is 2–5 m and depth is 15–30 cm in shallow sections to more than a meter in small pools, with considerable variation depending on the amount of precipitation. The bottom of the creek is mostly rocks interspersed with sand, pebbles, and larger boulders. Primary forest (trees 20–30 m tall, most covered with bromeliads) surround the stream; the shoreline is dominated by *Heliconia*, *Dieffenbachia*, and other Araceae. An abundance of fallen logs are products of sudden, rapid rises in water levels during the wet season. Access to the transect is through untouched rainforest, reaching a middle sector of the creek at an elevation of 460 m asl. The higher portions of the stream (above 690 m) are inaccessible due to the many substantial waterfalls and we never encountered harlequin toads below section 1.

We counted 113 individuals, uniquely identified by dorsal patterns, and recaptured seven toads once for a total of 120 sightings, including 79 adult males (Figs. 4A–D & 4F) and 10 adult females (Figs. 4E & G–H); 11 adults for which we could not definitively determine sex were tentatively classified as males. Reproductively active males have a distinctive dark brown nuptial pad only during the breeding season. Another 13 individuals were subadults with SVLs = 19–25 mm, and 11 were juveniles with SVLs = 12–18 mm. We did not find eggs, tadpoles, recent metamorphs, or calling males. Sections 2 and 3 were the most productive, with 32 (3 females) and 43 (5 females) individuals, respectively. Section 1 had 12 (1 female) and section 4 26 (1 female) individuals. Encounters were most common during the dry season (January–April), followed by June–July when juveniles are present (Fig. 9). In April, an apparently intentional aggregation of individuals, but especially females, was evident near waterfalls or in narrow canyons where humidity was highest. We saw three females in an area of less than 2 m^2 on a nearly vertical wet wall near a waterfall about 4 m high, but observed no interac-

Fig. 8. A dead Variable Harlequin Toad (*Atelopus varius*) in population A. A preliminary PCR tested positive for *Bd* (Barrio-Amorós and Abarca 2016). Photograph by C. Barrio-Amorós.

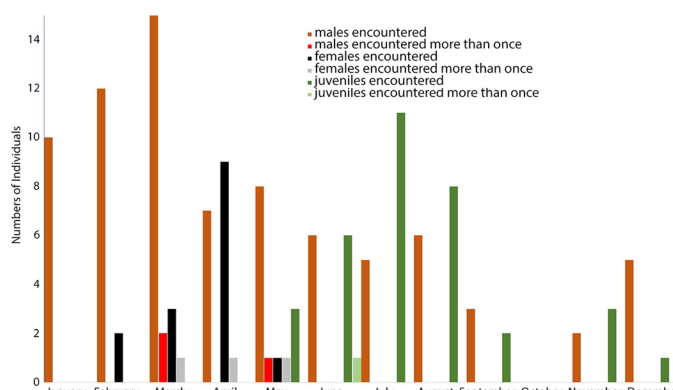

Fig. 9. Variable Harlequin Toads (*Atelopus varius*) encountered by month from May 2017 to May 2018 in Population A near Uvita de Osa, Puntarenas Province, Costa Rica, at elevations of 350–480 m asl.

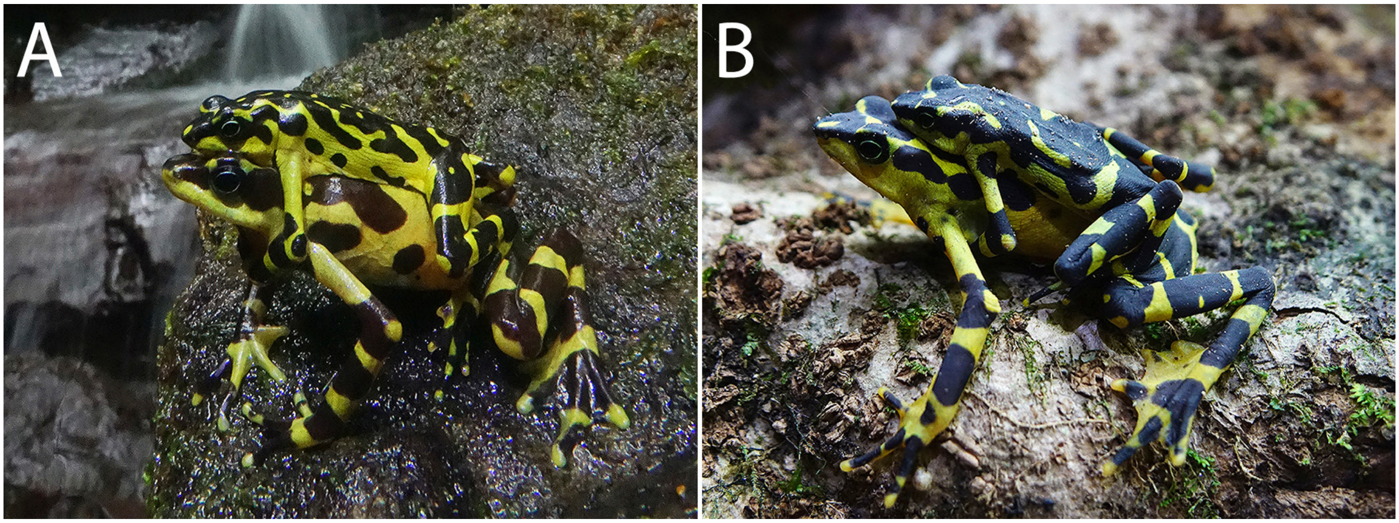

Fig. 10. Variable Harlequin Toads (*Atelopus varius*) in population A in amplexus: This male had grasped the female by the neck before assuming a typical axillary position after the female moved (A); typical axillary amplexus on a dry horizontal trunk in the middle of the stream (B). Photographs by C. Barrio-Amorós.

tions. Pounds and Crump (1987) noted similar concentrations at Monteverde during the dry season.

Toads on a mossy substrate often were difficult to see. However, individuals in this population are not as cryptic as morphs in populations B or C (see below).

Of the seven recaptures (3 females, 3 males, 1 juvenile), the longest distance moved was 27 m by an adult female, others moved 11, 9, 7, 4, 4, and 2 m, all upstream. One recapture was one month after the first sighting, four after two months, and two after three months. Although not counted as a recapture, one male was seen at 1323 h on a mossy rock wall on 18 March 2018, and the same individual was found sleeping on a leaf 4 m away (3 m downstream and 1.6 m across the stream) at 2047 h that night.

Most males in this population were active during the day, perched on bare or moss-covered rocks and boulders along the stream or on large boulders surrounded by water; a few were walking on leaf litter. Of all males observed, 62 were on boulders or tree trunks. Most were immobile but in positions that suggested that they had been moving. Some moved 4–15 cm after several minutes, with movements triggered in many instances by the discovery of a nearby prey item. We believe that males perched on top of boulders were engaged in territorial displays, but we never saw two males interact despite waiting hours for a male to call or wave a hand. We did see hand-waving while males were moving, but it did not appear to have a territorial connotation. For example, a male moving and searching for prey would suddenly wave its hand. Some males engaged in hand-waving more frequently than others. We never saw foot-waving in any context and we never observed a female waving its hand.

We encountered three amplectant pairs, two in April 2017 and another in April 2018, two close to waterfalls (Fig. 10A) and one on a dry horizontal trunk in the middle of the stream (Fig. 10B). The male in the first image had initially grasped the female by the neck; after 14 min the female moved and the male adjusted its grip. We saw another male in the interior of a hollow tree with a female deeper in the cavity. We waited an hour but saw no interaction. The male moved close to the female, but the latter apparently remained undetected.

At night, males and females slept on leaves at heights of 0.5–2 m above the ground, always near the stream and usually hanging over the water. We found many individuals that had not been disturbed during the day again at night a few meters away on leaves. We found no individuals, sleeping or awake, in phytotelmata or crevices, as reported by Gómez-Hoyos et al. (2018a) in a population on the Río Cotón (population B1). We rarely saw toads climbing, a few females moving upward on vertical or very steep waterfalls as high as 4 m above the ground and occasional males and juveniles foraging for prey or escaping after we disturbed them.

On 2 April 2017, we found the very fresh carcass of an adult ovigerous female on the bottom of a shallow rocky pool close to a waterfall (Fig. 11). The female was cut in half, exposing the eggs, but the anterior half (except for a missing forearm) and the eggs were intact. Only two reports of predation on *Atelopus* are known, one by a Fire-bellied Snake (*Erythrolamprus epinephelus*) (Savage 2002) and one by a giant waterbug (Belostomatidae) (González-Maya et al. 2019). We assumed by the clean cut that the predator in this case could have been a crab (Pseudothelphusidae) that, after tasting the poisonous toad and eggs (i.e., Pavelka et al. 1977), abandoned its prey. We did not find the rest of the carcass.

During a recent visit to the site in December 2020, we found that the storms and hurricane of October 2020 had a dramatic effect on the habitat. Two relatively extensive mudslides had entered the creek, affecting one of the breeding

Fig. 11. The fresh carcass of an ovigerous female Variable Harlequin Toad (*Atelopus varius*) presumably killed and bisected by a crab. Photograph by C. Barrio-Amorós.

Fig. 12. The Variable Harlequin Toad (*Atelopus varius*) is microsympatric with the Granular Poison Frog (*Oophaga granulifera*) at locality A. Photograph by C. Barrio-Amorós.

hotspots (where a number of juveniles had been found during prior visits). Such events can alter the dynamics of a small stream from year to year. How this might affect populations of *Atelopus varius* is unknown, but they might be adapted to such dramatic environmental changes. We did not detect any substantial decrease in the population numbers, as we found six individuals in December and 11 during a subsequent visit in March 2021 (normal numbers for those months), including juveniles (one in December, two in March), one female (in March), and the rest adult males.

We detected several other species of amphibians along the monitored transect. The most abundant of which was the Granular Poison Frog (*Oophaga granulifera*), which frequently occurs in the same microhabitats as *A. varius*, but is less prone to being exposed in clear areas. In two instances, we saw *A. varius* and *O. granulifera* within 5–10 cm of each other (Fig. 12) but observed no interactions. Also abundant during the day along the stream is the Rainforest Rocket Frog (*Silverstoneia flotator*) and, in leaf litter, the Pacific Litter Frog (*Craugastor stejnegerianus*). Present, but largely limited to the forested slopes of the creek, is the Green and Black Poison Frog (*Dendrobates auratus*). At night during the dry season, we encountered Common Rainfrogs (*Craugastor fitzingeri*), Cascade Glassfrogs (*Sachatamia albomaculata*), Drab Streamside Treefrogs (*Smilisca sordida*), and Granular Streamside Treefrogs (*S. sila*). We never spent nights during the wet season to record the presence of other amphibian species.

Population B1 is the best known of extant populations. González-Maya et al. (2013) reported the survival of the population since 2008 and published preliminary results of their monitoring. The main habitat (Río Cotón) is a montane river 6–15 m in width (pers. obs.). Surveys were conducted along a 2.2-km long transect including both disturbed (pastures, degraded habitat) and undisturbed primary forest. Monthly surveys conducted in 2011–2013, resulted in the identification of 204 individuals (222 sightings), 103 immature (23 juveniles and 80 subadults) and 113 male and female adults (González-Maya et al. 2018), with 14 individuals recaptured once and two recaptured twice. The mean number of individuals sighted monthly was 21.50 ± 10.18 (SD) during the dry season (November–March) and 6.25 ± 5.44 during the rainy season (April–October). Two of 15 individuals tested positive for *Bd*, but no mention was made of condition. That population should still be considered vulnerable to local extinction given low recruitment rates and high seniority (González-Maya et al. 2018), although Gómez-Hoyos et al. (2020) recorded tadpoles along the Río Cotón. During four months in 2016 (two in the dry season, two in the rainy season), Gómez-Hoyos et al. (2018a) recorded the use of phytotelmata (Araceae and Bromeliaceae) by some species of anurans, noting that *Atelopus varius* was the predominant species using these plants as shelters. *Atelopus varius* used Araceae in disturbed areas more than Bromeliaceae, and also used many more phytotelmata as shelters during the dry season than during the wet season (24 vs. 1). All of 21 tests for *Bd*, including 17 *A. varius*, were negative. Gómez-Hoyos et al. (2018b) reported an anecdotal observation of one individual moving slowly and eating ants at night. However, toads in the genus *Atelopus* are known to be diurnal with only a few exceptions (Rueda-Solano and Warkentin 2016). In recounting this observation, Gómez-Hoyos et al. (2018b) failed to mention substrate, time, phase of the moon (however, on 14 July 2016 the moon was a waxing crescent, indicating that only 9% of moonlight was present), or, most importantly, how the animal responded when surprised by the authors' light. In population C2, we have seen toads awakening very quickly when hit by the beam of a light, become active, then escape slowly, but even then pausing to catch and consume small prey — but the moon phase on that occasion (2 May 2020) was a waxing gibbous, with 75.2% of moonlight, the latter in particular possibly predisposing diurnal animals to awaken, escape, and even feed. González-Maya et al. (2019) recorded water bug (*Abedus* sp.: Belostomatidae) predation on an adult *A. varius* on 11 July 2012. Very recently (May 2021), during an expedition to the upper Cotón River system (elev. 2,000 m asl), R. Fallas (pers. comm.) reported sightings of *A. varius*.

Population B2 was discovered by Solano-Cascante et al. (2013), who found one individual at an elevation of 840 m. We managed to reach the locality and CBA and collaborators found four males (one in May 2017, none in February 2018, three in May 2018) (Figs. 4B–D). In May 2019, CBA returned with five collaborators and found along the Río Cotón and several small tributaries 14 males in 11 manhours (Figs. 4E & F). In a few hours in April 2021, we found a recent metamorph, three males (two with clear signs of *Bd*), and a healthy female. At an elevation of 800–1,000 m asl, the rapidly flowing main river has a gradient of 25% and is 4–8 m in width. This population exhibits the same pattern morph as B1 (Fig. 4A). We found these animals to be more cryptic than those in population A. They are much darker and less prone to move when approached. Some individuals remained stationary on mossy rocks close to the water (Fig. 13), allowing for close observations. However, one male that CBA was photographing, probably in response to his presence, released his hold and fell into the current. After 12 min of searching, we found it 10 m downstream on the same side of the stream. This behavior can serve both an escape strategy from potential predators and as a survival tactic when animals are surprised by sudden flooding. Individuals are very successful at returning to an original site after being naturally or artificially displaced (Crump 1986). We found several adult males sleeping at night (no signs of nocturnal activity) on leaves 0.5–1.5 m above the ground as distances of 0–2 m from the river (Figs. 4G & H). This population is relatively close to a small village where crops of pineapples and oil palms are expanding. The extensive use of pesticides and herbicides and an ongoing increase in cultivated areas (Fig. 14) is likely to have a negative effect on this population.

In **population C1**, Jiménez-Monge et al. (2019) found 25 individuals (person-hours not noted), 13 in February, 6 in June, and 1 in August, plus five incidental sightings at other times. With permission of the owners, CBA visited twice. In a few hour on 15 May 2019, he found only one male motionless on a mossy rock adjacent to the stream (Fig. 6A). On 2 April 2021, he found three males active during the day along the river and two males at around 1900 h sleeping on leaves in close proximity to the stream and about 2 m above the ground. This population is still being monitored by a team from the Universidad de Costa Rica and York University, Toronto, Canada. Animals at this site are hard to detect, as they are considerably more cryptic than Morphs A and B. Jiménez-Monge et al. (2019) detected males on the leaf litter, whereas females were on vegetation and boulders in and along the stream. Individuals in this population do not appear to aggregate near splash zones like those along the Río Lagarto at Monteverde (Pounds and Crump 1994). Jiménez-Monge et al. (2019) found that basking is more important than moisture-seeking behavior during the dry season. Also, these toads appeared to be more arboreal or inclined to climb than those in other populations, and adults and juveniles frequently were found far from the river and at heights greater than eye level. Interviews with local residents revealed the possibility that the elevational range of the population has shifted. In the past, toads were never encountered at elevations above 600 m but are now found at elevations as high as 1,000 m. Climate change and warmer temperatures in the area might have driven the surviving populations to higher/cooler areas. Alternatively, toads might always have occupied higher elevations but were not detected or reported. No evidence of *Bd*

Fig. 13. Variable Harlequin Toads (*Atelopus varius*) in population B2 tend to be more cryptic and less prone to move than toads in population A. This male allowed a close approach. Photograph by C. Barrio-Amorós.

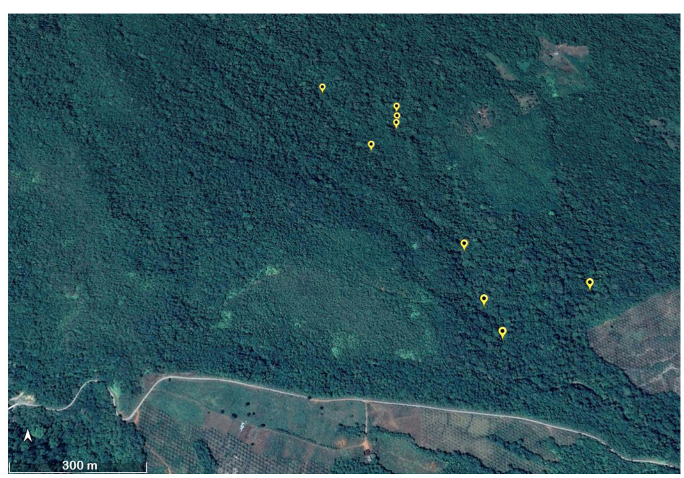

Fig. 14. Google Earth© image showing locations of nine sightings of Variable Harlequin Toads (*Atelopus varius*) in population B2. Note the proximity of land devoted to pineapple and oil palm crops.

has been found in this population, possibly because they tend to bask more than toads in other populations — but that hypothesis requires testing.

Population C2 was discovered in April 2020 thanks to a citizen-science endeavor. This provided an opportunity to interact with rural communities and start a local project with interested local residents. During two visits (21 April 2020 and 2–3 May 2020) we found seven individuals, six adult and one subadult male (Figs. 6B–G). all within a 200-m section of the river (of >500 m surveyed). Eleven person-hours during two later visits (10 August 2020 and 29 April 2021), when water levels were high, rocks very slippery, and cloudy skies after rain on the previous days, failed to locate any additional individuals. Two of the four males encountered during the first visit had been seen by our local guide (recognized through photos he took) a few days earlier on the exact same mossy wall of a pool below a low waterfall. The other three were seen during the second visit in the same sector. Toads in this population are virtually invisible, with the tricolored pattern blending into the moss-covered microhabitat (Fig. 15). They tend to remain motionless unless approached very closely. On one occasion, an adult male jumped into the water and curled into a ball (similar to the famous Tepui Bush Toads in the genus *Oreophrynella*; McDiarmid and Gorzula 1989), only to emerge on the bank of the creek 3 m downstream. Another individual escaped by jumping into the water and disappearing downstream. After searching for several minutes, we found it had emerged about 7 m downstream below a 2-m high waterfall, clearly demonstrating an ability to survive waterfalls and, presumably, sudden floods. Two individuals were sleeping at night on leaves about 2–3 m above the ground, one of them in the same spot, albeit on another leaf, the next night, whereas the other was 30 m into the forest and not as close to the stream. Our observations of this population largely coincide with those of Jiménez-Monge et al. (2019), who conducted the only study of this morph, albeit at locality C1. One difference was that toads in this population were never seen basking, which is common in population C1. However, Morph C at both locations appears to rely on crypsis, tending to remain motionless unless disturbed by our very close proximity. If disturbed, they walk or hop in search of a place to hide. They are very good climbers and often can be found high on mossy rocks or tree trunks. At night individuals appear to sleep higher (2–4 m above the ground, most frequently on leaves of bushes) than populations of morphs A and B. Sleeping toads are visibly stressed by headlamps, responding quickly to avoid the artificial lights, sometimes climbing to heights of more than 5 m in trees. This stress response might account for observations of apparent nocturnal activity in the species (e.g., Gómez-Hoyos et al. 2018). Under similar conditions Morphs A and B were not as affected by light as Morph C.

Population C3 also was found thanks to the involvement of local residents, when CBA was contacted to identify some photographs of an unknown anuran that was indeed *A. varius* of this morph. CBA and an assistant visited the area (intentionally not revealed) to verify the presence of the species. Although a logistically complicated and expensive expedition (2-day round trip on horseback), we did not find any *Atelopus*. Two local residents, however, showed us photographs of three individuals (Fig. 6H).

Figure 15. At Population C2, Variable Harlequin Toads (*Atelopus varius*) are highly cryptic and tend to remain completely motionless or seek to hide in crevices. The red arrow shows the position of an adult male that otherwise would be almost invisible. Photograph by C. Barrio-Amorós.

Discussion

The Variable Harlequin Toad (*Atelopus varius*) and the Golden Toad (*Incilius periglenes*) are the most publicized anurans used to exemplify amphibian declines. Whereas *I. periglenes* is recognized as recently extinct (IUCN SSC Amphibian Specialist Group 2020d), *A. varius* is considered a Lazarus species (one that has come back from apparent extinction). Herein we discussed the status and natural history of the surviving populations of this species in Costa Rica, which, along with those in Panama, retain a relatively wide gene pool (Ramírez et al. 2020). Three distinct morphs (A, B, and C) survive in Costa Rica, each with one to three distinct populations, while a single additional population includes individuals with patterns characteristic of three morphs. The history of recently rediscovered populations suggests that additional populations might be extant.

Whether the current populations are stable, declining, or thriving is difficult to assess. Population A appears to be stable, but ongoing monitoring will be necessary. Population B1 also appears to be stable, and it has been monitored and studied for at least 12 years. Too little is known about population B2 to make any inferences about its status; of concern is the fact that it seems to have a lower density than populations A and B1, and many individuals, although apparently healthy, show evidence of *Bd* infections. Population C1 has been monitored for only a short period and more effort is needed to assess its status; it appears to be stable but the population density is low. Recently, this population has been receiving attention from tourists who arrive and search for these toads in order to take pictures. Whether a number of persons invading the habitat and touching animals without following the correct bioprotocols has an effect is unknown — however, this practice is illegal. Population C2 has only recently been discovered and monitoring is necessary; that the upper and lower sections of the site (where toads are present) are very near areas with cultivated crops is a major concern. Population C3 also appears to have a very low density and no effort has been made to assess this population. Population D has not been visited by any herpetologist since 2007 and its current status is unknown.

Morph A is known from a single population and, if no other populations are rediscovered, the unique gene pool associated with this morph is in great peril of extinction. Thanks to the field notes of Eberhard Meyer and documentation at the University of Costa Rica, we know that at least one additional population existed near Palmar Norte, Puntarenas Province. Although currently thought to be extinct (the most recent visit by CBA and colleagues on 4 January 2021 failed to find any *Atelopus*), Meyer documented the presence of the species in the area in the 1990s. During four visits (January and May 1990 and two in March 1993) to Quebrada Benjamin (near Palmar Norte), Meyer saw nine females and at least 40 males.

Although multiple populations of morphs B and C are known, Meyer also documented additional populations in the 1990s that are currently thought to be extinct. During four visits (March, two in April, and July 1990) to the Centro Biológico las Quebradas (near San Isidro del General), Meyer saw "many" *Atelopus* (morph C) in March, a few, including a pair in amplexus, in April, and a single female in July. During two visits by CBA to that site in April 2021, he found no *A. varius*. During two visits in November 1989, Meyer also recorded the presence of the species (morph B) at the Jardín Botánico Las Cruces in San Vito, Puntarenas, where he saw one male and three females. Although visits by CBA to the site in December 2013, June 2015, and June 2017 failed to document any individuals, extant population B1 is nearby.

We strongly recommend additional monitoring of all known populations. We also urge ongoing searches for additional populations at localities where the species has been documented in the past and in new area with suitable habitat.

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