Pairing noninvasive surveys with capture-recapture analysis to estimate demographic parameters for *Dendrobates auratus* (Anura: Dendrobatidae) from an altered habitat in Costa Rica

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Abstract

Pairing noninvasive surveys with capture-recapture analysis to estimate demographic parameters for *Dendrobates auratus* (Anura: Dendrobatidae) from an altered habitat in Costa Rica. Amphibian populations are in decline worldwide. Monitoring programs are important, but many studies use invasive techniques to handle, mark, and identify individuals. We recommend a noninvasive technique in which individuals can be identified from photographs based on individual markings for capture-recapture analyses. As a case study, we examined the population dynamics of *Dendrobates auratus* at a highly altered habitat in northern Costa Rica. We applied the robust design to the capture-recapture data from the photographs of individual frogs at two 25-m transects, a parking lot and a gravel walkway. From these data, we estimated parameters for survival, emigration, immigration, abundance, and capture probability. The observed mean density estimate of 2.62 ± 0.60 individuals (CI = 1–4) per 100 m^2 is the first statistically rigorous estimate for this species in altered habitats. These results suggest that this species might be suited to occur in human-altered habitats and may be less susceptible to population declines than previously suggested. Our noninvasive methodology to obtain robust abundance and demographic parameter estimates is also applicable to citizen-science surveys for a variety of taxa of amphibians and reptiles that are individually identifiable.

Keywords: amphibian populations, capture-recapture, noninvasive surveys, photographic identification, robust design.

Resumo

Associando técnicas não-invasivas com análise de captura-recaptura para estimar parâmetros demográficos para *Dendrobates auratus* (Anura: Dendrobatidae) de um hábitat alterado na Costa Rica. Populações de anfíbios estão em declínio em todo o mundo. Programas de monitoramento são importantes, mas muitos estudos utilizam técnicas invasivas para manipular, marcar e identificar indivíduos. Recomendamos uma técnica não invasiva, em que os indivíduos podem ser identificados a partir de fotografias baseadas em marcas individuais para análises de captura-recaptura. Como estudo de caso, examinamos a dinâmica populacional de *Dendrobates auratus* em um hábitat altamente alterado no norte da Costa Rica. Aplicamos o design robusto a dados de captura-recaptura das fotografias de indivíduos em dois transectos de 25m, uma área de estacionamento e uma passarela de cascalho. A partir desses dados, estimamos os parâmetros para sobrevivência, emigração, imigração, abundância e probabilidade de captura. A densidade média estimada de 2.62 ± 0.60 indivíduos (CI = 1–4) por 100 m^2 é a primeira estimativa estatisticamente rigorosa para esta espécie em hábitats alterados. Esses resultados sugerem que essa espécie poderia ocorrer em hábitats antropizados e ser menos suscetível a declínios populacionais do que anteriormente sugerido. Nossa metodologia não-invasiva para obter estimativas robustas de abundância e parâmetros demográficos é igualmente aplicável à investigações feitas por leigos para uma variedade de táxons de anfíbios e répteis que são identificáveis individualmente.

Palavras-chave: captura-recaptura, design robusto, identificação fotográfica, populações de anfíbios, técnicas não-invasivas.

Introduction

It is well established that amphibian populations have declined dramatically in recent years (Carey 2000, Houlahan *et al*. 2000). Although there are various competing hypotheses as to the major causes of this trend, many contest that the influence is due to habitat alteration and loss, invasive species, disease, and human-induced changes to the environment (Blaustein and Kiesecker 2002, Young *et al*. 2001). Frogs, in particular, seem to be highly sensitive to environmental changes, climate change, and habitat alterations (Lips *et al*. 2003) making them important environmental indicators (Phillip 1990).

One study used species-specific ecological traits to evaluate and predict the risk of extinction and population decline for various Neotropical frogs; Lips *et al*. (2003) predicted that six of eight dendrobatid species of two genera (*Colostethus* and *Dendrobates*) had a high probability of population decline in Central America. *Dendrobates auratus* (Girard 1855)

was one of these species with a high probability (0.72) of regional decline. Thus, it would be expected that this species is intolerant, and hence, a good indicator of habitat change or degradation.

Many amphibian studies use indices of abundance and relative abundance such as counts during visual encounter surveys, counts at individual plots, or counts at cover boards without any consideration of detection bias (e.g., Reider *et al*. 2013). It is preferable to apply capture-recapture models to survey data to account for detection bias explicitly in estimating demographic parameters (Schmidt *et al*. 2002, Williams *et al*. 2002). To estimate such detection rates and bias in population monitoring, amphibian sampling strategies often are highly invasive because of variable capture methods, handling, and marking techniques to uniquely identify individuals in the populations under study (Bailey *et al*. 2004). However, digital photography and photo-recognition software offer noninvasive tools to monitor uniquely identifiable individuals of amphibian and reptile

populations. Additionally, citizen-science research might provide powerful data sets over large geographic scales, if data are collected in the context of noninvasive population monitoring (Dickinson *et al.* 2010).

Individual *Dendrobates auratus* can be identified based on their color patterns and anastomosing stripes (Summers 1989, Guyer and Donnelly 2005; Figure 1). Summers (1989) toe-clipped frogs to identify individuals for a behavioral study because he lacked the tools to record individuals with digital photography. We are unaware of any studies that have used the advantage of uniquely identifiable individuals paired with noninvasive techniques to estimate demographic parameters such as survival, emigration, immigration, and abundance in tropical frog populations. As a case study, we examined the population dynamics of two populations of *D. auratus* at a highly altered area in northern Costa Rica and draw inferences about the susceptibility of this species to population declines.

Materials and Methods

We conducted frog surveys at the Sarapiquí Conservation Learning Center (10º27'01.33" N, 84º04'04.25" W; Figure 2) in Chilamate, Costa Rica. The learning center is located on the property of the Selva Verde Lodge directly adjacent to, and lying between, the Sarapiquí River and a major paved road in the southern region of the San Juan—La Selva Biological Corridor. It has been suggested that a population of *Dendrobates auratus* was introduced by an employee of Selva Verde Lodge in 1986 (Guyer and Donnelly 2005), but it is unclear that the species was completely absent prior to that introduction. However, the lodge is well within the natural geographic distribution of *D. auratus*. The biological corridor is highly modified and the surrounding landscape consists mainly of fragmented forest reserves that serve as refugia for amphibians among cattle ranches, pineapple plantations, and urbanization. We surveyed two
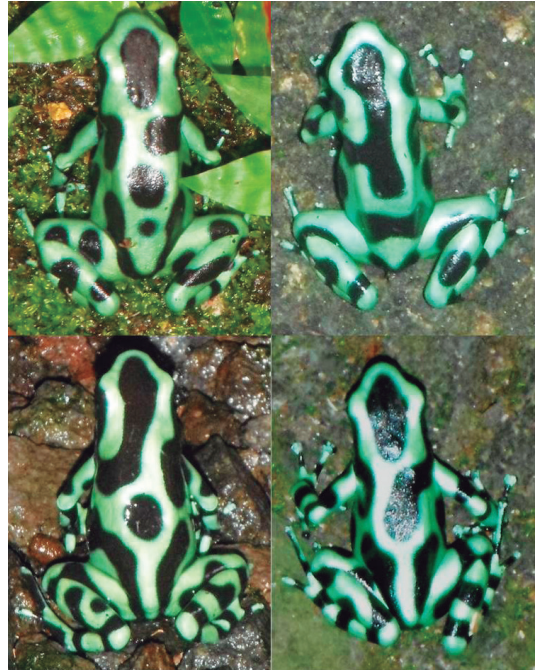

Figure 1. Examples of individually identifiable color patterns of *Dendrobates auratus* from photographic surveys conducted at the Sarapiquí Conservation Learning Center in the northern zone of Costa Rica.

25-m transects no less than 40 m apart. The first transect traversed a paved parking lot area and the second, a stretch of gravel and concrete walkway (Figure 2). We included frogs within 5 m on either side of the transect. The estimated area of each transect was approximately 250 m^2—a size similar to those examined by Summers (1989) in Panama with plots 352 m^2 and 240 m^2 in 1985 and 1986, respectively. Both transects included the open space of the human-altered substrate, but also vegetation, moss, and leaf litter debris along their peripheries.

Because *Dendrobates auratus* is terrestrial and typically lives in leaf litter, we predicted that individual detection probabilities would be less than 1.0, so we used likelihood models and repeated surveys to estimate demographic

Figure 2. Transect habitats from surveys of *Dendrobates auratus* conducted at the parking lot (**A**) and gravel trail (**B**) of the Sarapiquí Conservation Learning Center (arrow pointer, **C**) and surrounding landscape in the northern zone of Costa Rica.

parameters (Bailey *et al.* 2004). From 15 October 2011 to 18 December 2011, we conducted morning frog surveys in the context of fitting the data to Pollock's robust design for capture-recapture analysis (Pollock 1982). This analytical method later was adapted to estimate temporary emigration, which allows for the estimation of individual availability in the sampled population. This methodology was well suited to our data because frogs could use the edges of the transects, where bromeliads and plants were dense (Kendall *et al.* 1997). Following the protocols of Bailey *et al.* (2004), we conducted seven primary surveys (open population) with three or four secondary surveys (closed popu-

lation) contained therein. Primary surveys were separated by 6–10 days in which we considered the populations to be demographically open (Bailey *et al.* 2004). Surveys lasted up to 15 min each and took place in the morning between 06:30 and 09:30 h. For comparisons to other survey methods, we estimated the total survey effort in surveyor-hours, and then estimated the amount of time/effort for subsequent data management and analyses.

Using our noninvasive approach, we photographed every frog encountered along each transect for visual comparison to previously cataloged photos of individuals. We did not handle, manipulate, or disturb frogs any further

than taking photographs; as a result, we were unable to determine exact sizes or genders. Two to five photos were taken directly overhead of each frog observed to ensure clarity in the images for identification. When visually examining the photos, we first looked at the head and back for distinct markings and used the back leg markings as an extra marker if the back and head were not sufficient to distinguish individuals. We used this information to create binary "capture" histories (1 = "captured", 0 = "not captured") for each frog identified at each study transect. We think that the two sites are connected as a single meta-population, but we did not observe any individuals moving between the sites; thus, we considered transects to be independent and analyzed them separately. Independence is probable over the course of our study because the walkway in between the two sites was regularly cleaned of leaf litter and consistently traveled by center volunteers and students.

We developed 11 a priori population models to estimate demographic parameters. Three of the parameters of interest are estimated between the primary survey occasions (open population model), including survival (ϕ, which is confounded with permanent emigration), temporary emigration (γ''), and the complement of immigration (γ', probability of staying out of the sample area given that the individual has previously exited). Frog abundance (N), individual capture probability (p), and recapture probability (c) are all estimated from the secondary surveys (closed population model). Given the data, we applied relatively simple models to estimate each of the demographic parameters as constant (.) over the course of the study or variable by time (t) over the course of the study, and did not consider any other covariate effects. We also estimated capture probabilities as constant, variable by time, or effort (3- vs. 4-day surveys). Because we did not manipulate or disturb the frogs, we consider the probability of initial "capture" to equal the "recapture" probability ($p = c$) because it was

unlikely that there were any behavioral responses to the initial "capture." We also modeled movement as either Markovian (γ'' and γ' are modeled separately and dependent on the earlier stage) or random movement ($\gamma'' = \gamma'$). Symbology is explained further in Table 1. We calculated density estimates (individuals per 100 m^2) by dividing the abundance estimates by the area surveyed at each site and multiplied by 100.

We conducted all analyses using the robust design implemented in MARK (White and Burnham 1999). Models were ranked using an information theoretic approach (using AICc as the criterion) and models were only considered strong if they contained > 0.90 of the Akaike weight (w_i). In cases in which no model contained > 90% of the support, we performed model averaging to estimate derived population parameters from the 90% confidence set ($\sum w_i >$ 0.90; Burnham and Anderson 2002).

Results

We conducted 25 surveys at each of the two transects. In total, we observed 31 individual frogs from 84 total detections, of which 29 detections were at the parking-lot transect and 55 at the gravel walkway transect. One juvenile was observed at the gravel transect, but excluded from the analyses. The photographs captured enough distinct markings (Figure 1) to allow individual identification of all frogs encountered. Mean number of frogs detected per survey was 1.16 ± 1.07 SD and 2.20 ± 1.55 SD for the parking-lot transect and the gravel transect, respectively. Each survey lasted a maximum of 15 min; cataloging photos for visual identification and data management usually only required 30–45 minutes for a single surveyor. Therefore, our total effort for the surveys and all data management prior to analyses was ~30 hours during the 2-mo study.

The constant model with random movement ranked first (w_i = 0.505) for the parking-lot population; however, because it contained < 90% of the model support, we model averaged

Table 1. Model selection statistics for robust design analysis of capture data of *Dendrobates auratus* from the Sarapiquí Conservation Learning Center, Costa Rica. Included are the top-ranked models ($\sum w_i > 0.90$) for the parking-lot and gravel trail transects, AICc values (AIC_c), the information distance from the top ranked model (ΔAIC_c), Akaike weights (w_i), number of parameters (K), and deviance (Dev). Model notation: ϕ is survival, γ'' is temporary emigration, γ' is the inverse of immigration, p is capture probability, c is recapture probability, N is abundance, (.) is constant, (t) is variable with time, (3) and (4) are variable with survey effort, and parameters are equal as denoted by =.

Model Description	AIC_c	ΔAIC_c	w_i	K	Dev
Parking Lot Transect					
{ϕ(.), γ''(.) = γ'(.), p = c(.), N(.)}	136.91	0.00	0.505	4	104.44
{ϕ(.), γ''(.), γ'(.), p = c(.), N(.)}	139.00	2.08	0.178	5	103.58
{ϕ(.), γ''(.) = γ'(.), p = c(4), p = c(3), N(.)}	139.58	2.67	0.133	5	104.17
{ϕ(.), γ''(.) = γ'(.), p = c(t), N(.)}	139.85	2.94	0.116	7	97.71
Gravel Trail Transect					
{ϕ(.), γ''(.) = γ'(.), p = c(4), p = c(3), N(.)}	192.07	0.00	0.211	5	168.63
{ϕ(.), γ''(.), γ'(.), p = c(4), p = c(3), N(.)}	192.45	0.38	0.175	6	166.49
{ϕ(.), γ''(.) = γ'(.), p = c(t), N(.)}	192.51	0.44	0.170	7	163.91
{ϕ(.), γ''(.), γ'(.), p = c(t), N(.)}	192.73	0.66	0.152	8	161.38
{ϕ(.), γ''(.), γ'(.), p = c(.), N(.)}	192.79	0.72	0.147	5	169.35
{ϕ(.), γ''(.) = γ'(.), p = c(.), N(.)}	192.83	0.76	0.145	4	171.82

all parameters among the top four competing candidates ($\sum w_i = 0.932$; Table 1). There was more uncertainty among the models for the gravel-walkway population, with six competing models ($\sum w_i = 1.00$; Table 1) contributing to the model averaged parameter estimates. Individual survival estimates (ϕ) between surveys were relatively high for both transects at 0.95 ± 0.09 SE and 0.89 ± 0.08 SE for the parking lot and gravel walkway, respectively. Temporary emigration (γ'') for the parking lot was estimated at 0.54 ± 0.21 SE and was 0.45 ± 0.16 SE for the gravel walkway. The complement of immigration (γ', probability of staying out of the sample area given that the individual has exited) was 0.48 ± 0.26 SE for the parking lot and 0.24 ± 0.28 SE for the gravel walkway.

Daily capture and recapture probabilities for individuals were statistically equivalent (confidence intervals overlap) at 0.21 ± 0.07 SE and 0.20 ± 0.08 SE for the parking-lot transect. Daily capture probabilities for gravel transect frogs varied by survey effort with four day surveys resulting in slightly lower detection at 0.26 ± 0.07 SE and three survey occasions resulting in 0.31 ± 0.07 SE. There was no model support for varying abundance during the study, and estimates reveal gravel abundance was 6.23 ± 1.34 SE (95% CI = 3–9 individuals) and parking-lot abundance was 6.86 ± 1.65 SE (95% CI = 3–10 individuals) for any primary survey period. These abundance estimates equate to density estimates of approximately 2.62 ± 0.60 individuals (95% CI = 1–4 individuals) per 100 m².

Discussion

Our noninvasive survey protocol is applicable to other amphibians and reptiles if they have individually identifiable markings. Although we were able to visually compare photographs to identify individuals with high success, photographic recognition software might make this process easier for less distinguishable species in future studies. Given their environmental sensitivity, amphibians probably do not deal well with handling or other manipulations such as implanting elastomers (Bailey *et al*. 2004), pit tags, or toe clipping (Summers 1989). The methods outlined herein are superior to surveys that do not consider detection bias and allow for robust trends in abundance and other demographic parameters to be monitored through time (Williams *et al*. 2002). Furthermore, our study design required only limited effort by the surveyor and may be applicable to citizen-science type surveys at larger scales. Citizen science is also appealing because of the availability of digital cameras and GPS technology integrated into phones and tablets, which would only require limited training if any.

We observed *Dendrobates auratus* to be common in this altered habitat. Although the species may have been introduced at Selva Verde in the mid-1980s (Guyer and Donnelly 2005), it is difficult to document whether or not green and black dart frogs were always present or were stocked in the altered area. Regardless of the historic introduction, the species has persisted for more than 25 years and now is common throughout the zone in natural and unnatural microhabitats. This is likely to be considered the first successful intro/reintroduction of *D. auratus*, in which case the subsequent population monitoring may provide valuable information to consider when introductions or reintroductions of rare amphibians may be necessary in the future.

Few studies have examined the spatial ecology of *Dendrobates auratus*, but Summers (1989) monitored two populations and observed seven males at each site during his studies and reported 14 females at the 1986 site (~8 individuals per 100 m^2). Our study transects were of similar size and although primary survey abundance (3- or 4-day period) was lower than that observed in Panama, the cumulative numbers of frogs observed (12 and 19) were only slightly less. Our observed density estimates of 1–4 individuals per 100 m^2 are the first statistically rigorous estimates for this species in altered habitats and probably the first for any habitat. There is a multitude of probable causes for the difference in individual abundance between our surveys and those of Summers (1989). For example, Summers (1989) surveyed his sites much more vigorously to observe behavior of the frogs; this may account for the higher individual counts. Alternately, the lower abundance may be a combined result of lower productivity and higher transient adult movement in the altered habitats of this study. Nevertheless, the observations suggest that these populations might be more dynamic than those in natural areas in another Central American study (Summers 1989).

Frogs most likely visit the open areas to feed on insect prey and presumably retreat to the leaf litter and bromeliads on the outer edges of these transects later in the day because there is little cover for avoidance of sun or elements. Also, owing to the limited leaf cover available in the transects, frogs were relatively easy to detect when present. Therefore, the heightened detection rates of frogs in the gravel area might reflect higher use of that habitat as opposed to the parking lot. This is probably a result of denser leaf litter and bromeliads surrounding that site that may provide more diverse insect prey (Richardson 1999). This site was also within close proximity (<15m) to an unmaintained orchid garden which provided spawning habitat and elevated insect prey for transient frogs.

Survival often is an important demographic parameter to monitor in population ecology (Williams *et al*. 2002). Our analysis allowed us

to estimate survival between the primary periods, which equates to an approximate time interval of ~2 weeks. We did not document any mortalities, and it is probable that given the open-nature of the two transects, frogs can see predators and foot traffic and are able to avoid being trampled. As a result, the estimates are relatively high (confidence intervals approaching 1.0), and we suspect that future studies will benefit from extending the open period between primary surveys to allow for longer-term population monitoring.

Movement was random with relatively high temporary emigration γ″ rates (~0.50) between primary surveys at both sites, suggesting transient animals used the open areas to forage, regularly left the study sites and then returned. This corresponds with the findings of Summers (1989), who determined that transient males commonly crossed through his study transects and that transient females would often linger around the study area for 1–2 weeks before dispersing. In contrast, γ′ for the gravel site was relatively low and suggests that individuals in the population have a high probability of returning soon after temporary emigration. The γ′ estimate for the parking-lot site was only marginally less than the emigration parameter, suggesting that there is an "even flow" of immigration and emigration of marked individuals in the population and surrounding habitat. However, because the confidence intervals strongly overlap, we think that this may be an artifact of high initial detections and abundance at the gravel site versus the parking lot. Additionally, this may also result from transient frogs leaving the sites to the surrounding area (more natural) to set up territories for breeding and spawning, but returning to forage. As with survival estimation, we recommend that future surveys consider extending the open period between primary surveys to estimate these movement parameters more precisely.

Though our study was modest, the habitats surveyed were non-representative of natural areas and suggest the resilience of *Dendrobates*
auratus to survive in altered human habitats. Thus, they might not be as susceptible to population declines as previously suggested (Lips *et al*. 2003). Further study of this species and the integration of individually identifiable markings with noninvasive surveys for other species will improve our current knowledge for this and other poison dart frogs in Central America.

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