Changes in Population Size and Survival in *Atelopus spumarius* (Anura: Bufonidae) Are Not Correlated with Chytrid Prevalence

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ABSTRACT.—Approximately one-third of amphibian species are experiencing population declines. Among the most affected groups are the Harlequin frogs (Bufonidae: *Atelopus*), nearly all of which are threatened with extinction. We monitored one of the last known Ecuadorian populations of *Atelopus spumarius* (Pebas Stubfoot Toad) with a mark–recapture survey between February 2009 and December 2010. We aimed to determine the effect of the fungal pathogen *Batrachochytrium dendrobatidis* (*Bd*), previously recorded at the site, on population size and survival. We also analyzed the effect of selective logging which occurred along the transect in April 2010. We tested every individual captured or recaptured for *Bd* presence using end-point PCR. All 679 *Bd* swabs (from 356 individuals) were negative, suggesting that *Bd* did not influence population size and survival. Population size increased during the first 9 months of the study (August 2009–April 2010), from an estimated 47 to 92 individuals, but then decreased by November 2010 to an estimated 48 individuals. Probability of survival was 0.13 lower in months following selective logging compared to previous months; emigration decreased by 0.37 after the logging event. Pairs in amplexus were found between April and December, suggesting a long, if not year-round, reproductive period. Although most *Atelopus* spp. declines have been attributed to *Bd*, we present a case in which *Bd* has been detected in the area yet changes in population size cannot be attributed to chytridiomycosis. Analyses of survival and male body condition index suggest that the decline at the end of the study was the result of habitat destruction.

RESUMEN.—Aproximadamente un tercio de las especies de anfibios experimentan declives poblacionales. Entre los grupos más afectados están las ranas Arlequín (Bufonidae: *Atelopus*), casi todas se encuentran en peligro de extinción. Monitoreamos el tamaño poblacional y la supervivencia de una de las últimas poblaciones ecuatorianas de *Atelopus spumarius* con un muestreo de marca-recaptura entre Febrero 2009 y Diciembre 2010. Debido a que *Batrachochytrium dendrobatidis* (*Bd*) había sido previamente registrado en el sitio, quisimos determinar su efecto en el tamaño poblacional y supervivencia. También analizamos el efecto de tala selectiva, la cual ocurrió a lo largo del transecto en Abril 2010. Diagnosticamos la presencia de *Bd* en cada individuo capturado o recapturado usando PCR de punto final. Las 679 muestras de *Bd* (provenientes de 356 individuos) fueron negativas, sugiriendo que *Bd* no influenció el tamaño poblacional y la supervivencia. El tamaño poblacional aumentó durante los nueve primeros meses del estudio (julio 2009–abril 2010) de un estimado de 47 a 92 individuos pero luego disminuyó en noviembre de 2010 a 48 individuos. La probabilidad de supervivencia fue 0.13 más baja en los meses posteriores a la tala selectiva que en los meses previos; emigración también disminuyó por 0.37 en los últimos meses. Parejas en amplexus fueron encontradas entre abril y diciembre, sugiriendo un período reproductivo largo, o incluso de duración anual. Aunque la mayoría de declives de *Atelopus* han sido atribuidos a infecciones de *Bd*, presentamos un caso en el que *Bd* ha sido detectado en el área, pero los cambios en el tamaño de la población no pueden ser atribuidos a quitridiomicosis. Análisis de supervivencia y del índice de la condición corporal en machos sugiere que el declive al final del estudio fue resultado de la destrucción del hábitat.

Harlequin frogs (Anura: Bufonidae: *Atelopus*) have been experiencing rapid population declines and extinctions within the last few decades (La Marca et al., 2005). As of May 2013, 71 of 85 *Atelopus* species were Critically Endangered or Extinct (IUCN, 2010). *Atelopus* spp. seem particularly vulnerable to extinction because they occupy riparian habitats, have aquatic larvae, and inhabit small distribution ranges along high-altitude mountains. These characteristics, especially having a small geographical range (Sodhi et al., 2008), have been associated with amphibian declines and *Batrachochytrium dendrobatidis* (*Bd*) infection (Lips et al., 2003; Stuart et al., 2004; Queiroz-Carnaval et al., 2006).

Understanding the population dynamics of *Atelopus* spp. is important because this genus has been used as evidence for two prominent hypotheses to explain amphibian declines in the Neotropical region (Pounds et al., 2006; Lips et al., 2008; Rohr et al., 2008). According to the "climate-linked epidemic hypothesis," *Atelopus* spp. population declines are a consequence of *Bd* epidemic outbreaks caused by an increase in ambient temperature in the tropics (Pounds et al., 2006). An alternative explanation was proposed by Lips et al. (2008), who asserted that *Atelopus* spp. declines resulted from the wave-like geographic spread of *Bd* among previously unexposed popula-

tions. Both studies relied on estimates of the time of population decline throughout Central and South America. Unfortunately, these estimates were based on limited quantitative population data and, thus, their conclusions need to be interpreted with caution (La Marca et al., 2005). Detailed studies of the population size and survival of *Atelopus* spp. are required to identify plausible mechanisms for past population declines.

Despite the large number of amphibian extinctions and decreases in population sizes, few population declines have been monitored closely (Young et al., 2001). Herein we report the population dynamics of a declining population of the Amazonian Harlequin frog *Atelopus spumarius* (Pebas Stubfoot Toad) (Cope, 1871) in Ecuador estimated by mark–recapture surveys. We explored the influence of *Bd* on population size by monitoring its prevalence in the population and evaluating the potential impact of selective logging on survival, condition, and population size. Based on these results, we discuss the relative importance of habitat destruction and disease in influencing extinction risk.

MATERIALS AND METHODS

Study Species.—*Atelopus spumarius* is a bufonid frog distributed in the Amazon Basin of Brazil, Colombia, Ecuador, and Peru (Lötters et al., 2005). The species is considered Vulnerable under IUCN standards, yet it was thought to be locally extinct in Ecuador until it was rediscovered in 2008 (Azevedo-Ramos et al.,

2008; IUCN, 2010). The population at Río Pucayacu is at the upper elevational limit for the species (1,000 m a.s.l.).

Study Site.—We studied a population of *A. spumarius* at Río Pucayacu (1°22′22′′S, 77°51′8′′W), a river surrounded by steep banks of primary forest 2.4 km SE from the Reserva Zanjarajuno (km 9 on the road Puyo-Tena), Pastaza Province, Ecuador (Fig. 1). The site is located on the eastern Andean slopes at an elevation of 1,000 m a.s.l. Vegetation type, as defined by Sierra (1999), is Amazonian Mountain Range Evergreen Foothill Forest characterized by a mixture of Amazonian and Andean vegetation with a canopy of 30 m. Annual rainfall in the region ranges between 2,000–3,000 mm and temperature averages between 22–27°C (Cañadas-Cruz, 1983). A minor rainy season lasts from September to December followed by a major rainy season from January to March. A moderate dry season lasts from April to August.

River width at the study site varies between 6.4 and 14.0 m (mean: 10.3 m) and mid-river depth ranges between 15 and 150 cm (mean: 59 cm) (Acosta, pers. obs.). The river is surrounded by primary and secondary forest. Gravel paving of a road in 2009 allowed logging directly along half of the transect between April and October of 2010. As a result, areas were left without vegetation and covered with sawdust and planks of wood.

Population Sampling.—Population surveys were conducted between February 2009 and December 2010. Sampling was designed under a mark–recapture robust model (Pollock, 1982) which consisted of primary and secondary sampling occasions. The primary sampling occasions (PSOs) lasted between 5 and 10 nights (see Table 1). Each night within a PSO was a secondary sampling occasion (SSO) on which we surveyed a 500-m long transect along the south bank of river Pucayacu, thoroughly checking the foliage 2.5 m into each side of the trail to a height of 2.5 m. We carried out 102 SSOs grouped into 12 PSOs (Table 1).

On each SSO we began sampling at sundown (usually between 1830 h and 1900 h) for a period of 2–5 h, depending on weather conditions and the number of frogs found. Sampling was conducted at night because individuals were at rest over the vegetation and could be found easily with a headlamp. Dorsal and ventral color patterns were used as individual marks; females were distinguished from males by their larger adult size and ventral coloration (more yellow and a greater amount of larger black spots than males). Males with a snout–vent length (SVL) of 20.00 mm or greater and females with an SVL of 26.00 mm or greater were classified as adults; we chose these values based on SVL measurements of individuals in amplexus. Each individual found was photographed, measured with digital calipers to the nearest 0.01 mm, and mass was determined with a spring scale to the nearest 0.1 g. Photographs were stored and organized in FileMaker Pro 11.0v1 (FileMaker, Inc.) and each individual was given a unique identification number. Photographs from each survey were cross-referenced so that individuals could be identified by their distinctive dorsal and ventral patterns. Dorsa were black with variable green mottling and bellies were yellow with black spots of varying size and arrangement. Because the dorsal mottling and ventral spots were extremely variable, individual identification was unambiguous.

We swabbed every individual to test for the presence of *Bd*. To collect the sample we passed a swab (model MW100, Medical Wire and Equipment Co., Wiltshire, UK) 10 times along the dorsum, 10 times along the venter, 10 times on each flank, and 5 times on each palm and sole. We followed biosecurity protocols to avoid pathogen dispersal and sample contamination (Johnson et al., 2003). After swabbing, the individual was released at
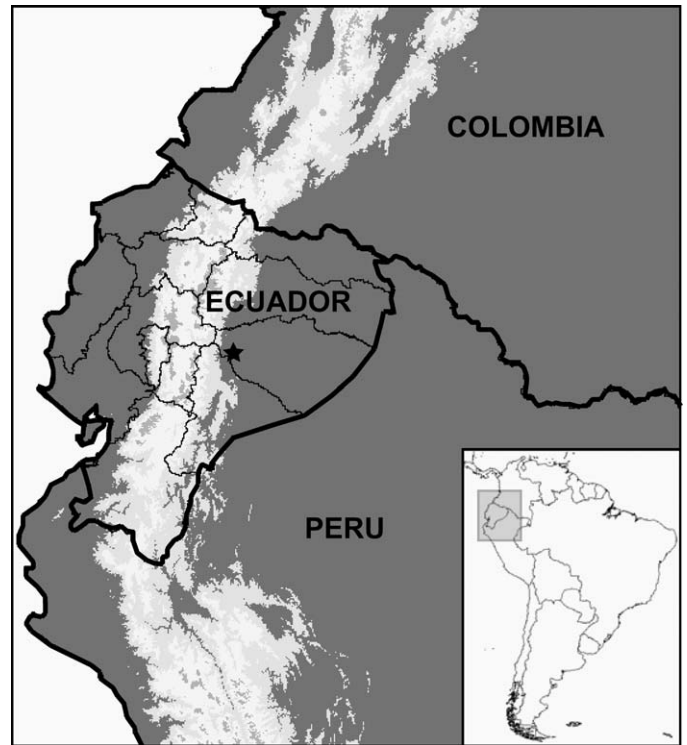

FIG. 1. Location of the study site at Río Pucayacu in Pastaza Province, Ecuador, indicated by the black star.

the same site as capture. We tested for the presence of *Bd* on swabs with end-point polymerase chain reaction (PCR) using the primers and PCR conditions described by Annis et al. (2004).

Territoriality and Movement.—The transect was marked every 5 m so that we could note where individuals were at each sighting. To assess long-term movement, we calculated the longest distance moved along the transect for each individual. We averaged these data among males, females, and juveniles to compare values among demographic classes. In addition, to examine short-term movement (average meter[s] moved per day) we first calculated the number of days between sightings for each individual. We then calculated the number of meters moved between consecutive dates, divided this value by the number of days between dates, and averaged values for each individual. To analyze the difference in average substrate height between adults and juveniles, we first tested for equal variances in distributions and normality and then conducted a one-way analysis of variance (ANOVA) to test the difference in means.

Capture–Recapture Analysis.—We analyzed the mark–recapture data using the robust design model (Pollock, 1982), which considers population sampling at two temporal scales: primary and secondary. PSOs span long time intervals between which the population is considered to be open and, thus, can change in size as a result of mortality and migration. Each PSO was subdivided into SSOs that spanned short periods during which the population was considered to be closed; a mark–recapture model with data from SSOs was used to estimate population size for each PSO (Pollock, 1982). The robust design has the advantage of providing robust estimates of population parameters, some of which are not estimable with separate open or closed models (Williams et al., 2002). We chose the robust design model over the Cormack-Jolly-Seber (CJS) model because assumptions that the CJS model makes regarding capture probabilities can bias estimates of population size; furthermore, estimates of popula-

TABLE 1. Sampling occasions and numbers of captures and recaptures of *Atelopus spumarius* during the mark–recapture study along the river Pucayacu, Provincia Pastaza, Ecuador.

Primary sampling occasion	No. secondary sampling occasions	No. captures (males)	No. recaptures (males)	No. captures (females)	No. recaptures (females)	No. captures (juveniles)	No. recaptures (juveniles)	No. pairs in amplexus
Feb 2009	5	21	1	5	1	7	1	0
Jul 2009	5	16	2	8	6	4	3	1
Oct 2009	9	34	18	12	7	7	5	2
Dec 2009	8	27	6	13	8	8	6	1
Feb 2010	10	35	21	13	6	8	7	0
Apr 2010	10	58	63	18	9	10	5	2
Jun 2010	10	38	32	10	7	13	2	0
Aug 2010	10	48	45	8	10	14	4	2
Sep 2010	10	46	46	10	9	8	3	2
Oct 2010	10	54	43	11	12	15	3	1
Nov 2010	5	17	5	9	2	5	0	0
Dec 2010	10	38	16	11	5	17	5	0

tion size and survival by the robust design model tend to be more precise (Kendall et al., 1995). The structure of the robust design reduces bias in capture and survival probabilities by allowing finer control over parameter precision (Kendall and Pollock, 1992; Kendall and Nichols, 1995).

We estimated population size within PSOs and survival and emigration rates between PSOs using the program MARK (White and Burnham, 1999). Females and males were grouped together because a preliminary analysis (not shown) indicated that male and female survival was not significantly different. The test consisted of a comparison between two robust models with a likelihood ratio test. In one model there was a single parameter for male and female survival while in the other the survival parameters for males and females were separate. The test favored the less parameterized model.

Under the maximum likelihood models implemented by MARK, model overparameterization is indicated by unrealistically narrow or wide confidence intervals for population parameters. To avoid model overparameterization, we tried a number of model simplifications: setting capture (p) and recapture (c) rates to be constant within each PSO, which assumes that capture (and recapture) efforts were constant within PSOs but not among PSOs; setting p equal to c; setting p and c estimates equal for two consecutive PSOs (rather than having one estimate per PSO); and setting γ'' and γ' (probability of being outside the study area during the current PSO given that during the last PSO the individual was inside or outside the study area, respectively; henceforth, emigration) equal to each other and with one estimate for each pair of consecutive PSOs or a single estimate for the entire study (see Table 2). We also tested models with two values for emigration, as initial estimates were high in the first five PSOs and low in the last four PSOs. To choose among competing models, we used Akaike's Information Criterion with small sample size correction (AICc). Even after reducing the number of parameters, only a few models were estimable.

We excluded the first PSO (February 2009) from our mark–recapture analyses because the searching skills of the surveyors at the beginning were not comparable to those of subsequent surveys. We also excluded the last PSO (December 2010) because its inclusion generated unrealistic confidence intervals for some population parameters. This was likely a result of the low number of captures per SSO towards the end of the study. However, data from individuals captured during the first and last PSOs were used in all other analyses.

We used two likelihood ratio tests to determine if survival and emigration were significantly different before and after the logging event. In each test we compared two variations of our selected model: one in which the survival or emigration parameter was constant throughout the study and one in which survival or emigration was separated into two estimated parameters. For survival, the first parameter represented survival before the logging event (October 2009–April 2010), and the second parameter represented survival following the logging event (June 2010–November 2010). However, for emigration we included June 2010 in the first parameter (October 2009–June 2010) rather than in the second (August 2010–November 2010) because our models showed a decrease in emigration starting after June 2010 rather than April 2010; this is the same division as in our selected model.

Body Condition Index.—Body condition is predicted to decrease as a result of habitat degradation (Stevenson and Woods, 2006). We averaged individual SVL and mass for each PSO and calculated body condition index as the ratio between average mass and average SVL. We compared body condition indices before and after logging. Because the data were non-normally distributed and contained repeated measures of the same individuals, we used nonparametric two-sample Wilcoxon tests to compare indices before and after logging in both the logged and unlogged areas of the transect. Because logging affected males and females differently, we analyzed male and female datasets separately. We performed all statistical analyses in R version 3.0.0 (R Development Core Team, 2013). Unless otherwise noted, results are reported as mean ± SE.

RESULTS

Detection of Batrachochytrium dendrobatidis (Bd).—All 679 *Bd* samples from 356 individuals (average number of tests per individual = 1.91 ± 0.07) tested negative for *Bd* DNA.

Population Size and Survival.—During 102 surveys (SSO) from February 2009 to December 2010, we encountered 356 individuals of which 200 were adult males, 72 were adult females, and 84 were juveniles. Males were more abundant than females (average PSO sex ratio = 4.1 males : 1.0 females), and adults were found more often than juveniles (absolute counts: average PSO adult to juvenile ratio = 5.3 adults : 1.0 juveniles). On average, each male was encountered 3.7 ± 0.3 times (range 1–26, N = 738 sightings), each female was encountered 2.8 ± 0.3 times (range

TABLE 2. Robust design models from MARK used to estimate population size and survival rates for the Río Pucayacu *Atelopus spumarius* population. Abbreviations: PSO = primary sampling occasion, SSO = secondary sampling occasion, S(t) = survival probability estimated between each PSO, N(t) = population size estimated for each PSO, p(.) = capture probability constant within each PSO, p(t) = capture probability estimated for each SSO, c(.) = recapture probability constant within each PSO, c(t) = recapture probability estimated for each SSO, γ' = probability of unavailability given unavailability in the last PSO, γ'' = probability of unavailability given availability in the last PSO, AICc = Akaike's information criterion with sample size correction, * = estimates for two consecutive PSOs, $\wedge$ = selected model.

Model	AICc	No. parameters	Model likelihood	Deviance
$\wedge$S(t)N(t)p*(.)c*(.), $c* = p*$, $\gamma' = \gamma'' = 2$ values	2,233	26	1.0000	2,470
S(t)N(t)p*(.)c*(.), $c* = p*$, $\gamma'* = \gamma''*$	2,241	28	0.0161	2,474
S(t)N(t)p(.)c(.), $c = p$, $\gamma' = \gamma'' = $ constant	2,254	30	0.0000	2,483
S(t)N(t)p(.)c(.), $\gamma' = \gamma'' = $ constant	2,257	40	0.0000	2,465
S(t)N(t)p(t)c(t), $\gamma' = \gamma'' = $ constant	2,349	105	0.0000	2,340

1–16, N = 200 sightings), and each juvenile was encountered 1.8 ± 0.2 times (range 1–11, N = 157 sightings). Fifty-one percent of males, 65% of females, and 43% of juveniles were captured more than one time. Ninety-two percent of the individuals found in the first two PSOs were not found in the last two PSOs (samplings 11, 12) and none of the individuals found in the first PSO were found in the final PSO.

After reviewing all possible parameter combinations in MARK, five models were estimable with zero confidence errors. We report the values from the model predicted to be the best by AICc, S(t)N(t)p*(.)c*(.), $c* = p*$, $\gamma' = \gamma'' = 2$ values (Table 2): survival (S) and population size (N) fluctuated over time while capture (p) and recapture (c) probabilities were held constant within each PSO but varied among PSOs. Estimates of p and c were constant for each pair of consecutive PSOs; γ', and γ'' estimates were set equal to each other and best represented by two values, one encompassing October 2009–June 2010 and the other August 2010–November 2010.

Between August 2009 and April 2010, the population size increased from 47 to 92 individuals. Following the logging event (April 2010), population size decreased to 59 individuals by the next PSO (June 2010), increased slightly in subsequent PSOs, but then decreased overall by November 2010 (to 48 individuals; Fig. 2). Probability of survival fluctuated between 0.57 and 0.97 during the study (Fig. 2). Average survival before the logging event (0.88) was significantly higher than survival following the logging event (0.75; likelihood ratio test: df = 1, $\chi^2 = 11.38$, P = 0.0007). Estimates of emigration (γ' and γ'') were high in the first part of the study (0.61) but significantly decreased two PSOs after the logging event for the remainder of the study (0.24; likelihood ratio test: df = 1, $\chi^2 = 17.81$, P < 0.0001).

Reproduction and Movement Patterns.—During the study we encountered 11 pairs in amplexus during the months of April, July, August, September, October, and December (Table 1). Mean SVL for adult males was 23.45 ± 0.06 mm (range 20.00–30.10, N = 725) with an average mass of 0.95 ± 0.01 g (range 0.2–2.1, N = 717); mean adult female SVL was 30.18 ± 0.17 mm (range 26.30–36.10, N = 183) with a mean mass of 2.1 ± 0.03 g (range 1.1–3.5, N = 179). Frequently, individuals were found nightly at the same meter of the transect or close nearby; sometimes individuals were found night after night (and in one case, month after month) on the same leaf. During this study the average maximum distance moved by individual males was 13.4 ± 2.6 m (range 0–295), for females 11.0 ± 2.5 m (range 0–63), and for juveniles 7.2 ± 2.8 m (range 0–100). Short-term movement averaged between 1.1 and 1.6 m per day (males: 1.1 ± 0.3 m/day, range 0–31, N = 668 sightings, 130 individuals; females: 1.6 ± 0.6 m/day, range 0–20, N = 168 sightings, 37 individuals; juveniles: 1.4 ± 0.5 m/day, range 0–15, N = 157 sightings, 84 individuals). Daily movement

was not significantly different among demographic classes (multi-way ANOVA: df = 2, F = 0.34, P = 0.71). Juveniles were found significantly closer to the ground than were adults (juvenile average height = 74.6 ± 3.5 cm; adults = 102.3 ± 1.5 cm; one-way ANOVA: df = 1, F = 52.0, P < 0.001).

Body Condition Index.—Overall, females had higher body indices than did males (0.065 g/mm vs. 0.041 g/mm, respectively), as is expected during the mating season, and the effect of logging was different for males versus females. Male body index decreased significantly in the logged (from 0.041 ± 0.0006 g/mm to 0.039 ± 0.0004 g/mm), but not in the unlogged, area (from 0.041 ± 0.0007 g/mm to 0.040 ± 0.0005 g/mm) following the logging event (two-sample Wilcoxon test, logged: W = 5798, P = 0.0020; unlogged: W = 3583, P = 0.18). On the contrary, female body indices were unaffected by the logging event in either transect area (logged area: before = 0.069 ± 0.002 g/mm; after = 0.070 ± 0.002 g/mm, two-sample Wilcoxon test, W = 889, P = 0.81; unlogged area: before = 0.057 ± 0.003 g/ mm, after = 0.60 ± 0.003 g/mm, W = 129, P = 0.74).

Discussion

We estimated *A. spumarius* survival, body condition, population size, movement, reproductive activity, and *Bd* prevalence for 18 months. Our detailed demographic information allows us to demonstrate that *Bd* did not have a significant impact in the size and survival of the studied population. Population declines in *Atelopus* spp. have been linked to disease outbreaks caused by *Bd* (Bonaccorso et al., 2003; La Marca et al., 2005; Lips et al., 2008), but the evidence has been inconclusive because it lacked detailed information on pathogen prevalence and host survival. Our study is the first designed to explore the link between *Bd* prevalence and population size and survival in *Atelopus* spp.

Batrachochytrium dendrobatidis was not found during the study despite the intensive sampling effort (679 samples). Absence of *Bd* was unexpected because *Bd* had been recorded previously at the site using the same diagnostic technique. In 2008, two *Engystomops petersi* (Peters' dwarf frog) and one *Leptodactylus wagneri* (Wagner's White-lipped Frog) tested positive for *Bd* (out of 127 tested individuals belonging to 35 species, none of them *Atelopus*; Ron, unpubl. data). The fact that *Bd* is present in the area suggests that *A. spumarius* can either avoid becoming infected or, if infected, the zoospore load per individual is too low to be detected by end-point PCR. Although we cannot rule out the presence of mildly infected individuals (end-point PCR cannot detect less than 10 zoospores; Annis et al., 2004) it is unlikely that those infections have a significant impact on individual survival. Hence, we conclude that in this study the
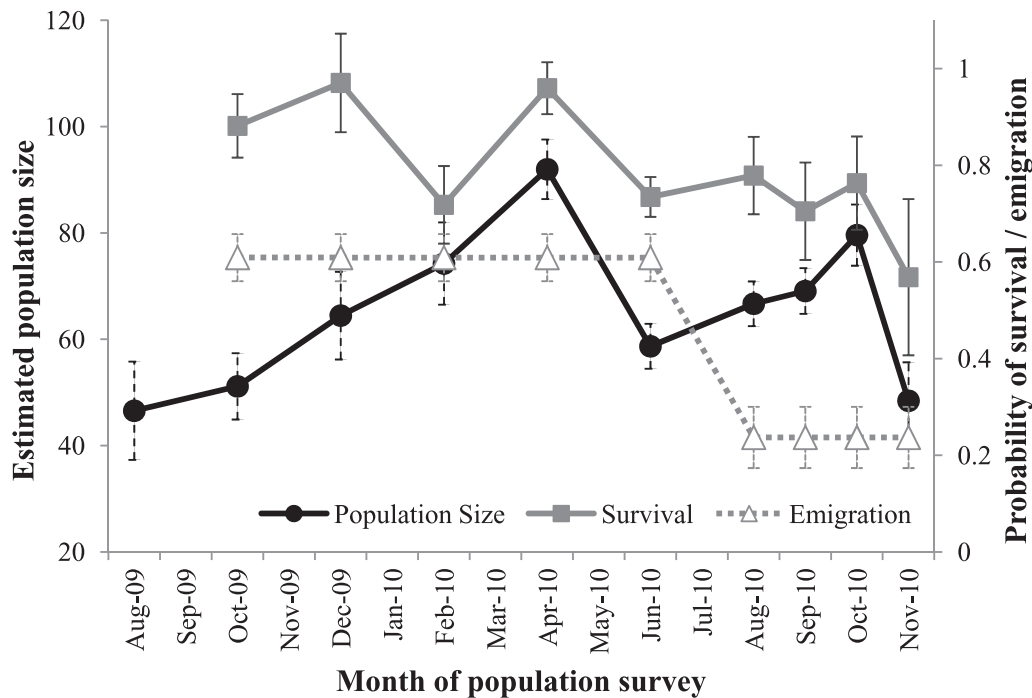
FIG. 2. Estimated number of adults and probability of survival and emigration (γ; unavailability) of the *Atelopus spumarius* population along the River Pucayacu, Pastaza Province, Ecuador. Bars represent standard error.

changes in population size and survival cannot be attributed to an effect of *Bd*.

Our results are similar to two studies on *Atelopus* spp. in which *Bd* was present at populations of stable or increasing size. The first study was carried out on *Atelopus cruciger* (Rancho Grande Harlequin Frog) in Venezuela (Lampo et al., 2012). As in our study, prevalence of *Bd* was low (only 1.4% of tested individuals had spore loads >10). The study lasted over 1 yr, during which the population showed a slight increase in abundance, indicating that *Bd* did not have severe demographic effects. The second study was carried out in a population of *Atelopus elegans* (Elegant Stubfoot Toad) in Colombia (Flechas et al., 2012). At that site, *Bd* was detected with low prevalence in 2007 and 2010. Although individual counts were not systematic, there were not noticeable changes in population size between 2007 and 2010.

The results from *A. cruciger*, *A. elegans*, and *A. spumarius* suggest that, at least at present, *Bd* is not adversely affecting lowland (below 1,000 m) populations of *Atelopus* spp. in tropical South America. Additional studies are necessary to determine if this pattern can be generalized to other species and regions. The lack of effect of *Bd* on current population survival does not rule out severe negative effects in the past, as predicted by the novel pathogen hypothesis of *Bd* (Fisher et al., 2009). The epidemic outbreak resulting from the arrival of the exotic pathogen could have generated high mortality and, thus, strong natural selection for disease resistance. This evolutionary response would explain the low prevalence of *Bd* in our study.

Recent genetic studies, however, show that *Bd* has high genetic diversity, a pattern unexpected for a novel spreading pathogen (Rosenblum et al., 2013). In addition, the Rosenblum et al. (2013) phylogeny shows that the earliest diverging lineages of *Bd* are from South America, suggesting a South American origin. In light of these findings, our results seem more consistent with an endemic *Bd* rather than a novel geographic spread of *Bd* because long-term host–pathogen

coevolution usually results in increased host resistance or decreased pathogen virulence (Woolhouse et al., 2002; Thrall and Burdon, 2003); conversely, see Claessen and de Roos (1995).

We report for the first time demographic estimates on population size, survival, and movement patterns of males, females, and juveniles of *A. spumarius*. As described for *Atelopus varius* (Clown Frog) (Crump, 1986), males and females of *A. spumarius* were found often in the same vicinity over periods of more than a year, suggesting that both sexes are territorial; juveniles also exhibited high site fidelity. Mating in *A. spumarius* was recorded between April and December and may occur over the entire year, as has already been suggested by Azevedo-Ramos et al. (2008).

The population increased in size during the first 9 months but declined toward the end of the study after a portion of the transect was logged (Fig. 2). The concurrent decrease in estimates of emigration suggests that individuals were not leaving the study site, regardless of the habitat degradation. Starting in April 2010, local residents began felling the largest trees along the transect. By October 2010, the majority of the old growth trees were gone and many planks from felled trees were left behind, exposing half of the transect to increased sunlight and temperature. A second 250-m section of forest across the river, where more *A. spumarius* have been seen, was also logged. It is likely that these habitat changes affected this *Atelopus* population negatively, as individuals were found most often under closed canopy, near medium-to-large sized trees, and were almost never seen adjacent to felled trees. Indeed, probability of survival was lower following the logging event. Males appeared to be particularly affected, as their body indices following deforestation were significantly lower in the logged area. Conversely, female body indices were not affected by the logging event, suggesting that males and females are differentially affected by habitat disturbance.

Lampo et al. (2012) suggests that *Atelopus* spp. may have short life spans and high recruitment rates, contrary to previous

reports (e.g., La Marca, 1984). Our study supports this finding, as only 8% of the individuals seen in the first two surveys were seen in the last two (after 18 months). Nevertheless, even if *A. spumarius* has a high population turnover rate, a low probability of survival can still contribute to population decline. For example, in the long-lived Western Toad (*Anaxyrus* (= *Bufo*) *boreas*), high recruitment rates in a population with low survival were insufficient to rescue the population from overall decline (Muths et al., 2011).

Although these results suggest a role of selective logging in the decline of this population, we are unable to determine conclusively if logging was a causal factor. The initial population size in August 2009 was the same as the final population size in November 2010; thus, it is conceivable that the population decline during the last part of the study was the product of a natural fluctuation unrelated to the habitat degradation that began in April–June 2010. Nevertheless, in Amazonian Ecuador, *A. spumarius* is only known from three additional localities, all in primary forest (at Parque Nacional Yasuní; Ron et al., 2012). The lack of records of *A. spumarius* in logged forests and open areas throughout its range in Ecuador suggest that it has a high sensitivity to deforestation. If individuals are not leaving the study site, as our estimates of emigration and evidence of high site fidelity suggest, this population may be at risk for extinction.

Unlike previous accounts of *Atelopus* spp. declines, the decreasing size and survival of this *A. spumarius* population cannot be attributed to chytridiomycosis. Even though most *Atelopus* spp. declines have been attributed to *Bd*, other factors such as habitat destruction, an important global driver of amphibian decline (Sodhi et al., 2008), should not be over-looked. If selective logging along Río Pucayacu continues, all prime habitat for this *A. spumarius* population will disappear, and the effect of logging will likely become more prominent. With declining probabilities of survival, low rates of emigration, and an already decreasing population size, we predict that the Río Pucayacu *A. spumarius* population may soon go extinct.

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