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Original research article

The demography of *Atelopus* decline: Harlequin frog survival and abundance in central Panama prior to and during a disease outbreak

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ABSTRACT

Harlequin frogs (Bufonidae: *Atelopus*) are a species-rich genus of Neotropical toads that have experienced disproportionately severe population declines and extinctions caused by the amphibian chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*). The genus *Atelopus* is of high conservation concern, but relatively little is known about the population dynamics and life history of the majority of species. We examined the demography of one population of *Atelopus zeteki* and two populations of *A. varius* in central Panama using three to six years of mark-recapture data collected prior to and during an outbreak of *Bd*. We estimated male survival probabilities prior to the arrival of *Bd* and sex-specific population sizes for these three populations using state-space Bayesian population models. Prior to the arrival of *Bd*, monthly apparent survival probabilities were higher for *A. varius* males than for *A. zeteki* males, and recaptures among years were low in both species. Abundance of both species varied over time and declined rapidly after the arrival of *Bd*. Male densities were generally greater than female densities, though female densities were higher or equivalent to males after the arrival of *Bd*. Estimates of survival and abundance over time may be explained by differences in the use of stream habitat by the two sexes and three populations, both during and between breeding seasons. These estimates provide key baseline population information that can be used to inform reintroductions from captive assurance colonies and studies of extant *Atelopus* populations as part of conservation and management programs.
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1. Introduction

Harlequin frogs (Bufonidae: *Atelopus*) are among the most threatened amphibian taxa in the world (La Marca et al., 2005), and are emblematic of tropical amphibian declines caused by the amphibian chytrid fungus *Batrachochytrium dendrobatidis*, *Bd* (Lips et al., 2006, 2008; Crawford et al., 2010). At least 40 of 97 described species have disappeared in the past 20 years, with three species listed as extinct (IUCN, 2014), 82 species listed as Endangered or Critically Endangered (IUCN, 2014), and only 10 stable species (La Marca et al., 2005; Lips et al., 2008). Declines have been particularly severe at elevations above 1000 m, although lower elevation populations have also been affected. Species have disappeared from throughout the range of this large genus, from Costa Rica and Panama to Colombia, Ecuador, Venezuela and Peru (La Marca et al., 2005). The

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alarming declines in this genus have prompted biologists to conduct extensive surveys of habitats within the genus' range to determine the presence of remnant populations in areas affected by *Bd*, identify new populations, and initiate monitoring efforts for remaining populations. Despite the attention to population declines in these species, we know relatively little about their natural history and population dynamics. Because of this, studies of *Atelopus* population dynamics are a critical missing component of ongoing research and recovery programs.

Past studies of *Atelopus* species have focused on general distribution patterns, ecology, and behavior. Species in this large genus are quite similar in their general ecology (Lötters, 1996; Savage, 2002). These toads are typically small to medium-bodied, with bright and contrasting aposematic coloration (Wells, 2007). They are typically diurnal and found on stream banks or on rocks in the stream where they breed during the dry season or year-round. Territoriality and aggression by males of certain species have been well-documented (Crump, 1988; Lindquist and Hetherington, 1996), and males appear to exhibit high site fidelity (Crump, 1986). In two recent studies, researchers have quantified population parameters for a remnant *Atelopus cruciger* population in Venezuela (Lampo et al., 2012), and a rediscovered *Atelopus spumarius* population in Ecuador (Tarvin et al., 2014). These estimates provide a baseline for comparing demographic rates to other South American *Atelopus* species. Analyses such as these can provide information on demographic rates in rediscovered *Atelopus* populations where *Bd* has been present (Tarvin et al., 2014), as well as on demographic responses to *Bd* outbreaks across species, populations, and time periods (Lampo et al., 2012). Additionally, they can help with designing monitoring programs, and can provide critical demographic information to inform captive breeding programs and potential reintroduction efforts in critically endangered species. For example, understanding natural population densities may be useful for determining how many individuals to reintroduce into stream habitat, and estimates of survival from *Bd*-free and infected populations provide an important basis with which to compare survival in captive and reintroduced populations of interest.

Capture–recapture studies provide a powerful design for estimating survival and population size in amphibian populations. By tracking individuals, researchers can estimate survival, recruitment, and other population parameters of interest while accounting for probability of detection, where raw counts of individuals are corrected for imperfect detection (Schmidt et al., 2002; Funk et al., 2003; Mazerolle et al., 2007). Detection probabilities are rarely constant over time, so indices of population size like visual counts often do not capture true population dynamics (Lampo et al., 2012; Guimarães et al., 2014). Capture–recapture studies are relatively rare in the amphibian literature (Mazerolle et al., 2007), and are particularly infrequent in studies of amphibian populations in tropical systems (Guimarães et al., 2014). However, their importance in Neotropical amphibian ecology has been recognized and several recent papers have estimated survival and abundance parameters from capture–recapture data in the past ten years (Ryan et al., 2008; Murray et al., 2009; Longo and Burrowes, 2010; Lampo et al., 2012; McCaffery and Lips, 2013; Cole et al., 2014; Tarvin et al., 2014). In tropical studies, capture–recapture analyses of amphibian populations have led to a greater understanding of the natural population dynamics of several species, including baseline survival estimates, density estimates, and population growth rates (e.g., McCaffery and Lips, 2013). Furthermore, they have contributed to our understanding of how habitat disturbance and climate may impact species demography (Cole et al., 2014), provided insight into the demographic mechanisms of decline due to *Bd* (Ryan et al., 2008; Murray et al., 2009), and yielded information on survival rates in populations persisting with disease (Murray et al., 2009; Lampo et al., 2012).

We examined the abundance and survival of two species of *Atelopus* found in central Panama prior to and during an outbreak of *Bd*. *Atelopus varius* is a species that is native to Costa Rica and Panama, and was historically found in moist lowland and montane rainforest localities along fast-flowing, high gradient streams (Savage, 2002). The species experienced dramatic population declines and disappearances across its range, starting in northwestern Costa Rica in the 1980s and moving into central Panama by the 2000s. In 2008 it was listed as Critically Endangered on the IUCN Red List (Pounds et al., 2010). In recent years, a few individuals of *A. varius* have been found in several areas where they were presumed extirpated following the arrival of *Bd*, including sites in Costa Rica (González-Maya et al., 2013) and Panama (Hertz et al., 2012; Perez et al., 2014). *Atelopus zeteki*, also known as the Panamanian golden frog, is endemic to a small area of central Panama, where it is typically found in low to middle elevation dry and moist forest habitat (Zippel et al., 2006). It has experienced dramatic declines over the past 15 years as *Bd* has moved from west to east through Panama, and is also listed as Critically Endangered on the IUCN Red List (Lips et al., 2010). It is considered extinct in the wild (Hertz et al., 2012). Both species are being maintained and bred in several zoos for eventual reintroduction (Zippel, 2002).

Between 1999 and 2006, we collected capture–recapture data for three populations of these two species as part of larger projects addressing other research questions. Because of the need for demographic data for ongoing conservation and reintroduction programs we analyzed these two datasets together and present results to maximize possible application by practitioners. Our aims for this study were to: (1) estimate survival probabilities in male *Atelopus* prior to the outbreak of *Bd*; (2) estimate abundance of male and female *Atelopus* prior to and during the disease outbreak; and (3) determine whether the three populations differed in survival and abundance patterns.

2. Methods

2.1. Study areas and field methods

We studied *Atelopus varius* in two neighboring areas in central Panama (Fig. 1). The two sites were both located in the 25,000 ha Parque Nacional G. D. Omar Torrijos, located in Coclé Province. We considered each site to be a separate population.

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