From hope to alert: demography of a remnant population of the Critically Endangered Atelopus varius from Costa Rica

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From hope to alert: demography of a remnant population of the Critically Endangered *Atelopus varius* from Costa Rica

José F. González-Maya, Diego A. Gómez-Hoyos, Ivan Cruz-Lizano and Jan Schipper

ABSTRACT
Harlequin frogs have suffered severe declines across the Neotropics. We present a population assessment for a recently discovered population of *Atelopus varius* from Costa Rica. Using mark-recapture methods from September 2011 to February 2013, we estimated survival and recruitment parameters using Cormack-Jolly-Seber models. We obtained 222 captures and estimated low recruitment rates and high seniority. Given estimates of population growth rates close to zero, the observed population seems to be stable during the study. However, contrary to expectations for seasonally reproducing species like *A. varius*, we did not find an increase in recruitment rates between dry and rainy season. We provide details on ongoing threats for the population, as well as propose conservation actions to mitigate these threats.

RESUMEN
Las Ranas Arlequín han sufrido declives severos en el Neotrópico. Presentamos una evaluación poblacional para una población recientemente descubierta de *Atelopus varius* de Costa Rica. Usando métodos de marca-recaptura desde septiembre de 2011 hasta febrero de 2013, estimamos parámetros de supervivencia y reclutamiento usando modelos Cormack-Jolly-Seber. Obtuvimos 222 capturas y estimamos bajas tasas de reclutamiento y alta ‘antigüedad’ (seniority). Dadas que las tasas de crecimiento poblacional se acercaron a cero, la población observada parece estar estable durante el estudio. Sin embargo, contrario a lo esperado para especies con reproducción estacional como *A. varius*, no encontramos un incremento en las tasas de reclutamiento entre las estaciones lluviosa y seca. Proveemos detalles de amenazas actuales para la población, así como propuestas de acciones de conservación para mitigar estas amenazas.

Introduction
Frogs of the *Atelopus* genus, known as harlequin frogs, are distributed from Costa Rica down to Bolivia and the Guianas in the south and east of their range, respectively (Lötters 1996, 2007; La Marca et al. 2005). Except for some populations in Colombia, the Amazon and the Guianas, harlequin frogs have suffered from rapid and severe population declines across their entire distribution, leading to concerns regarding the potential extinction of the entire genus (Lötters 2007). According to the IUCN Red List of Threatened Species (IUCN 2012), 74 of the 93 species are categorized as Critically Endangered, from which a large proportion is considered potentially extinct (Lötters 2007).

Despite these dark prospects, some species that were thought to be extinct, or were classified as data deficient, have been ‘rediscovered’ and studied (Carvajalino-Fernández et al. 2008; Flechas et al. 2012; Rueda-Solano 2012; González-May et al. 2013a; Gómez-Hoyos et al. 2014, 2017). These remnant populations offer a unique opportunity for the study and development of conservation actions, providing hope for other *Atelopus* species (González-May et al. 2013a; Perez et al. 2014; Gómez-Hoyos et al. 2017).

Of the four harlequin frog species recorded in Costa Rica, only *Atelopus varius* has been rediscovered from two localities during 2008 and 2015 (González-May et al. 2013a; Barrio-Amorós & Abarca 2016). For these surviving populations, management and conservation actions seems warranted, since several factors considered to pose potential threats for amphibians – such as pathogens, habitat degradation and invasive species – are operating in these areas (JFGM & DAG-H, pers. obs.). Furthermore, post population decline surveys are
critical for amphibian conservation in general (Perez et al. 2014), because they help to identify threat factors driving population declines, and help refine the management actions required. Here we estimated population parameters for an A. varius population in Talamanca, Costa Rica and identified the main threats for population persistence. Based on our results we specify urgent research needs and propose management measures for A. varius.

Materials and methods

Study area

Our study site is located in the Las Tablas Protected Zone (LTPZ), Puntarenas Costa Rica. LTPZ is located in Southeastern Costa Rica, specifically in the Talamanca mountain range, one of the regions with higher levels of endemism of the country (González-May et al. 2013b). LTPZ spans over 19,000 ha, and it is part of La Amistad Biosphere Reserve (González-May & Mata-Lorenzen 2008). Our study site is located in the Cotón river, at 1300 m asl, with a mean annual precipitation of 3500 mm and mean annual temperature of 19°C, corresponding to very humid premontane tropical forest (González-May & Mata-Lorenzen 2008). In this site, the landscape is dominated by mature and secondary forest, with some scarce patches of crops and pastures.

Survey

Our surveys were conducted during the day on a 3 km transect along both sides of the Cotón river. The transect was surveyed monthly between September 2011 to February 2013, by a herpetologist and a trained field assistant. The surveyors walked along the river margin covering at least 2 m from the river bank, searching post-metamorph individuals as well as eggs and tadpoles. Detected post-metamorph individuals were captured, measured (i.e. weight and snout-to-vent length) and their dorsal and ventral surfaces were photographed. Samples from the skin of each individual were obtained using cotton swabs for the study of Batrachochytrium dendrobatidis (Bd) presence (Krger et al. 2006), that were stored and refrigerated dry on sterile vials for posterior testing. Data on location (i.e. geographic coordinates), time and substrate were recorded for each individual, and a unique ID was assigned to each capture. Given that each individual of A. varius exhibits a unique spotting pattern, capture histories were built based on dorsal/ventral pictures of each captured individual. With the aim of avoiding transmission of Bd between localities, we used exclusive wear and boots for our study area.

Data analysis

We used the Cormack-Jolly-Seber (CJS) model based on live animal recaptures in an open population (Lebreton et al. 1992) in order to estimate apparent survival. Apparent survival is the probability that the animal remains alive and available for recapture and, technically, not the survival probability of marked animals in the population (White & Burnham 1999). To confirm that the CJS model adequately fitted the collected data, we used bootstrap goodness-of-fit test (GOF). Analyses were conducted in program MARK 8.0 (White & Burnham 1999). Models were constructed based on apparent survival (\( \phi \)) and recapture rates (\( p \)) with constant (.), temporal (\( t \): each monthly capture session) and seasonal variation (\( season \): dry or rainy month during the surveys) of such parameters, and for two age groups (immature individuals, including juveniles and sub-adults: < 27 mm and mature individuals: > 27.1 mm). We used two seasons (dry: December to March; rainy: April to November) as a temporal variation within models, because Costa Rica has a marked bi-seasonal climatic pattern and A. varius is a seasonally reproductive species. A multi-state model was not considered because it assumes that all individuals make the transitions at the same time, which is difficult to test for small sample sizes such as in our study.

Seniority (\( Gamma \)) was estimated through Pradel ‘seniority only’ model. Since this model computes encounter histories identical to the CJS model, we use the \( \hat{c} \) achieved by the GOF test of the CJS model. Seniority probability (SP) is defined as the probability of an individual to be alive and in the population at times \( i \) and \( i + 1 \) (Pradel 1996). Thereby, SP is useful for identifying the proportion of the population that was previously in the population before and during reproductive season. In order to estimate the parameters involved in population growth, we estimated recruitment and survival, and their interaction, as a baseline characteristic of the population (Nichols et al. 2000). Also, the estimation of these parameters is useful to plan conservation actions for threatened species (Schmidt et al. 2005; Muths et al. 2011). The Pradel survival and recruitment (PSR) model was used to estimate recruitment. Recruitment accounts for the number of individuals added to a breeding population (Muths et al. 2011). In most bufonid species, recruitment is not equal to reproduction given that individuals spend multiple years as juveniles or immatures.
before joining the breeding population (Schmidt et al. 2005; Muths et al. 2011); according to our field observations, in a seasonal breeding species such as *A. varius*, new individuals entering the breeding population should come from cohorts near to complete two years of development. Survival and recruitment parameters were used to calculate *Atelopus varius* population growth (*Lambda*), or population size change rate, which has values >1 indicating growth, and values <1 indicating decline (Muths et al. 2011).

The best-fitting models were selected based on the Aikake information criteria with a correction for small sample sizes (AICc) and derived measures (Burnham & Anderson 1998; Cooch & White 2015). When we found uncertainty about the best fitting model, we used a model-averaging method with the top-ranked models (delta AICc < 2), including only those models with reliable estimations. All statistical results are presented with the respective standard error (±SE) and 95% confidence intervals (LCI–UCI).

**Threat assessment**

Swab samples were analyzed to confirm *Bd* presence in the population. Of 222 samples, we selected 15 random sub-samples and these were tested for *Bd* using standardized methods (Hyatt et al. 2007). We extracted DNA from the swabs with PrepMan Ultra (Applied Biosystems, Carlsbad, CA, USA), and analyzed the samples using the standard real-time quantitative polymerase chain reaction assay. We followed the standardized procedures in Boyle et al. (2004) with the following exception: the nucleic acids were extracted using 50 µl PrepMan, a negative control (H2O) and a positive control swab dipped in a broth of *Bd* culture from Costa Rican strain JGA01. The presence of other potential threats such as habitat perturbation and invasive species (e.g. rainbow trout) were registered (though not quantified) during surveys in order to provide a first insight on possible influence of such pressures, since these threats have been reported as potential drivers of decline in other populations (Pounds et al. 2010).

**Results**

We detected 222 individuals of *A. varius*, which included 103 immatures (23 juveniles and 80 sub-adults), as well as 113 male and female adults (six undetermined; Figure 1). Uncertainty on the identification between males and sub-adult females did not allow discrimination by sex categories. Since it is expected that mature females present snout-to-vent length (SVL) usually above 40 mm, our sample include at least 22 mature females. We did not detect any *A. varius* eggs or tadpoles during our surveys, or individuals under 18 mm SVL (Figure 1).

According to bootstrap GOF the CJS model adequately fits the data (*ĉ* = ~ 1). Due to uncertainty in selecting the best-fitting models, the model averaging method was applied to the four top-ranked models (Table 1); although model 5 was also competent (delta AICc = 1.912), the estimate was not reliable. Considering model averaging, estimated apparent survival was (estimate ± standard error [95% confidence interval]) 0.87 ± 0.09 [0.59–0.97] in the rainy season and 0.78 ± 0.16 [0.37–0.95] in the dry season. The capture probability varied over time from 0.011 ± 0.01 [0.002–0.069] to 0.1 ± 0.098 [0.013–0.48]. Regarding the estimation of SP, the two best-fitting models explaining the data both included a capture probability depending on season, and gamma depending on season or constant, respectively (Table 1). Although the selection of models including both a seasonal SP as well as a constant SP, and therefore the difference in SP between seasons, was not substantially important, lower parameters were estimated from model averaging for the dry season (0.5 ± 0.17 [0.20–0.79]) compared to the rainy season (0.88 ± 0.07 [0.66–0.97]). Capture probability was different between seasons; however, estimations were imprecise (rainy: 0.01 ± 0.007 [0.005–0.04], dry: 0.095 ± 0.05 [0.03–0.26]). Meanwhile, the best-fitting model including the estimation of recruitment

![Figure 1](image-url) Distribution of age proportions of *Atelopus varius* individuals from Las Tablas Protected Zone, Costa Rica. (a) Metamorphs: 7 mm; (b) juveniles: <21.5 mm; (c) subadults: 21.5–27 mm; and (d) adults: 27–43 mm (adult females: 33–43 mm).
Table 1. Top-ranked models for *Atelopus varius* apparent survival, recruitment and seniority probability from Las Tablas Protected Zone, Costa Rica. Model averaging was performed to models with delta AICc < 2.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>Delta AICc</th>
<th>AICc weights</th>
<th>Model likelihood</th>
<th>k</th>
<th>Deviance</th>
</tr>
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<tr>
<td><strong>Apparent survival</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phi(.)(season)</td>
<td>178.470</td>
<td>0.000</td>
<td>0.234</td>
<td>1.000</td>
<td>3</td>
<td>84.275</td>
</tr>
<tr>
<td>Phi(.)</td>
<td>179.535</td>
<td>1.065</td>
<td>0.137</td>
<td>0.587</td>
<td>16</td>
<td>56.652</td>
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<tr>
<td>Phi(season)(p)(t)</td>
<td>179.828</td>
<td>1.358</td>
<td>0.118</td>
<td>0.507</td>
<td>17</td>
<td>54.578</td>
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<tr>
<td>Phi(season)(p)(season)</td>
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<td>0.111</td>
<td>0.474</td>
<td>4</td>
<td>83.688</td>
</tr>
<tr>
<td>Phi(age)(p)(season)</td>
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<td>1.912</td>
<td>0.089</td>
<td>0.384</td>
<td>4</td>
<td>84.109</td>
</tr>
<tr>
<td>Phi(.)</td>
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<td>3.190</td>
<td>0.047</td>
<td>0.203</td>
<td>2</td>
<td>89.524</td>
</tr>
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<td>Phi(season)(p)(t)</td>
<td>181.867</td>
<td>3.397</td>
<td>0.043</td>
<td>0.183</td>
<td>17</td>
<td>56.617</td>
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<tr>
<td>Phi.(p)(season)^<em>age</em></td>
<td>182.206</td>
<td>3.736</td>
<td>0.036</td>
<td>0.154</td>
<td>5</td>
<td>83.834</td>
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<tr>
<td>Phi(.)</td>
<td>183.093</td>
<td>4.623</td>
<td>0.023</td>
<td>0.099</td>
<td>3</td>
<td>88.698</td>
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<td><strong>Pradel seniority</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gamma(season)(p)(season)</td>
<td>179.635</td>
<td>0.000</td>
<td>0.522</td>
<td>1</td>
<td>4</td>
<td>−935.597</td>
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<tr>
<td>Gamma(.)</td>
<td>180.215</td>
<td>0.579</td>
<td>0.390</td>
<td>0.748</td>
<td>3</td>
<td>−932.943</td>
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<tr>
<td>Gamma.(p)(.)</td>
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<td>4.765</td>
<td>0.048</td>
<td>0.092</td>
<td>2</td>
<td>−926.702</td>
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<tr>
<td>Gamma(season)(p)(.)</td>
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<td>6.711</td>
<td>0.018</td>
<td>0.035</td>
<td>3</td>
<td>−926.811</td>
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<td>7.180</td>
<td>0.014</td>
<td>0.028</td>
<td>16</td>
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<td>0.013</td>
<td>17</td>
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<tr>
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<td>18.422</td>
<td>0.000</td>
<td>0.000</td>
<td>17</td>
<td>−946.004</td>
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<td>20.814</td>
<td>0.000</td>
<td>0.000</td>
<td>16</td>
<td>−941.264</td>
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<td>Gamma(t)(.)</td>
<td>203.244</td>
<td>23.609</td>
<td>0.000</td>
<td>0.000</td>
<td>27</td>
<td>−965.637</td>
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<tr>
<td><strong>Pradel recruitment</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Phi(.)</td>
<td>1209.240</td>
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<td>0.502</td>
<td>1</td>
<td>18</td>
<td>62.807</td>
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<tr>
<td>Phi(.)</td>
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<td>2.025</td>
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<td>0.362</td>
<td>19</td>
<td>62.367</td>
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<tr>
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<td>0.333</td>
<td>19</td>
<td>62.614</td>
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<tr>
<td>Phi.(p)(t)</td>
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<td>2.449</td>
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<td>0.294</td>
<td>22</td>
<td>55.332</td>
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<tr>
<td>Phi.(p)(season)(t)</td>
<td>1228.038</td>
<td>18.797</td>
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<td>0.000</td>
<td>12</td>
<td>95.491</td>
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<tr>
<td>Phi(t)(p)(t)</td>
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<td>21.635</td>
<td>0.000</td>
<td>0.000</td>
<td>33</td>
<td>45.828</td>
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<td>0.000</td>
<td>12</td>
<td>103.409</td>
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<tr>
<td>Phi(season)(p)(t)</td>
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<td>28.811</td>
<td>0.000</td>
<td>0.000</td>
<td>13</td>
<td>103.246</td>
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<td>Phi(t)(p)(t)</td>
<td>1238.551</td>
<td>29.311</td>
<td>0.000</td>
<td>0.000</td>
<td>26</td>
<td>72.267</td>
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</table>

Comprised constant survival, constant recruitment, as well as a capture probability varying over time (Table 1). Survival estimates for this model (0.86 ± 0.07 [0.66–0.96]) were similar to the estimates with the CJS model, and recruitment was estimated as 0.23 ± 0.07 [0.12–0.39]. Based on the estimates of recruitment and survival, population size rate of change was 1.1 (0.78–1.35).

Tests for chytrid fungus were positive for two of the 15 individuals tested. Additionally, during our surveys rainbow trout (i.e. invasive species) were detected repeatedly. Furthermore, up to a distance of at least 500 m away from the survey area, the vegetation was under clearing maintenance, indicating ongoing habitat transformation within the study area.

**Discussion**

Population parameter estimates showed that the *A. varius* population from Las Tablas Protected Zone was stable, with survival contributing more than recruitment as empirically observed on both rates for our population; the estimation of these demographic components allows questions to be answered regarding population growth rates and the process that represents the most important determinants for such phenomena (Nichols et al. 2000). This is expected for long life expectancy species belonging to the *Atelopus* genus (Lötters 1996; Muths et al. 2011; Lampo et al. 2012). *Atelopus varius* is considered a seasonal breeding species (Lötters 1996; Savage 2002); however, population parameters such as seniority and recruitment were either not or weakly explained by seasonal reproduction, contrary to expectations, possibly due to the low capture rate. Although the population was stable during the survey, we argue that it can still be considered vulnerable to local extinction given the low recruitment rates and high seniority, and considering as baseline the elevated pre-decline population estimates; the species was considered locally abundant in the same area at least 20 years before our surveys (Pounds & Crump 1994; La Marca et al. 2005; González-Mayá et al. 2013a).

Our apparent survival estimates were similar to those estimated for the species in El Copé and Santa Marta in Panama prior to the arrival of *Bd* (McCaffery et al. 2015). They were also similar to the survival parameter estimated for a population of *A. spumarius* from Ecuador that tested negative for *Bd* (Tarvin et al. 2014). The similar survival estimates among these populations, all under *Bd* pre-outbreak scenarios, indicate adult individuals are potentially not severely
affected by the infection, as shown in our population at least during our survey. Our capture probabilities were similar to the lower limit estimates in these localities from Panama (McCaffery et al. 2015), but were substantial lower than those estimated for A. spurrelli and A. elegans in Colombia (Gómez-Hoyos et al. 2014, 2017), which likely contributed to the considerably large confidence intervals of parameter estimates in our study.

No data are available concerning survivorship of froglets, tadpoles or eggs of the species in our study or elsewhere (Lötters 1996), and we did not detect any tadpoles or eggs during our surveys. We found no evidence for seasonal differences in recruitment, and only weak influence of season on seniority (Table 1), contrary to what would be expected for species with marked seasonal reproduction (during the dry season) (Lötters 1996; Savage 2002). However, the absence of individuals below 18 mm SVL could be explained by their very low capture probability.

We found that threats to the population are still operating in the area, as was previously detected by Lips et al. (2003). Habitat loss has not ceased since the reported disappearance of the population in the area. During the last half of the twentieth century our study area was subject to logging and forest cover change due to the expansion of coffee production and pastures for cattle. Even though in the first decade of the twenty-first century logging was stopped in the area, and coffee plantations and cattle raising were considerably reduced, the area inhabited by A. varius is still subject to a low degree of cattle grazing. Chytrid fungus was detected and still potentially threats the survival of this population. Although these results are based on a small sample size, and should be regarded only as confirmation of presence of the fungus in the population, we consider this information relevant for our study; not only this is the first record to Bd presence in A. varius population from LTPZ, but also it is likely the most important threat based on the severe consequences detected in populations of other species upon the arrival of Bd (Ryan et al. 2008; Crawford et al. 2010).

Previous studies have suggested habitat degradation as one of the main causes of Atelopus decline throughout its range (La Marca et al. 2005); for instance, survival of A. spumarius decreased after selective tree harvest within its habitat (Tarvin et al. 2014). Also, rainbow trout has shown constant presence in recent years; the species was introduced to Costa Rica as early as 1927–1928, but it was extensively cultured only since 1988, mainly on the higher parts of Talamanca and other mountain ranges (Vargas 2003). During our field surveys we frequently detected the presence of the species both in the main river and isolated ponds and tributaries. We hypothesized that rainbow trout might cause population decline by predating on eggs, and probably to a minor extent on tadpoles and metamorphs. Atelopus varius lay egg strings on streams and rivers (Lötters 1996) and are probably very susceptible to predation by trout (La Marca et al. 2005; Martín-Torrijos et al. 2016) and other aquatic predators.

We do acknowledge that our results did not test causality or positive/negative relationships between potential threats and population parameters. However, we believe these causes have plausible probability to be affecting the survival of the population, especially since they were already positively related with Atelopus decline both globally and in Costa Rica (Blaustein et al. 1994; Berger et al. 1998; La Marca et al. 2005).

In order to avoid the local extinction of this population, we propose three main conservation/management actions: (1) entrance of other strains of Bd must be avoided by establishing a biosafety protocol, including disinfection of potential carriers of zoospores (e.g. tires, equipment, boots, etc.) for accessing the river; (2) enclosures around located breeding sites to reduce predation on eggs or tadpoles; (3) habitat loss and degradation must be stopped (e.g. maintenance of legal protection areas in the river banks) to maintain suitable conditions around the core population. All proposed measures will need to be assessed through permanent population monitoring in order to test its effectiveness on reducing the risk for this population.

Finally, the good and encouraging news of the rediscovery of this ‘Lazarus’ population also brought the serious challenges of ensuring its survival in spite of the continuing threats. The stable/positive growth rate of the population estimated in our study is promising, although this result has to be interpreted with great caution due to the low capture rates in this study. However, these low capture rates are at the same time an indication that abundance is considerably lower than estimated before (Pounds & Crump 1994; La Marca et al. 2005), which calls for the incorporation of the suggested measures plus continuing close monitoring and research of the population in order to obtain more clues on how to secure these unique populations in the long term.

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**Disclosure statement**

No potential conflict of interest was reported by the authors.

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