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## Ineffectiveness of Call Surveys for Estimating Population Size in a Widespread Neotropical Frog, *Oophaga pumilio*

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**ABSTRACT.**—Call surveys offer a valuable method to monitor anuran populations attributable to their temporal breeding habits and close association with water. Many temperate locations have adopted citizen science programs to monitor local anuran populations using call surveys and road transects. These surveys, however, are not commonly conducted in the tropics. I tested use of call surveys for estimating population density of a small terrestrial poison frog, *Oophaga pumilio*, in six different populations in Bocas del Toro, Panama. By conducting three-minute call surveys, and searching for all individual frogs in a 10 m radius of the survey point, I directly compared the number of calling males to the observed number of frogs in a given area. I found call density to be a poor predictor of population density. Despite there being differences in population densities, the lack of a relationship between the number of calls and population density highlights the limited use for call surveys for terrestrial, territorial species. Although call surveys may be useful in some taxa for general abundance estimates, this study clearly demonstrates a startling deficiency of call surveys for anuran monitoring and highlights the need for species-specific analysis to further explore the utility of this method.

Because most amphibians have limited sites to rear their larvae, they will often congregate around suitable locations during the breeding season. These aggregations of amphibians, especially anurans, provide researchers the opportunity to sample species that otherwise may be difficult to sample during nonbreeding times (e.g., hylid tree frogs). Because these allow observation of population trends, demographics, and reproductive output all at once, such breeding gatherings are important for managing threatened species. Although no accurate method has been developed to analyze population trends quantitatively using call surveys, methods exist to qualitatively assess population trends (Mossman et al., 1998; Genet and Sargent, 2003).

Wildlife managers commonly conduct call surveys around breeding sites to estimate relative abundance of frogs. Many areas in the United States and Canada have active, citizen-science-based programs to qualitatively assess population trends (e.g., Lepage et al. 1997, Mossman et al. 1998, Genet and Sargent 2003). These programs typically will rank the number of calls on a standardized scale to estimate the number of males calling over the course of the breeding season (Mossman et al., 1998). This qualitative method is primarily used because of oversaturation of calling males and the inability to distinguish individuals in a chorus (Genet and Sargent, 2003). It is particularly useful in temperate areas where most amphibians depend on seasonal bodies of water to breed. Biologists generally assume a linear relationship between calling intensity and population size, but few studies have tested this (Mossman et al., 1998).

Call surveys are not commonly used for tropical anurans. This may be in part attributable to the climatic aseasonality as compared to temperate regions (Janzen, 1967). Despite this reduced amount of seasonality, many anuran species show punctuated breeding seasons based on the amount of rainfall over the course of a year (Gottsberger and Gruber, 2004). Given the number of species (especially threatened species; Myers et al., 2000) found in tropical regions, a method such as call

surveys that allows for detection and qualitative analysis of populations may provide a useful tool for assessing and monitoring tropical amphibians.

Further complicating the utility of call surveys is the role of weather on encouraging breeding congregations and choruses (Brooke et al., 2000; Bandoni de Oliveira and Navas, 2004). Amphibians are well known to migrate to breeding sites during precipitation events; that certainly holds true for many tropical amphibians as well (Gottsberger and Gruber, 2004). Although this offers a predictable method for determining when to conduct surveys, it presents two problems when interpreting survey results. First, population estimates may be high because of the large congregation of animals at a breeding site. This congregation may be the result of animals migrating great distances and only temporarily be in such high densities because of optimal weather conditions. Second, calling frequency may be a result not of population density but of optimal weather conditions. During suboptimal conditions, animals may be present but not calling. For example, some centrolenid frogs reach full breeding chorus only during heavy downfalls (pers. obs.). While animals may be present, they are not calling, thereby skewing conclusions drawn from call surveys.

*Oophaga pumilio* (Strawberry Dart Frog) is a species of poison frog that occurs in the Caribbean lowland rain forests from Nicaragua to Panama. Unlike many anurans, this species uses small volumes of water in phytotelmata (e.g., Bromeliaceae) for larval deposition (Lötters et al., 2007). Given that these epiphytes are broadly distributed through a lowland rain-forest landscape (Fischer and Araujo, 1995), *O. pumilio* is not constrained to common breeding locations in a forest patch. Although a majority generally call within a few meters of the ground, individuals have been observed calling high in the canopy (Lawrence, 2011). This species, like most dendrobatids, has a prolonged breeding season with no noticeable spike in reproductive effort in relation to environmental conditions (Gottsberger and Gruber, 2004). As a result, opportunistic call surveying around a water source is not an option for species such as *O. pumilio*.

*Oophaga pumilio* is common in suitable habitat, including disturbed habitat. In such areas, I have observed this species to

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be one of the most abundant vertebrates in the area. While females and males do seem to congregate around areas for reproduction (i.e., trees with access to phytotelmata), they have broad distributions throughout suitable habitat and can be found away from such areas (McVey et al., 1981). This species is highly territorial (Gardner and Graves, 2005); thus, large congregations of individuals, particularly males, is rare. This trait makes identification of individuals easy as compared to breeding choruses found in other species of anurans. Phytotelmata in epiphytic bromeliads (e.g., *Guzmania*, *Werauhia*, *Aechmea*, and *Vriesea* species) are a common feature throughout the tropical forests where these frogs occur, largely favoring canopy and emergent tree species (pers. obs.). Indeed, in other areas of the Neotropics, researchers have found that bromeliads have high densities within the canopy, and although individual species likely have clumped distributions (Nieder et al., 2000), bromeliads are known to capitalize on a wide variety of niches in the forest canopy (Fischer and Araujo, 1995), likely providing a large distribution of reproductive sites available to frogs. Given the abundance of reproductive sites, *O. pumilio* should be broadly distributed in suitable habitat. As few studies have examined the use of call surveys quantitatively, this broad distribution of calling males through a landscape (McVey et al., 1981) provides an ideal system with which to explore the utility of quantitative call surveys as a method of population assessment. This study quantitatively examines the hypothesis that call density varies with population density in six populations of *O. pumilio*. In addition to population density, I also examined other factors that could influence call density, including temperature and humidity.

#### MATERIALS AND METHODS

**Study Area.**—I conducted call surveys in May and June 2010 in six different *O. pumilio* populations in a series of Caribbean islands, the Bocas del Toro archipelago in Panama. Seasonality in this area is very subdued with the wet season typically occurring from May through August and another spike in precipitation in October and November (STRI, 2010). Over the course of a year, Isla Colon, the largest island and the site of the Smithsonian Tropical Research Institute's (STRI) weather station, receives an average of 3,312 mm of precipitation per year (STRI, 2010). Seasonal temperatures range from 23.2°C to 28.6°C with daily temperatures ranging from 28°C during the day to 24.9°C at night. Average daily relative humidity ranges from 75.9 – 88.3% (STRI, 2010).

The populations used for this study were located on the islands Isla Colon, Solarte, San Cristobal, Pastores, Isla Popa, and Loma Partida (Fig. 1). Isla Popa has two distinct phenotypes on the northern and southern portions of the island. To clarify in what area surveys were conducted, I will henceforth reference the northern population as "Popa North." These sites were chosen because of the variety of *O. pumilio* phenotypes (size, color) and habitat present (Siddiqi et al., 2004). By sampling broadly across the region, trends can be attributed to the species rather than population specific patterns.

**Call Surveys.**—Observers surveyed each population at five different sites on at least two different days between 0830 and 1500. Surveys took on average 74 min ( $N=30$ ) to complete. Two observers conducted call surveys by standing at a single point and listening for calling males. Observers conducted each call survey at least 100 m from any other survey point and was



FIG. 1. Map of the different sampling locations for six different populations in Bocas del Toro, Panama. Populations were 1) Isla Colon, 2) Loma Partida, 3) Pastores, 4) Popa North, 5) San Cristobal, and 6) Solarte. Five surveys were done on each island. Surveys were at least 100 m apart. Because of restriction of suitable habitat on Solarte, two surveys were conducted approximately 1.5 km away from the other three. Compared to the first site, this second site had a high abundance of frogs.

located within a forested area where frogs could be heard calling. Sites were situated in forest where there was very little undergrowth to minimize any muffling of calls. All sites were similar across populations. Following site selection, observers recorded environmental data on humidity, temperature, and weather conditions for each survey. Observers then conducted a 3-min call survey, followed by an intensive survey of the surrounding area for any resident frogs. The two observers recorded the number of distinct calling males for the survey, which then was averaged to estimate the number of calling males.

To estimate maximum distance an individual male could be discerned, I located a calling male of Isla Colon (one of the largest, and hence loudest, morphs) and walked away until the frog could not be individually identified from background noise. Based on preliminary findings, I estimated 10 m to be the maximum distance a call would travel and still be distinguishable as an individual male, allowing me to directly link call estimates to population density estimates within the same area. Once observers completed call surveys, they established the sampling perimeter (10-m radius) and intensively surveyed for resident individuals. They delimited circles by the use of flagging after call surveys were completed to avoid disturbing calling males. Starting at the outside of the circle, observers slowly walked in a spiral toward the center of the circle conducting a visual encounter survey of frogs within the survey area. The spiral method allowed for thorough coverage and overlap of the survey area such that all frogs could be found within the survey plot should some individuals be more skittish than others. This spiral method helps account for these individuals because this method will result in the coverage of an area several times from a varying degree of distance, thereby limiting the number of individuals that may not be detected. As observers encountered frogs, they were collected to avoid counting individuals multiple times. For

TABLE 1. Demographics of six *Oophaga pumilio* populations. Male snout-vent length (SVL) determined from all males found in surveys for each population. Call density was determined by dividing the number of calling males by the total area of the survey ( $100 \pi \text{ m}^2$ ). Data are mean  $\pm$  SD. Two surveys were conducted in a high-density area on Solarte, which explains the large standard deviation. Because Popa North has dark blue venters, sex was not reliably determined by discoloration of a gular patch; hence, total number (rather than males/females) is reported.

Population	Male SVL (mm)	Population density (frogs/100m <sup>2</sup> )	Call density (calls/m <sup>2</sup> )	Total males/females
Isla Colon	19.36 $\pm$ 0.66	3.7 $\pm$ 1.7	0.019 $\pm$ 0.003	36/18
Solarte	17.88 $\pm$ 0.59	14.3 $\pm$ 14.3	0.02 $\pm$ 0.003	117/80
San Cristobal	18.65 $\pm$ 0.77	11.6 $\pm$ 4.9	0.022 $\pm$ 0.002	91/72
Pastores	17.71 $\pm$ 0.54	25.9 $\pm$ 11.9	0.024 $\pm$ 0.004	113/139
Popa North	15.54 $\pm$ 0.57	12.9 $\pm$ 3	0.017 $\pm$ 0.002	173 total
Loma Partida	17.95 $\pm$ 0.7	15.2 $\pm$ 4.5	0.014 $\pm$ 0.001	114/86

each collected frog, I recorded snout-vent length (SVL) and sex. I identified males by the presence of a melanistic gular patch that indicated recent vocal sac expansion (Gardner and Graves, 2005). Popa North frogs were small and had blue venters; therefore, vocal sac discoloration was not a reliable method for sexing those frogs. On several occasions, I sexed frogs from this population as female based on lack of a gular patch only to start calling while handling them. For this reason, I excluded the Popa North population from data analysis involving sex differences.

*Data Analysis.*—I first determined differences in population density using a linear mixed-effects model with the surveys within each population as a random effect. If I found population densities to be statistically different, I examined the expectation that calling density was related to population density (i.e., if differences in call density vary predictably with population density).

A number of factors could influence call density including overall population density, humidity, and temperature. Researchers have well established that precipitation (and by extension, humidity) influences call rates among anurans (Brooke et al., 2000; Bandoni de Oliviera and Navas, 2004; Gottsberger and Gruber, 2004). Likewise, researchers have shown that temperature has a correlative effect on call rate (Pröhl, 1997). Consequently, I ran a mixed-effects model first examining the environmental variables (temperature and humidity) and whether they predict call rate with population as a random effect. Following this model, I removed any nonsignificant variables for the final model. The final model used population density and significant environmental variables as independent variables and population being a random effect to predict call rate. I  $\log_{10}$ -transformed humidity to ensure a normal distribution. Because frog calls vary in intensity (i.e., decibels) in relation to body size (Wilbur et al., 1978), I standardized call densities to body size by dividing the observed call density by the average SVL of males of each respective population to eliminate any bias in being able to hear large males better than small males. I used a representative subset of males from each population to determine mean SVL. I conducted all analyses in R (R v2.15.2; R Core Development Team, 2014).

I also examined sex ratios to determine whether they varied with population size using a simple linear regression. Several factors including behavior (i.e., satellite males) or actual sex ratios (i.e., female-heavy populations) could explain differences in call density among populations. If the percentage of apparent males varies among populations, this could suggest that populations are sex skewed or alternative mating tactics

vary by population. Summary statistics are reported as mean  $\pm$  SD.

## RESULTS

The spiral surveys were successful in detecting frogs using both the visual encounter and the acoustic estimation surveys. On average, the difference between observers' estimates of calling males was  $1.76 + 1.48$  individuals ( $N = 30$ ).

Loma Partida and Pastores varied significantly in population density compared to the overall average ( $P = 0.036$  and  $P < 0.001$ , respectively), and Solarte approached significance ( $P = 0.051$ ). Populations exhibited as much as an eight-fold difference in density across populations (Table 1). Isla Colon had the lowest density with an average of  $3.6 \pm 1.7$  frogs/100 m<sup>2</sup> ( $N = 5$ ) and Pastores the highest density with an average of  $25.9 \pm 11.9$  frogs/100 m<sup>2</sup> ( $N = 5$ ). Populations varied in male SVL with the smallest examined (Popa North) at mean =  $15.54 \text{ mm} \pm 0.57$  ( $N = 40$ ) and largest (Isla Colon) at mean =  $19.36 \pm 0.66 \text{ mm}$  ( $N = 32$ ).

In my first mixed-effects model, humidity was significant in predicting standardized call rate ( $P = 0.014$ ), whereas temperature was not ( $P = 0.251$ ). Consequently, humidity, but not temperature, was included in the final mixed-effects model. Although call densities (number of calls/m<sup>2</sup>) differed among populations (Table 1), frog density did not show any significant relationship to standardized call density ( $P = 0.562$ ); humidity, however, was correlated with call density ( $P = 0.024$ ; Fig. 2).

Sex ratios varied among populations, with some populations having an excess of males and others an excess of females (Table 1). Regressing the proportion of apparent males against population density yielded an  $R^2$  of 0.324 ( $P = 0.0029$ , Fig. 3).

## DISCUSSION

The spiral survey technique allows an examination of the assumptions of call surveys to estimate population density. Call surveys rely on the predictable relationship between the absolute abundance of individuals in a population and the number of calling males (Lepage et al., 1997; Mossman et al., 1998), although this assumption has not yet been tested. This could be largely attributable to the difficulty of assessing absolute abundance of individuals and directly correlating that with calls. The spiral survey outlined here tested this assumption. There was some error for acoustic surveys, and this low error likely was because the majority of these frogs were found within a few meters of the ground. Additionally, by spiraling inward to a given point, observers can have great confidence in capturing the vast majority of frogs within the

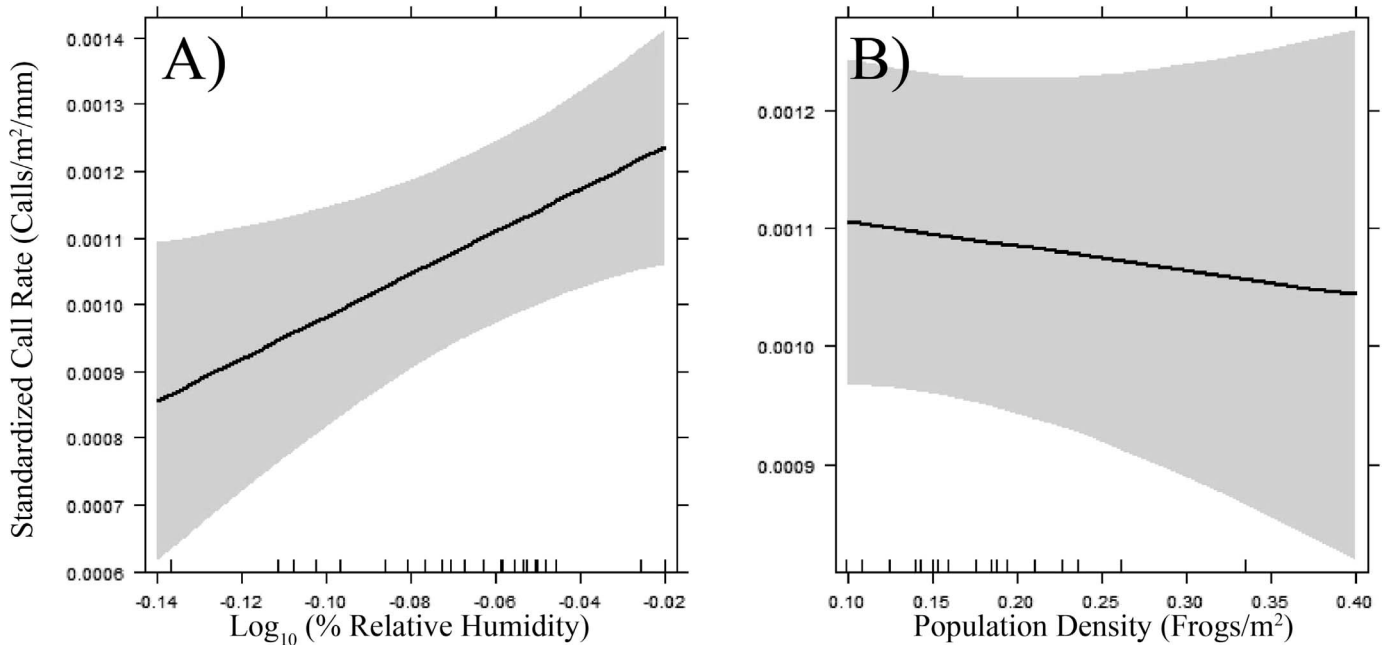


FIG. 2. Effects plots of the final mixed-effects model for (A)  $\log_{10}$ -transformed relative humidity and (B) population density in relation to standardized call rate. Call rates were standardized by dividing the observed call density by the average male snout-vent length of the representative population to remove potential impacts body size has on calling intensity.

survey area, therefore, validating the use of this method. Although this method may not work for all species, it is a valuable tool for testing broad assumptions of standard survey techniques.

Despite as much as an eight-fold difference in population density among sites, I found no apparent trend suggesting calling density represented a good indicator of frog density. This is of particular note because of the territorial nature of *O. pumilio* (McVey et al., 1981; Pröhl, 2005) as one would expect an increase in territorial displays (e.g., calling) as population density increases. Particularly interesting is the variation among populations in male density, and despite this, an absence of

any apparent difference in calling effort by males among populations.

Calling density showed a strong relationship to relative humidity, with the number of calling males increasing in a linear fashion with increasing humidity; this is consistent with previous research on *O. pumilio* (Pröhl, 1997). Indeed, temperature and humidity are well known to affect breeding efforts in amphibians (Aichinger, 1987; Duellman, 1995; Bandoni de Oliveira and Navas, 2004; Poelman and Dicke, 2007). Humidity appears to be the most predictive variable for the number of frogs calling at any given time. Humidity, therefore, possibly has greater influence on calling density than population density does in other anurans. Given this, any management that takes place based on results from call surveys needs to take environmental conditions into account.

Using gular patches as a method of sex identification can cause one-way misidentification of sexes (noncalling males being confused for females; females are unlikely to be confused for males). Interestingly, some surveys resulted in proportions of males greater than 50%, which seems counterintuitive, but could be explained by life history. Females in this species are highly mobile, often going from phytotelmata to phytotelmata caring for offspring (Brust, 1993). Males, however, are more likely to defend territory and move little (Pröhl, 1997). As a result, in the surveys where few frogs were found, females likely were not on the ground but working through phytotelmata in the canopy while males defended terrestrial territories.

Sex ratios varied linearly with population density estimates. This relationship provides interesting insight into possible function of these populations. Gular patches are visible only in actively calling males, but once a reproductively mature male stops calling for a period of time (Kao et al., 1994), it loses the gular patch, potentially biasing sex ratio counts. Once a population reaches a particular density, the number of males calling decreases relative to the whole population, making a population appear to be more dominated by females. This

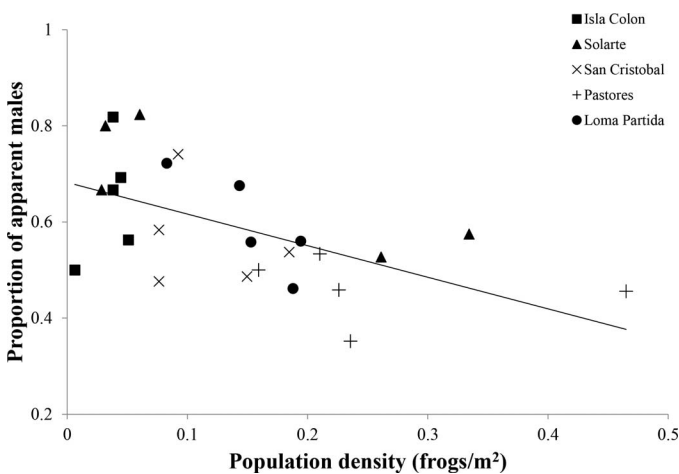


FIG. 3. Relationship of the proportion of males and population density for Isla Colon, San Cristobal, Solarte, Loma Partida, and Pastores. Proportion of males was the total number of apparent males (identified by gular patch) to total number of frogs found in each survey plot. Regressing male density against population density yielded a negative relationship ( $R^2$ -value of 0.324;  $P = 0.0029$ ), possibly suggesting alternative reproductive strategies (i.e., acoustic niche partitioning, satellite males) in *Oophaga pumilio*.

suggests that, as population density increases, individual males are less likely to call. How noncalling males contribute to overall reproductive fitness currently is unknown. Many of these males, for example, could act as satellite males to increase mating success with minimal energy devoted to calling and defending territories (Forester and Czarrowsky, 1985). This reduction in the amount of calling males could have implications for conservation methods. If, for example, estimates of population size based on call surveys assume equal sex ratios, this assumption is clearly violated in *O. pumilio*, as only a portion of males will call at a given time, resulting in an underestimate of population size. And further, because call density appears relatively stable compared to population density, relying on call surveys could make changes in population density difficult to detect over time.

The question, then, is why are a number of the males in *O. pumilio* populations not calling? One of three scenarios could explain noncalling males: acoustic niche partitioning, sneaker/satellite males, or lack of territory establishment. Acoustic niche partition generally relates to short-term adjustment to "crowded" acoustic space (Bourne and York, 2001; Duellman and Pyles, 2009). With the highly territorial nature of this species (Gardner and Graves, 2005), one would expect territorial interactions to increase as population density increases. Because males compete with one another in acoustic space, males would benefit from alternate calling such that individuals do not overlap and reduce the fitness for both parties. Sneaker/satellite reproductive strategies are well documented in anurans (Wells, 1977; Forester and Czarrowsky, 1985; McCauley et al., 2000), and although such a phenomenon has not been described in *O. pumilio*, as population size increases and defendable territories become more limited, a sneaker/satellite strategy may be more likely to develop. Alternatively, noncalling males could simply lack territories to defend and, therefore, lack impetus to call. Understanding why many males in the population do not call, or do not call enough to develop gular patches, requires more investigation.

A large variety of reproductive modes have evolved in tropical anurans (Haddad and Prado, 2005) and among them include terrestrial breeders like *O. pumilio*. Although terrestrial breeding behavior is vastly different from the reproductive modes used by temperate anurans, the concept of using call surveys to monitor population trends in an intriguing option for threatened or endangered terrestrial breeders (i.e., *O. lehmanni*, *Andinobates bombetes*, *Phylllobates terribilis*). If these species are similar to that of *O. pumilio*, however, then call surveys likely would be limited to detecting individuals rather than estimating population size or trends. Some tropical amphibians, however (i.e., *Dendropsophus* sp., *Scinax* sp., *Agalychnis* sp.), are likely excellent candidates for call surveys, because they have life histories similar to those of temperate zone anurans. Further research is necessary to determine whether the assumptions of call surveys are met (i.e., calling density varies with population size) for other species, including gregarious breeders such as those in the temperate zone. Not all males, even in temperate anurans, actively call during breeding congregations (i.e., sneaker/satellite males; Forester and Czarrowsky, 1985; Wells, 1977; McCauley et al., 2000), and if this phenomenon is widespread in a species of interest, this, too, could skew population estimates.

The use of citizen science can be a very powerful tool for managing wildlife populations and understanding community trends over time, as evidenced by the successful National

Audubon Society Christmas bird count initiative (Butcher et al., 1990). With the current decline in amphibian populations around the world (Houlahan et al., 2000) and especially in Latin America (Lips et al., 2005), methods to monitor population trends are sorely needed. Call surveys offer a cheap and effective method to observe presence or absence of species in a given region, but the current methods allow for collection only of presence-absence data. Wildlife managers may be tempted to use such methods to infer population trends over time, but they must use caution with this approach. This method may be valid for examining population trends of some species, but for others (such as *O. pumilio*), this method appears to be invalid. Results from this study highlight the need to further test the accuracy of surveys for tracking population sizes over time. For many species, environmental factors such as humidity (this study), or rainfall (Gottsberger and Gruber, 2004), drive calling density in anuran populations, not population density.

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