

Potential causes of population declines in forest fragments in an Amazonian frog

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Abstract

Forest fragmentation results in population declines and extinctions for many forest vertebrates, but little is known about the mechanisms causing declines in fragments. We investigated potential causes of declines in forest fragments for an Amazonian forest frog (*Colostethus stephni*) at an experimental fragmentation study site in central Amazonian Brazil using field estimates of abundance and vital rates coupled with population simulations. Although adult male survival was not reduced by fragmentation, mean clutch size was reduced by 17%. Population simulations demonstrate that a reduction in clutch size of this magnitude is sufficient to cause the observed magnitude of population declines in fragments. Female snout-vent length was also reduced in fragments and may be related to the observed reduction in clutch size.

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1. Introduction

Forests throughout the world are becoming increasingly fragmented as they are cleared for timber extraction, road construction, agriculture, mining, and other types of development (Whitmore, 1997; Laurance, 1998). This is a major conservation concern given that many forest vertebrate populations are known to decline or disappear in forest fragments (Terborgh and Winter, 1980; Laurance, 1994; Bierregaard and Stouffer, 1997; Tocher et al., 1997; Marsh and Pearman, 1997). In order to manage forests in a way that minimizes the negative impacts of fragmentation on vertebrates, it is critical to understand the mechanisms causing declines in fragments (Sieving and Karr, 1997).

Fully understanding the mechanisms of declines in forest fragments requires identification of both the proximate and ultimate causes of declines. Proximate causes of declines are changes in one or more of the

demographic vital rates that determine population growth: survival, fertility, immigration, and emigration. A reduction in survival, fertility, or immigration rates or an increase in emigration rates are all potential proximate causes of declines. However, vital rate changes are not all equal in terms of their effects on population growth, necessitating a link between vital rate changes and effects on population growth using modeling approaches (Biek et al., 2002; Mills and Lindberg, 2002).

Underlying the proximate causes of declines are the ultimate causes which are the physical and biological changes in forest fragments that reduce vital rates. Potential ultimate causes of declines include, but are not limited to, increased drying of microhabitat, increased treefall disturbances, alteration of vegetative composition, increased levels of predation and competition, and reduced prey base (Terborgh and Winter, 1980; Kapos et al., 1997; Laurance et al., 1998). These factors may directly reduce vital rates or indirectly reduce vital rates by reducing other fitness traits such as size, growth rates, and/or physiological performance.

The objective of the present study was to investigate potential causes of decline of an Amazonian forest frog,

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Colostethus stepheni, in forest fragments. Previous work has shown that the abundance of *C. stepheni* was reduced in fragments relative to continuous forest 8–14 years after isolation of fragments, but the causes of its decline were not determined (Tocher et al., 1997). Specific objectives of the present study were to: (1) test whether the abundance of *C. stepheni* is still reduced in fragments 15–19 years after isolation; (2) test whether adult survival probability and/or clutch size are reduced in a focal study site fragment; (3) use population simulations to assess whether the magnitude of any observed reductions in adult survival and/or clutch size in the focal study site fragment is sufficient to cause the observed declines in abundance in fragments; and (4) investigate the factors causing any observed reductions in adult survival and/or clutch size in the focal study site fragment.

2. Methods

2.1. Study area and species

Field work was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), an experimental fragmentation study site located approximately 70 km north of Manaus, Amazonas, Brazil (Bierregaard and Stouffer, 1997), from December 1998 through February 1999. Fifty by fifty meter study plots were set up in continuous forest, 10-ha fragments, and secondary forest matrix habitat dominated by *Cecropia* and *Vismia* species surrounding fragments at two different fazendas (ranches): Dimona and Esteio. One plot was placed in each treatment at each site for a total of six plots. Plots were placed near the center of 10-ha fragments and at least 150 m from the forest edge in continuous forest. The 10-ha fragment used at Dimona (BDFFP reserve number 2206) was isolated from continuous forest in 1984 and the 10-ha fragment at Esteio (reserve number 1202) was isolated in 1980. The relative abundance of *Colostethus stepheni* was estimated in both of these fragments in Tocher et al.'s (1997) study. Dimona served as the focal study site for detailed investigation of the mechanisms of declines.

The focal species of the present study was *Colostethus stepheni*, a small, terrestrial frog in the neotropical poison frog family Dendrobatidae (Martins, 1989). Like most dendrobatids, *C. stepheni* lays its eggs in leaf litter nests on the forest floor and exhibits territoriality and parental care of its embryos and tadpoles (Duellman and Trueb, 1986). In *C. stepheni*, males provide parental care by guarding embryos and tadpoles from potential invertebrate and vertebrate predators. In most dendrobatids, tadpoles are also carried to bodies of water where they complete larval development. However, in *C. stepheni*, non-feeding tadpoles remain in their nests

on the forest floor until metamorphosis (Juncá et al., 1994). *C. stepheni* breeds for 7–10 months of the year in synchrony with the rainy season (Moreira and Lima, 1991; Juncá, 1994).

Colostethus stepheni is a good species for studying mechanisms of decline in forest fragments for several reasons. First and most importantly, previous work has already shown that *C. stepheni* has declined in abundance in forest fragments (Tocher et al., 1997). In addition, it is possible to estimate abundance and survival probabilities using capture–recapture methods for adult male *C. stepheni* because males advertise their locations by calling and are relatively easy to catch. This provides high capture probabilities and precise estimates of abundance and survival probabilities. Finally, *C. stepheni* will lay its eggs in “artificial nests” made of cup-shaped dead leaves which facilitates finding clutches for estimating clutch sizes (Juncá, 1996).

2.2. Capture–recapture data collection and analysis

Three capture sessions were conducted at Dimona and one at Esteio. All capture sessions lasted 6 days except for the first session at Dimona which lasted only 5 days. Capture sessions at Dimona were separated from each other by approximately 4 weeks. During each day of capture sessions, the 50 × 50 m plots in each treatment were intensively searched for *C. stepheni*. Individuals were caught by gently tapping them into a small glass jar to minimize handling. The sex of animals was determined from the calling activity and laterally expanded third toes of males (Martins, 1989). New individuals were marked by clipping a unique combination of toes using a modified version of the system used by Hero (1989) in which thumbs are not cut.

Daily capture histories of adult males were used from the second and third capture sessions at Dimona and the first and only capture session at Esteio to examine variation in male abundance (N) over treatments and in capture probabilities (p) and recapture probabilities (c) over days and treatments using closed population capture–recapture models (White et al., 1982) in program MARK (White and Burnham, 1999). The assumption of closure (no births, deaths, immigration, or emigration) within the six-day period of capture sessions was likely met because previous work has shown that adult *C. stepheni* tend to remain in small home ranges during the breeding season (Juncá, 1994). Capture histories from the first session at Dimona were not analyzed using closed models because capture probabilities during this session were low.

A total of 37 different models were compared for each site and capture session, including the most general, global model with variation in p and c over days and treatments and in N over treatments in order to assure adequate model structure to fit the data. Competing

models were compared using Akaike's information criterion adjusted for sample size (AICc; Akaike, 1973). The best models, based on the criteria of parsimony and fit to the data, were those with the lowest AICc values. Models with ΔAICc values less than 4, where ΔAICc is the difference between the AICc value of the given model and the model with the lowest AICc value, were used to examine variation in p and c . Because these models gave similar estimates of N due to high capture probabilities, we did not average estimates of N (Buckland et al., 1997), but instead used N estimates from the best models (with ΔAICc values of zero).

Monthly capture histories of adult males were used from all three capture sessions at Dimona to examine variation in apparent survival probabilities (ϕ) and capture probabilities (p) over months and treatments using open population Cormack–Jolly–Seber (CJS) models (Cormack, 1964; Jolly, 1965; Seber, 1965) in program MARK. Sixteen different models were compared, including the most general, global model with variation in ϕ and p over months and treatments. The goodness-of-fit of the global model was tested using a bootstrap GOF test which was not significant ($P=0.92$), indicating that this model had adequate structure to fit the data. As with the closed model analysis, competing models were compared using AICc. Models with ΔAICc values less than 4 were averaged to estimate ϕ in order to take into account model selection uncertainty (Buckland et al., 1997).

2.3. Clutch size and snout-vent length data collection and analysis

Three artificial nests, each consisting of a cup-shaped leaf on the bottom and another leaf as a roof, were placed on the forest floor approximately 0.5 m from each of 48 calling males (for a total of 144 nests) in the continuous forest and 10-ha fragment plots at Dimona following Juncá (1996). Artificial nests and potential natural nests were then checked approximately 4 weeks later for clutches and the number of embryos in each clutch was counted. Snout-vent length (SVL) was measured using dial calipers by adpressing frogs to a flat plastic surface in order to prevent animals from arching their backs. All SVL measurements were made by the same researcher to prevent measurement bias.

We tested the hypothesis that mean clutch size was smaller in the fragment than in the continuous forest plot at Dimona using an extension of the Behrens–Fisher T test that allows for unequal variances between treatments (Rice and Gaines, 1989). We used the same approach to test the hypothesis that mean SVL was shorter in the fragment than in continuous forest for both males and females. Our a priori expectation was that the observed reduction in *C. stephensi* abundance in fragments was caused by vital rate reductions and that

the observed reduction in clutch size was caused by a reduction in SVL. The latter hypothesis is based on the well-known positive relationship between female SVL and clutch size in anurans (Crump, 1974; Townsend and Stewart, 1994). Because we had these a priori directional hypotheses, we used directed tests in which the Type-I error rate (α) is partitioned into two segments, $\alpha = \gamma + \delta$, the larger of which (γ) is associated with deviations between means in the anticipated direction (Rice and Gaines, 1994). For $\alpha=0.05$, the suggested ratio of $\gamma/\alpha=0.8$ (Rice and Gaines, 1994) gives $\gamma=0.04$ and $\delta=0.01$. We report $P_{1\text{-tailed}}$ and P_{dir} which is the P -value for directed tests.

We predicted the expected reduction in clutch size resulting from the observed reduction in female SVL in the fragment at Dimona using an equation that relates SVL to clutch size for small, neotropical frogs like *C. stephensi* with terrestrial, direct-developing eggs. This equation allowed us to assess whether the observed reduction in SVL could explain the observed reduction in clutch size. The equation is: $\ln(\text{clutch size}) = 2.644 \times \ln(\text{SVL}) - 6.142$ (Crump, 1974). An expected clutch size was calculated from the SVL of each female found in continuous forest and fragment plots at Dimona. The mean expected clutch size was then calculated for each treatment and the difference between expected means was qualitatively compared to the difference between observed means.

2.4. Population simulations

Population simulations were used to test whether the magnitude of the observed reduction in clutch size in the 10-ha fragment at Dimona could cause the observed reductions in N in fragments at Dimona and Esteio. We did this by running simulations with and without the reduction in clutch size and comparing the mean final abundances to calculate an expected reduction in N from the reduction in clutch size. Although it would be possible to use a simpler approach calculating final abundances from deterministic population growth rates, we favored a simulation approach that allowed us to account for variation and uncertainty in vital rates.

Simulations were performed using program RAMAS/metapop 1.0 (Akçakaya, 1994) for four different scenarios: (1) continuous forest at Dimona (no reduction in clutch size); (2) 10-ha fragment at Dimona (with the observed reduction in clutch size); (3) continuous forest at Esteio (no reduction in clutch size); and (4) 10-ha fragment at Esteio (with the observed reduction in clutch size). For each scenario, 2000 simulations were run for a single population whose growth was projected monthly over a time period equivalent to the number of years that 10-ha fragments have been isolated from continuous forest at each site (15 years at Dimona and 19 years at Esteio). Each simulation included both

demographic (binomial and Poisson distributions for survival rates and fecundity, respectively) and environmental (lognormal distribution for both survival rates and fecundity) stochasticity and was started with an initial adult abundance equivalent to the estimated abundance of adult males in continuous forest plots at each site (29 males during the first capture session at Dimona and 25 males at Esteio) at stable stage distribution.

In order to run simulations, male-based, post-birth pulse Lefkovitch matrices (Caswell, 2001) were constructed with monthly projection intervals representing a life history consisting of three stages: prejuvenile (embryo + larva), juvenile, and reproductive adult (Fig. 1). Vital rate data used in the Lefkovitch matrices were obtained from this study and the scientific literature (Table 1; for derivations of vital rates and matrix elements see Appendix at http://www.forestry.umd.edu/frog_fragmentation.pdf). In most cases, standard deviations (SD) associated with vital rates had to be inferred from observed ranges (maximum and minimum reported values). In addition, the available data did not allow us to distinguish between temporal, spatial, or sampling variation which ideally should be separated (Gould and Nichols, 1998).

Because of uncertainty associated with some of the vital rates used, we assessed the robustness of predicted reductions in *N* to potential inaccuracies in vital rate means and standard deviations. For each of the four previously mentioned scenarios (continuous forest and 10-ha fragments at Dimona and Esteio), simulations

were run with mean vital rate values of 0.5 (low) and 1.5 (high) times the magnitude of baseline values for each individual vital rate with all other vital rates held at baseline values. Simulations were also run with standard deviations that were 0.5 (low) and 1.5 (high) times the magnitude of baseline standard deviations for each vital rate with baseline mean values and the S.D. of all other vital rates held at baseline values. The robustness of predicted reductions in *N* was assessed by the degree to which predicted reductions with low and high vital rate means and standard deviations differed from predictions with baseline means and standard deviations.

Table 1
Demographic vital rates used in Lefkovitch matrix models for *Colostethus stepheni*^a

Vital rate ^b	Mean	S.D.
Embryo + larval survival	0.51	0.03
Juvenile survival	0.80	0.07
Age at sexual maturity	8	0.50
Probability of a juvenile staying a juvenile	0.75	0.06
Probability of a juvenile becoming an adult	0.05	0.03
Adult survival	0.90	0.07
Number of clutches/male/month	0.47	0.11
<i>Clutch size</i>		
Continuous forest	2.32	0.53
10-ha fragment	1.92	0.21

^a For derivations of vital rates and matrix elements see appendix at http://www.forestry.umd.edu/frog_fragmentation.pdf.

^b All vital rates are monthly and for males only.

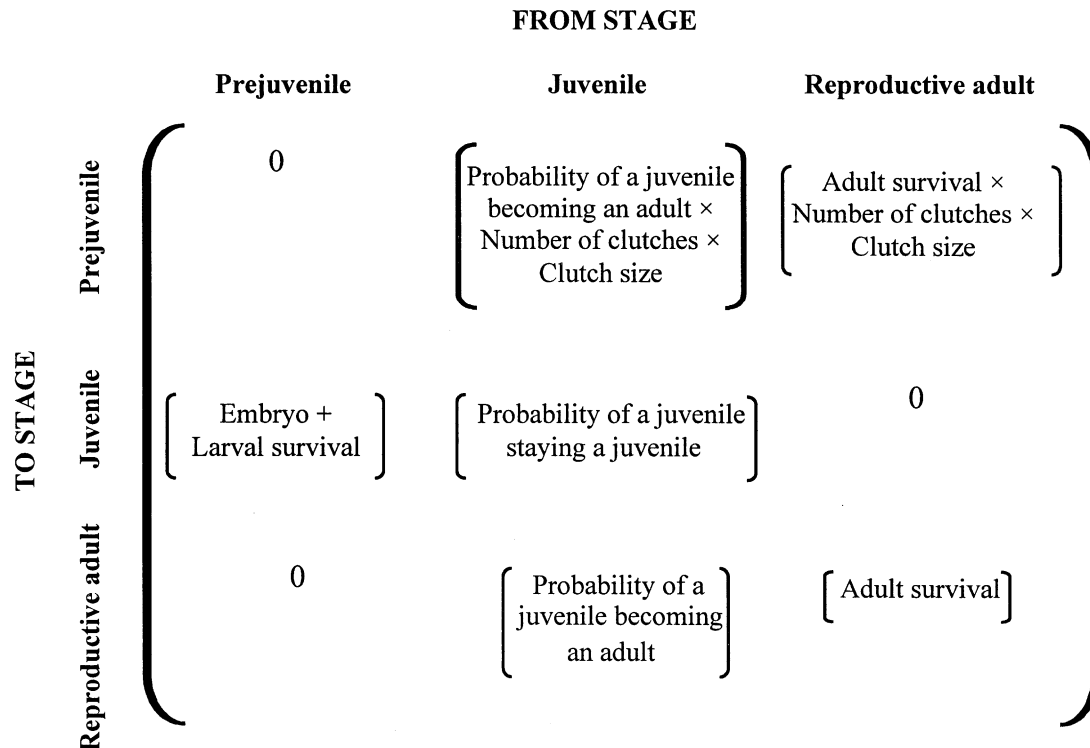


Fig. 1. Male-based, post-birth pulse Lefkovitch matrix with monthly projection intervals used in population simulations for *Colostethus stepheni*.

Table 2

Best supported (ΔAICc ^a values <4) closed population capture-recapture models used to examine variation in capture (p) and recapture (c) probabilities over days (t , T) ^b and treatments (g) ^c and in abundance (N) over treatments at Dimona and Esteio for *Colostethus stepheni*

Site (capture session)	Model	Description	ΔAICc	No. of parameters
Dimona (second)	$p_{g \times T} c_g N_g$	Linear trend in p over days with different slopes among treatments, c constant over days	0.00	8
	$p_{g \times T} c N_g$	Linear trend in p over days with different slopes among treatments, c constant over days and treatments	0.31	7
	$p_{g \times T} c_{g+T} N_g$	Linear trend in p over days with different slopes among treatments, linear trend in c over days with the same slope in both treatments	2.13	9
	$p_{g \times T} c_T N_g$	Linear trend in p over days with different slopes among treatments, linear trend in c over days and constant over treatments	2.36	8
	$p_{g \times T} c_{g \times T} N_g$	Linear trend in p and c over days with different slopes among treatments	3.09	10
	$p_{g \times t} c_g N_g$	c constant over days	3.13	16
	$p_{g \times t} c N_g$	c constant over days and treatments	3.31	15
Dimona (third)	$p_t c_{g \times T} N_g$	p constant over treatments, linear trend in c over days with different slopes among treatments	0.00	12
	$p_{g+t} c_{g \times T} N_g$	Constant difference in p among treatments over days, linear trend in c over days with different slopes among treatments	2.30	13
Esteio (only)	$p_{g \times t} = c_{g \times t} N_g$	p and c the same over days (no capture response)	0.00	21
	$p_{g+t} c_g N_g$	Constant difference in p among treatments over days, c constant over days	2.98	14

^a ΔAICc is the difference between the AICc (adjusted Akaike information criterion) value of the given model and the model with the lowest AICc value.

^b t indicates variation in p or c over days, whereas T specifies a linear trend in p or c over days.

^c The three treatments were continuous forest, 10-ha fragment, and matrix, but because no *Colostethus stepheni* were found in the matrix plot at Dimona, capture–recapture data was only available for continuous forest and 10-ha fragment treatments at this site.

3. Results

3.1. Abundance in continuous forest, forest fragments, and matrix

At Dimona, a total of 48 male *Colostethus stepheni* were captured during the second 6-day capture session and a total of 32 frogs were captured during the third session. During the second capture session, 28 frogs were captured in the continuous forest plot, 20 in the 10-ha fragment plot, and none in the matrix plot. During the third capture session, 19 frogs were captured in the continuous forest plot, 13 in the 10-ha plot, and none in the matrix plot. Capture histories from these two capture sessions were used to estimate abundance (N) using closed population models. Seven closed population models were well-supported (had ΔAICc values <4) for the second capture session and two for the third session (Table 2). All seven models for the second capture session had variation in capture probabilities (p) over days and treatments and capture probabilities that were different than recapture (c) probabilities. For the third capture session, both models had variation in c over days and treatments and, once again, capture probabilities that were different than

recapture probabilities. Male N estimates for continuous forest, 10-ha fragment, and matrix plots, respectively, were 29, 21, and 0 during the second capture session (Fig. 2a) and 20, 14, and 0 during the third capture session (Fig. 2b). Abundance estimates based on the best model were only slightly higher than the number of individuals sampled because of very high capture probabilities which allowed almost a complete census of all individuals in each plot.

At Esteio, a total of 35 male *Colostethus stepheni* were captured during the single 6-day capture session. Of these frogs, 22 were captured in the continuous forest plot, 10 in the 10-ha fragment plot, and 3 in the matrix plot. Two closed population models were well supported (had ΔAICc values <4; Table 2). The best supported model did not show a difference between capture and recapture probabilities, but both models did have variation in p among days and treatments. Abundance estimates were 25, 13, and 6 males in the continuous forest, 10-ha fragment, and matrix plots, respectively (Fig. 2c).

3.2. Vital rates in continuous forest and forest fragment

A total of 66 different *Colostethus stepheni* males were captured during all three capture sessions at Dimona.

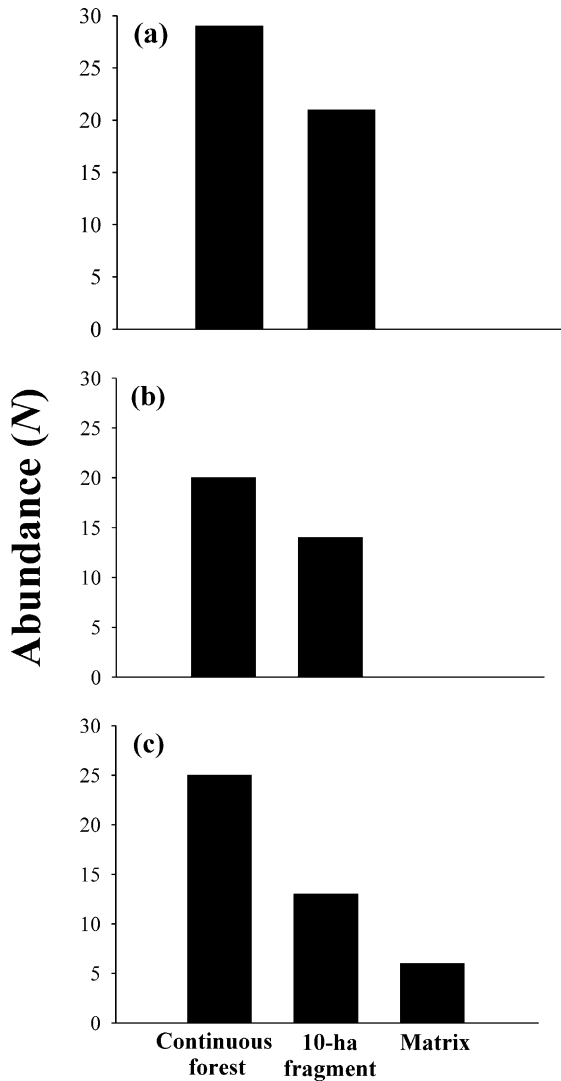


Fig. 2. Abundance (N) estimates for *Colostethus stepheni* in continuous forest, 10-ha forest fragment, and matrix plots at: (a) Dimona during the second capture session; (b) Dimona during the third capture session; and (c) Esteio. No 95% confidence intervals are visible because high capture probabilities allowed almost a complete census.

Of these frogs, 40 were captured in the continuous forest plot and 26 in the 10-ha forest fragment. Capture histories from these capture sessions were used to estimate apparent survival probabilities (ϕ) using CJS open population models. Seven CJS models were well-supported (ΔAICc values <4 ; Table 3). The best supported model had no variation in apparent survival probability (ϕ) or capture probability (p) over months or treatments, but the other six indicated potential monthly or treatment variation in these parameters. Estimates of monthly apparent survival probabilities during the first and second time intervals, respectively, were 0.602 (95% CI: 0.455–0.733) and 0.585 (95% CI: 0.446–0.712) in continuous forest and 0.614 (95% CI: 0.462–0.747) and 0.597 (95% CI: 0.449–0.729) in the 10-ha fragment (Fig. 3).

We placed a total of 144 artificial nests by 48 males (three nests by each male) in the continuous forest and 10-ha forest fragment plots at Dimona. Approximately 4

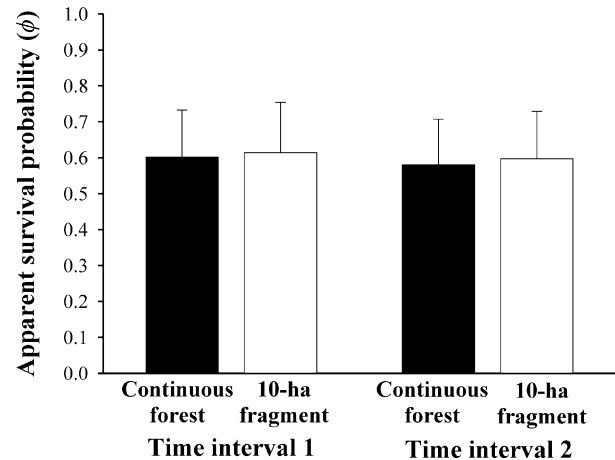


Fig. 3. Apparent survival probability (ϕ) estimates for *Colostethus stepheni* in continuous forest and 10-ha forest fragment plots at Dimona for the first and second approximately 4-week intervals. Error bars represent upper 95% confidence intervals.

Table 3

Best supported (ΔAICc^a values <4) Cormack–Jolly–Seber (CJS) capture–recapture models used to examine variation in capture (p) and apparent survival (ϕ) probabilities over months (t) and treatments (g)^b at Dimona for *Colostethus stepheni*

Model	Description	ΔAICc	No. of parameters
ϕp	ϕ and p constant over months and treatments	0.00	2
ϕp_t	ϕ constant over months and treatments, p constant over treatments	1.79	3
$\phi_g p$	ϕ constant over months, p constant over months and treatments	1.79	3
$\phi_t p$	ϕ constant over treatments, p constant over months and treatments	1.79	3
$\phi_t p_t$	ϕ and p constant over treatments	1.79	3
ϕp_g	ϕ constant over months and treatments, p constant over months	2.15	3
$\phi_g p_t$	ϕ constant over months, p constant over treatments	3.63	4

^a ΔAICc is the difference between the AICc (adjusted Akaike information criterion) value of the given model and the model with the lowest AICc value.

^b The two treatments were continuous forest and 10-ha forest fragment.

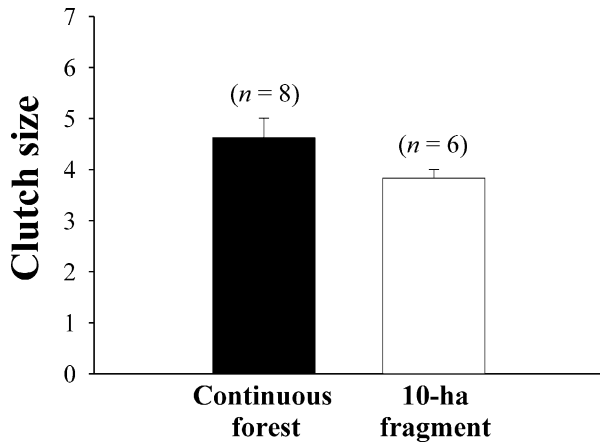


Fig. 4. Mean clutch size estimates for *Colostethus stephensi* in continuous forest and 10-ha forest fragment plots at Dimona ($P_{1\text{-tailed}}=0.049$, $P_{\text{dir}}=0.061$). Error bars represent standard errors (SE).

weeks later, we found clutches of one to six embryos in 11 artificial nests (7.6%) and five natural nests. Only two clutches (one in continuous forest and one in the fragment) had sizes of one embryo and all other clutches had at least three embryos. The two clutches with only one embryo were excluded from the analysis because they likely had been preyed upon before we checked them given that the previously reported minimum clutch size for *C. stephensi* is two based on a sample size of 143 clutches (Juncá, 1999). Exclusion of these two clutches did not qualitatively affect our results. Mean clutch size for the remaining clutches was 17% smaller in the 10-ha fragment (mean = 3.83 ± 0.17 SE) than in continuous forest (mean = 4.63 ± 0.38 SE, $n=14$, $P_{1\text{-tailed}}=0.049$, $P_{\text{dir}}=0.061$) (Fig. 4).

3.3. Expected reduction in abundance in forest fragments from reduced clutch size

The predicted reduction in N in forest fragments based on simulations incorporating the observed reduction in clutch size was 92% at Dimona and 96% at Esteio (Fig. 5). These reductions are substantially higher than the observed reduction in N at Dimona of 29% (which is an average of the 28% reduction seen in the second capture session and the 30% reduction seen in the third) and at Esteio of 48%. Moreover, this result is robust to potential inaccuracies in vital rate mean and S.D. estimates. With low and high vital rate means and standard deviations, the lowest reduction in N at Dimona expected from the observed decrease in clutch size is 70% and the highest expected reduction is 98%. The lowest and highest expected reductions in N at Esteio are 95 and 100%, respectively (Fig. 5). Therefore, even if the baseline vital rate mean and S.D. estimates used are not all accurate, the overall result still holds that expected reductions in N in fragments from the observed reduction in clutch size are much greater than the observed reductions.

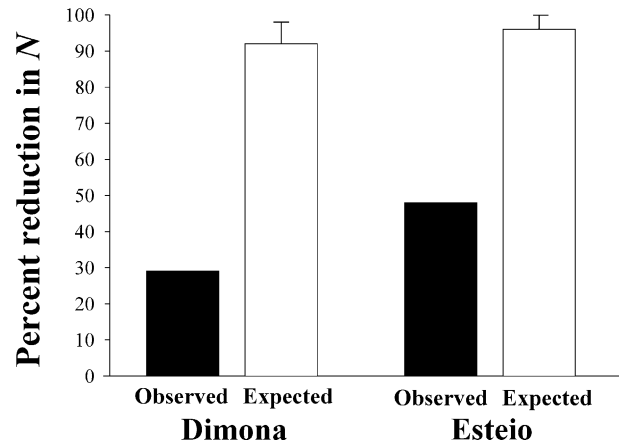


Fig. 5. Observed and expected percent reductions in abundance (N) of *Colostethus stephensi* in 10-ha forest fragment plots compared to continuous forest plots at Dimona and Esteio. Observed reductions in N were calculated from N estimates in continuous forest and 10-ha fragment plots. Expected reductions in N were calculated from mean N estimates from population simulations for continuous forest populations without a reduction in clutch size and for 10-ha fragment populations with a reduction in clutch size of 0.8 eggs/clutch (equivalent to that observed in the 10-ha fragment plot at Dimona). Error bars represent the maximum expected reductions in N from simulations with low and high vital rate means and standard deviations to test the robustness of simulations to potential inaccuracies in the estimates used.

3.4. Snout-vent length in continuous forest and forest fragment

Mean male snout-vent length was smaller in the 10-ha fragment (mean = 16.31 ± 0.12 SE) than in continuous forest at Dimona (mean = 16.56 ± 0.09 SE, $n=66$, $P_{1\text{-tailed}}=0.047$, $P_{\text{dir}}=0.059$; Table 4). Similarly, mean female SVL was also smaller in the 10-ha fragment (mean = 16.53 ± 0.29 SE) than in continuous forest (mean = 17.83 ± 0.06 SE, $n=10$, $P_{1\text{-tailed}}=0.004$, $P_{\text{dir}}=0.005$; Table 4).

Table 4

Mean snout-vent lengths (SVL) of adult male and female *Colostethus stephensi* in continuous forest and 10-ha fragment plots at Dimona

Treatment	Snout-vent length (mm)	
	Male ^a	Female ^b
Continuous forest	16.56 ± 0.09^c $n=40$	17.83 ± 0.06 $n=4$
10-ha fragment	16.31 ± 0.12 $n=26$	16.53 ± 0.29 $n=6$

^a $P_{1\text{-tailed}}=0.047$ and $P_{\text{dir}}=0.059$ for a Behrens–Fisher T test of the hypothesis that mean male SVL was shorter in the fragment than in continuous forest.

^b $P_{1\text{-tailed}}=0.004$ and $P_{\text{dir}}=0.005$ for a Behrens ± Fisher T test of the hypothesis that mean female SVL was shorter in the fragment than in continuous forest.

^c Standard error (SE).

The predicted mean clutch size in continuous forest for the observed female snout-vent lengths is 4.37 eggs/clutch. The predicted mean clutch size in the 10-ha fragment for the observed female snout-vent lengths is 3.60. Therefore, the reduction in clutch size in the 10-ha fragment expected to result from the observed reduction in female SVL is 0.77 eggs/clutch which is very close to the observed reduction (4.63 eggs/clutch in continuous forest – 3.83 eggs/clutch in the 10-ha fragment = reduction of 0.80 eggs/clutch).

4. Discussion

Colostethus stephensi abundance is reduced in forest fragment plots at Dimona and Esteio relative to continuous forest plots, suggesting that populations within fragments have declined as a result of fragmentation. The evidence from the present study suggests that reduced clutch sizes resulting from decreased female snout-vent lengths is the cause of the decline of *C. stephensi* in these forest fragments. The first line of evidence supporting this conclusion is that adult survival was not reduced in the 10-ha forest fragment at Dimona (Fig. 3), suggesting that a different vital rate reduction was responsible for the decline. Secondly, clutch size was reduced by 0.80 eggs/clutch in the fragment at Dimona (Fig. 4). Next, female SVL was reduced by 1.3 mm in the fragment at Dimona (Table 4) which, according to an equation relating clutch size to SVL, is expected to result in almost exactly the clutch size reduction observed. Moreover, male SVL was also reduced in the fragment at Dimona, demonstrating that reduced SVL in the fragment was a general phenomenon for both sexes. Finally, population simulations demonstrated that a reduction in clutch size of this magnitude is more than sufficient to cause the reduction in abundance observed at Dimona and Esteio, a result that is robust to potential inaccuracies in the vital rate estimates used (Fig. 5). The observed reduction in abundance may be less than expected from simulations because of immigration into fragments, compensatory increases in other vital rates, and/or a lower average reduction in clutch size over time than that observed during the period of this study.

Snout-vent length was measured and vital rates were estimated at Dimona only, so it is unknown whether clutch size and SVL are also negatively impacted by fragmentation at Esteio or other sites. Nonetheless, it is clear from the population simulations that a reduction in clutch size of the magnitude observed at Dimona is more than sufficient to have caused the observed decline in abundance at Esteio, suggesting that reduced clutch size resulting from a reduction in SVL could be the mechanism of decline at Esteio as well. The generality of this mechanism should be tested in future studies by estimating vital rates and SVL at other sites. The effect

of fragmentation on other vital rates such as juvenile survival probabilities and embryo + larval survival probabilities should also be tested in order to assess whether other mechanisms may be involved in declines as well.

The equation used in this study did an excellent job of predicting the observed reduction in clutch size from the observed reduction in SVL, yet it may not be the most suitable equation given that it was not developed for *C. stephensi*. Previous work did not find a positive correlation between clutch size and SVL in *C. stephensi* (Juncá, 1999), but this may be an artifact of small sample size and/or the fact that data were not log-transformed in order to reduce the curvilinear relationship between clutch size and SVL in anurans (Crump, 1974). Therefore, it would be useful to develop a regression model relating the natural logarithm of clutch size to the natural logarithm of SVL for *C. stephensi* in order to assess whether the observed reduction in clutch size could be caused by the observed reduction in SVL.

The reason for the observed reduction in SVL is unknown. Potential explanations include: (1) increased predation in fragments resulting in lower survival and a size structure skewed towards smaller individuals; (2) increased interspecific competition in fragments resulting in slower growth rates; (3) reduced prey base in fragments resulting in slower growth rates; and/or (4) delayed reproduction in fragments resulting in younger, smaller females. The first explanation seems unlikely given that no difference in survival probabilities was seen between continuous forest and the 10-ha fragment. The three other possibilities seem more probable. In particular, there could be increased interspecific competition in fragments between *C. stephensi* and other small, terrestrial leaf-litter frogs such as *Eleutherodactylus fenestratus* which may increase in abundance in fragments (Tocher et al., 1997) and eats similar prey items as *C. stephensi* (Zimmerman and Rodrigues, 1990; Lima and Magnusson, 1998). The abundance of the invertebrate prey items preferred by *C. stephensi* also could have been reduced. Previous work has not demonstrated an effect of fragment size on invertebrate abundance (Didham, 1997), but the responses of the smaller invertebrate prey preferred by *C. stephensi* are unknown. Finally, reproduction could occur later in fragments if fragments are drier than continuous forest so that juveniles would have less time to grow to sexual maturity by the following breeding season. This could result in younger, smaller females in fragments than in continuous forest at any given point in time.

5. Conclusions

Testing the effects of forest fragmentation on demographic vital rates and placing observed vital rate

reductions in a population level context using population modeling are important avenues of investigation for identifying potential causes of declines in fragments. The first step for generating hypotheses about the causes of declines in fragments is to look for correlations between species responses, life history characteristics, and changes in microhabitat. This approach has been successful in identifying life history characteristics that make species susceptible to forest fragmentation and potential microhabitat changes underlying declines (Laurance, 1994; Mills, 1995; Tocher et al., 1997). However, in order to dissect the proximate and ultimate causes of declines, it is also important to test the effect of fragmentation on vital rates and assess whether any vital rate reductions are consistent with observed reductions in abundance using population modeling methods. Once one or more vital rate reductions have been identified as potential proximate causes of declines, hypotheses for the ultimate causes of declines can be tested. Detailed studies of this nature will help us understand the mechanisms causing declines in forest fragments and, from this understanding, will help in the development of strategies for managing forests for the persistence of vulnerable species in increasingly fragmented forest landscapes.

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