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Spatial and temporal variation in population dynamics of Andean frogs: Effects of forest disturbance and evidence for declines

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ABSTRACT

Biodiversity loss is a global phenomenon that can result in the collapse of food webs and critical ecosystem services. Amphibian population decline over the last century is a notable case of species loss because amphibians survived the last four major extinction events in global history, their current rate of extinction is unprecedented, and their rate of extinction is greater than that for most other taxonomic groups. Despite the severity of this conservation problem and its relevance to the study of global biodiversity loss, major knowledge gaps remain for many of the most threatened species and regions in the world. Rigorous estimates of population parameters are lacking for many amphibian species in the Neotropics. The goal of our study was to determine how the demography of seven species of the genus *Pristimantis* varied over time and space in two cloud forests in the Ecuadorian Andes. We completed a long term capture–mark–recapture study to estimate abundance, survival, and population growth rates in two cloud forests in the Ecuadorian Andes; from 2002 to 2009 at Yanayacu in the Eastern Cordillera and from 2002 to 2003 at Cashca Totoras in the Western Cordillera. Our results showed seasonal and annual variation in population parameters by species and sex. *P. bicantus* experienced significant reductions in abundance over the course of our study. Abundance, apparent survival, and population growth rates were lower in disturbed than in primary or mature secondary forest. The results of our study raise concerns for the population status of understudied amphibian groups and provide insights into the population dynamics of Neotropical amphibians.

1. Introduction

Amphibians survived the last four major extinction events in the history of earth (Wake and Vredenburg, 2008), yet their current extinction rates and risk for future population decline are among the highest of any taxonomic group (Stuart et al., 2004). Drivers of amphibian population declines include land use change, climate change, disease, environmental contaminants, invasive species, and exploitation for the food, pet, and medical trade (Beebee and Griffiths, 2005; Blaustein and Kiesecker, 2002). Despite the severity of the threats they face and their significance to research focused on biodiversity loss, amphibians are one of the least studied taxonomic groups (Lawler et al., 2006).

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Baseline population vital rates, including abundance, survival, and population growth rates, are critical for determining extinction risk and population trends. Mark–recapture studies are a particularly robust method for determining population vital rates because they can control for a number of variables that might influence the detection of individuals, including survival, probability of capture, population growth rate, movement of individuals, and any variables that might co-vary with these parameters. Deforestation has contributed to population declines in tropical amphibians (Brook et al., 2003; Gardner et al., 2007; Pandit et al., 2007). Yet the effect of deforestation could may only be detected over a longer time frame (Todd and Rothermel, 2006). Long term monitoring is essential to accurately distinguish drivers of population dynamics, assess extinction risk (Bonebrake et al., 2010; Pechmann et al., 1991), and rigorously estimate population parameters (Funk et al., 2003).

The tropical Andes are an important focal region for studies on amphibian population dynamics because little is known about this biodiversity hotspot where high levels of diversity and endemism are at high risk of loss (Myers et al., 2000). Amphibian species in the tropics are more likely to experience threats from pathogens, climate change, and land-use change (Hof et al., 2011). High elevation, aquatic species in central and South America are generally thought to be the most susceptible to population decline (Stuart et al., 2004), but this conclusion may be biased because so little is known about the status of other amphibian groups. While there are some examples of studies that have competed completed robust estimates of population parameters of amphibians in the Neotropics (Ryan et al., 2008; Lampo et al., 2011; McCaffery and Lips, 2013), many amphibian population studies lack rigorous methods. An evaluation of studies published from 2006 to 2013 in South American herpetology journals showed that the majority (81%–95%) did not take into account bias related to imperfect detectability (Guimaraes et al., 2014). Mark–recapture analyses have not been used to estimate population vital rates for frogs from the genus *Pristimantis*. The absence of rigorous estimates of population parameters prevents accurate assessments of extinction risk, spatial patterns in population dynamics, and species differences for vulnerable regions and taxonomic groups.

The genus *Pristimantis* contains 462 described species (AmphibiaWeb, 2014), with more being discovered each year, making it the most speciose vertebrate genus in the world. *Pristimantis* frogs are distributed widely throughout the Neotropics from 0 to 4100 m above sea level (Carvajalino-Fernández et al., 2011). *Pristimantis* species are direct-developing (i.e. they hatch from eggs as small froglets) and are considered to have a lower population threat status and risk of population decline (Green, 2003), in part because they are not dependent on aquatic habitat for reproduction (Becker et al., 2007). There are many data deficient species in this group, but population decline or local extinction have been reported for some *Pristimantis* species in Costa Rica, Panama, Puerto Rico, Guatemala, Dominican Republic, Columbia, and Brazil (Hedges, 1993; Lips, 1999; Young et al., 2001). Reliable estimates of vital rates across more species in this genus are required to determine whether the species are persisting more successfully than other groups or if *Pristimantis* species are declining un-noticed by scientists and conservation professionals. Understanding how population parameters such as abundance, survival, and population growth vary across time, space, species, and sex is the first step in determining conservation status and trends.

We conducted a long-term study to understand the population dynamics and demography of *Pristimantis* frogs in the Ecuadorian Andes. We collected 4 years of data, from 2002 to 2009, and used mark–recapture modeling to determine (1) whether populations of seven *Pristimantis* species are growing, stable, or in decline, and (2) whether apparent survival, population growth rates, and abundance estimates differed among forest patches and/or species. Our study attempts to fill a critical gap in amphibian decline research by testing models that evaluate the effect of local variation in habitat, seasonal and interannual variation, species, and sex on population vital rates of seven *Pristimantis* species using a long-term capture–mark–recapture analysis. The results of our study are relevant to the conservation of an understudied, diverse, and potentially at-risk taxonomic group in one of the most vulnerable regions of the world.

2. Materials and methods

2.1. Study regions

We monitored populations of *Pristimantis* species in two regions in Ecuador, Bosque Protector Cashca Totoras, Bolivar Province (1° 43′ S, 78° 58′ W, 3000–3200 m) and Yanayacu Biological Station, Napo Province (0° 35′ S, 77° 53′ W, 1900–2400 m; Fig. 1). In each region, we randomly selected three, 50 m × 50 m grids within a 500 m × 500 m area for population monitoring (Fig. 1). At Yanayacu Biological Station, we monitored all grids 11 times from May 2002 to May 2009 (May 2002, August–September 2002, April 2003, August–September 2003, December 2003, January 2007, April 2007, June–July 2007, January–February 2009, March–April 2009, and May 2009). Thus, there was a gap of approximately three years in the middle of our sampling period due to a lapse in research funds. At Bosque Protector Cashca Totoras, we monitored all grids 6 times approximately every other month from March 2002 to November 2003. We estimated population vital rates at both sites but population declines could only be detected robustly at Yanayacu, where the sampling period spanned 8 years.

The sampling sites differed in terms of habitat composition, temperature, precipitation, and timing of the wet season. Undisturbed, primary forest dominates the region at Yanayacu Biological Station and the plant community is diverse. For trees greater than 5 cm in diameter breast height, Lauraceae is the most speciose family, followed by Moraceae, Fabaceae, and Solanaceae (Valencia, 1995). The forest at Bosque Protector Cashca Totoras is more disturbed, consisting of a mixture of pasture, primary cloud forest, secondary cloud forest, and stands of evergreen bamboo (genus *Chusquea*). Yanayacu