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The reproductive success of *Colostethus stepheni* (Anura: Dendrobatidae)

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Abstract

The mating and clutch development success of *Colostethus stepheni,* a small dendrobatid frog with terrestrial development and parental care, was studied in both primary and secondary amazonian forests, near Manaus, Brazil. Males mated twice on average, but their size influenced neither their mating frequency nor the number of eggs and tadpoles preyed upon. Individual clutches contained approximately four eggs and their survival rate (until the completion of metamorphosis) was approximately 50%. Multiple clutches were present. Predation was the principal cause of death of eggs and tadpoles. The number of eggs and tadpoles preyed upon in primary forest was approximately 10% larger than in secondary forest. During the two-year study, the number of eggs and tadpoles preyed upon was positively correlated with rainfall, although the number of clutches produced was not.

Resumo

O sucesso de acasalamento e desenvolvimento das desovas de *Colostethus stepheni,* um pequeno dendrobatídeo com desenvolvimento terrestre e cuidado parental, foi estudado em mata amazônica primária e capoeira próximo a Manaus, Brasil. Machos acasalaram em média duas vezes e seu tamanho não influenciou no número de acasalamentos nem no número de ovos e girinos predados. Mais de uma desova em um mesmo ninho foi observada. Cada desova apresentou em média 4 ovos e a taxa de sobrevivência destes foi de aproximadamente 50%. A predação foi a principal causa da morte de ovos e girinos. O número de ovos e girinos predados na mata primária foi aproximadamente 10% maior que na capoeira. Durante os dois anos de estudo o número de ovos predados mostrou-se positivamente correlacionado com a precipitação, embora o número de desovas produzidas não.

Keywords: Dendrobatidae, *Colostethus stepheni*, reproductive success, predation, eggs, predators

Introduction

Reproductive success can be defined as the relationship between the number of descendents produced by an individual and those produced by other individuals of the same species (Ryan, 1985). It has been measured variously in different taxa. For species of territorial lizards, for example, the number of females found within a male's territory has been used as a measure of his reproductive success (Stamps, 1983). In many bird species, the reproductive success of a male can be estimated by counting the number of clutches produced within his territory (Hiebert et al., 1989). For species with internal fertilization, such as birds, the success of the newly hatched chicks and the recruitment of young individuals into the population can be readily calculated, although it is practically impossible to be certain about the clutches' paternity in non-monogamous species. Anurans, with few exceptions, practice external fertilization. This would, in theory, permit a greater degree of certainty concerning the paternity of egg clutches (Lamotte & Lescure, 1977; Duellman & Trueb, 1986). Therefore, mating success of males can be measured with greater precision by quantifying number of eggs fertilized

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as well as the number of larvae that hatch (Shaffer et al., 1994). Tadpoles, however, are difficult to follow after hatching, because they rapidly disperse. Thus for anurans, mating success and hatching success provide the principal quantitative data which can measured to estimate the variation in reproductive success among individuals in a population (Ryan, 1983, 1985; Howard, 1983; Townsend, 1989b; Pough et al., 1998). In species of anurans with explosive reproduction males have few mating opportunities, since the reproductive period is extremely short. In these cases sex ratios are approximately one and most of the males will only be able to mate once. Then there will be little variation in the mating success among individuals (Pough et al., 1998). In species with longer reproductive seasons, however, mating opportunities may be numerous, providing for greater variation in mating success among males.

Although most species of the Dendrobatidae produce semi-terrestrial tadpoles (Wells, 1977a, 1977b, 1978, 1980a, 1980b; Limerick, 1980; Duellman & Trueb, 1986; Weygoldt, 1986; Aichinger, 1991; Pough et al., 1995), tadpoles of *Colostethus stepheni* Martins, 1990, develop fully on dry land (Juncá, 1998; Juncá et al., 1994). In this species it is possible not only to determine mating and hatching success, but also the success of the clutch through metamorphosis. *Colostethus stepheni* is a diurnal small frog (SVL 16.6 mm for males and 17.1 for females) occurring in both primary and secondary forests of Central Amazonia. Males vocalize with an advertisement call from perches usually only a few centimeters above the litter of forest and defend a territory with favorable nesting sites through the rainy season (Juncá, 1998). The nests are cup shaped, partly rolled up leaves with another leaf acting as a roof. The territory defence consists of an encounter call, display and aggressive attack, lasting up to 18 min (Juncá, 1996) and the home range varies from 4.9 to 6.7 m^2 (Juncá, unpublished data). Nesting sites are selected before the females appear and their distance from the male calling site varied from 30 to 150 cm (Juncá, 1998). This species has a very characteristic reproductive mode, for the couple engages in two amplexi (separated by 3 – 6 h) before ovipositing (Juncá, 1998). After having been attracted by a potential mate, the female is led to the nest where the first amplexus occurs. Shortly thereafter, the male leaves the nest while the female remains for a period of approximately five hours. When the male returns after this period, they engage in a second amplexus, followed by spawning. The clutch consists of 3 – 6 pigmented eggs, each one surrounded by a gelatinous capsule and glued together with a thick transparent jelly, that was initially formed by tens of hydrophilic colloidal spheres, similar in size to eggs. Development from oviposition to metamorphosis takes approximately 30 days and the male cares for the clutch, visiting it regularly during the first days of development. During parental care the male constantly remains close (20 cm) to the nest, sometimes enters it and sits on the clutch. During the nest guarding period, the male continues to exhibit territorial and mate attraction behaviours (Juncá, 1996).

Juncá (1996, 1998) found that males use artificial nest sites similar to natural nests. Artificial nests are made by joining two cup-shaped leaves of approximately equal size with their concave sides facing inward (Figure 1) and placed on the litter. The cavity thus formed can be used by anurans for mating and egg laying. In order to determine the reproductive success of *C. stepheni*, males as well as the principal causes of death of the tadpoles, artificial nest sites were placed within the territories of vocally active males in order to record the number of matings, the number of tadpoles which survived until the end of metamorphosis, and the principal causes of egg and tadpole mortality.

Materials and methods

Study sites

This study was undertaken in areas of primary and secondary forest located approximately 80 km north of Manaus, Amazonas State, Brazil (2° 25' S,

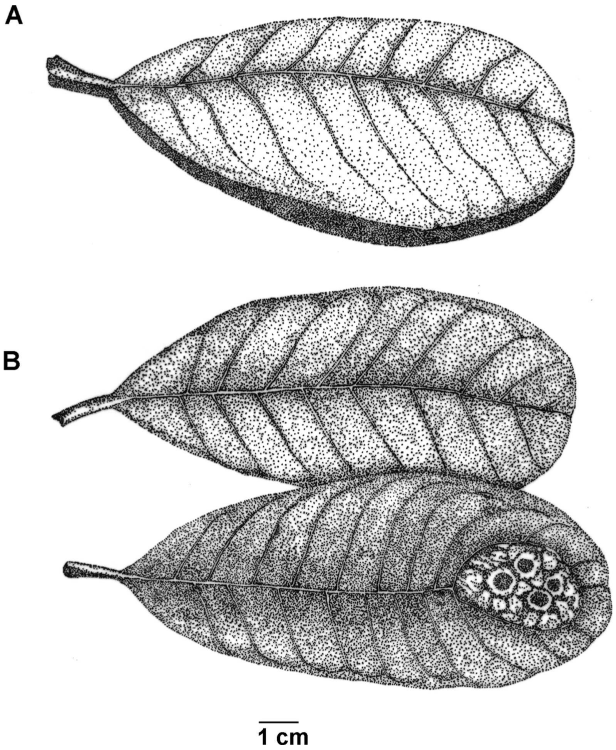

Figure 1. Example of an artificial nest offered to *Colostethus stepheni*. (A) closed and (B) opened to exhibit one clutch.

59° 50' W) which make up part of the Biological Dynamics of Forest Fragments Project (BDFFP) (Lovejoy & Bierregaard, 1990). The areas of primary forest were located in the "41" (100 000 m^2) and "Florestal" (75 000 m^2) reserves located approximately 15 km one from another. Within the "Florestal" reserve, an area of secondary forest was also delimited (50 000 m^2). The primary (A1) and secondary (A2) forest areas in "Florestal" reserve were separated from each other by more than 2 km. Area A1 was located approximately 600 m from the border of the secondary forest, while area A2 was approximately 300 m from the border of the primary forest. The fragments were not totally isolated, but had at least one of their sides in contact with continuous and intact forest. Two areas of primary forest (approximately 100 m^2) located 500 m (B1) and 200 m (B2) from the margins of areas "A1" and "A2", respectively, were also part of this study to increase the number of clutches used in the survival experiments (see below).

The climate in the study area is influenced more by rainfall patterns than by temperature fluctuations, monthly means vary from 26 to 27°C. Monthly rainfall during the rainy season can reach 300 mm, while during the dry season (June to September) it varies between 82.6 and 136 mm (Marques Filho et al., 1981). Daily precipitation was measured with pluviometers located in reserves "41" and "Colosso", the latter being approximately 5 km from the study area in "Florestal". Study area A2 was dominated by *Cecropia* spp.

Artificial nests

Potential nesting sites were prepared by joining leaves of approximately equal size with their concave sides facing inwards and placing them near vocally active males (Juncá, 1996). The cavity thus formed can be used by the frogs for mating and egg laying. Leaf size, shape and color were as similar as possible to those of natural nests. Four hundred and twenty-four artificial nests were constructed in "41" reserve between January and February 1995 offering two potential nests each of 212 males. Potential nests were placed approximately 10 cm from each male, leaving a distance of approximately 20 cm between each nest. These nests were observed until May 1995.

Four hundred and sixty-eight artificial nests were constructed in "Florestal" reserve between February and April 1996 and offered to each of 129 vocally active *C. stepheni* males in area "A1" and 105 in area "A2" respectively. In order to increase the number of clutches studied, 100 additional males also received two potential nests each. These males were located in B1 and B2. All nests were observed until May 1996, but those in B1 and B2 were used to increase the number of clutches in experiments.

If males remained in their territory, 45% of the nests were reused for one or two clutches (Juncá, 1996), whereas when males were removed after reproduction, less than 1% of the nests were reused. These results suggest that a takeover of nests by other males is rare and that multiple clutches are likely produced by a resident territorial male. In order to not disturb the frogs and thereby lower their mating chances, we did not mark males individually.

In the present study, all nests (except those in B1 and B2) were observed until development was completed on a repeated schedule of 10 days of daily observations separated by four day intervals without observation. Artificial nests were inspected by lifting the upper leaf, counting the number of clutches or mates, the number of eggs per clutches and recording the developmental stage of the embryos. In the secondary forest, we obtained clutches in natural nests placed in *Cecropia* leaves that were unrolled and inspected in the same way.

Predation was evaluated after direct inspection of the nests. Depending on the type of predation suffered, egg clutches will show either of two distinctive marks: (1) eggs or embryos in early stages of development still inside the nest, but "perforated" and with most of the yolk lost; (2) eggs, embryos and tadpoles lost, leaving, in some cases, remains of the vitellus dispersed in the jelly which protects the clutch.

Six developmental stages were recognized for clutches, according to the number of days after egg laying and corresponding to the developmental stages defined in Gosner (1960) (in parenthesis): (1) eggs and early stage embryos 0 to 5 days (stages 1–20), (2) embryos 6 to 10 days (stages 21–30), (3) tadpoles 10 to 15 days (stages 31–35), (4) tadpoles with hind limbs 16 to 20 days (stages 36–40), (5) tadpoles with fore and hind limbs 21 to 25 days (stages 41–44) and (6) recently metamorphosed frogs 26 to 30 days (stages 45–46).

Survival experiments

In order to compare the breeding success of *Colostethus stepheni* in primary and secondary forests, experiments were performed with clutches located in areas A1 and A2, as well as in two areas of primary forest adjacent to them (B1 and B2).

Forest 1 (F1): A group of clutches obtained in area A1 was not exposed to any form of treatment. The clutches underwent normal development in the primary forest and experienced male parental care.

Forest 2 (F2): A group of clutches obtained in B1 and was transferred to area A1, approximately 24 h after oviposition and placed approximately 3 m distant from existing nests in that area. These clutches would develop in the same forests type but were deprived of parental care.

Forest 3 (F3): A group of clutches obtained in area A1 remained there undisturbed, but was deprived of parental care by removing the male within 24 h after oviposition. This group served as a control to determine if the transport of clutches in itself influenced survival.

Secondary Forest 1 (SF1): A group of clutches was maintained in an area of secondary forest (A2) and experienced male parental care.

Secondary Forest 2 (SF2): A group of clutches obtained in an area of primary forest (B2) but subsequently transferred to secondary forest (A2) approximately 24 h after spawning and placed 3 m distant from existing nests in that area.

For the statistical analyses of the results we used Chi-square tests or Pearson correlation coefficient (Zar, 1984). The significance level considered was 0.05.

Results

Male mating success in primary and secondary forests

In 1995, 127 nests (29.9%) were used by 85 males (40.1%), resulting in 175 clutches. In that year, 42 (49.4%) males used the two nests offered. In 1996, 50 males (38.8%) utilized the nests in A1, and a total of 75 clutches were obtained. Of the 27 males that stayed in their territories (F1), nine (33.3%) used the two nests offered. Although the number of clutches per male varied from 1 to 5 in both areas studied, average numbers of clutches per male are similar ("41" reserve: $\bar{x} = 2.07$; $SD = 1.00$; $N = 85$ males; and "Florestal" reserve: $\bar{x} = 2$; $SD = 1.29$; $N = 27$ males).

In both reserves 2–6 eggs were laid per clutch ("41" reserve: $\bar{x} = 3.9$; $SD = 0.7$; $N = 170$ clutches; and A1: $\bar{x} = 3.66$; $SD = 0.76$; $N = 52$ clutches). There was no significant correlation between the number of eggs and the snout vent length (SVL) of the females, which varied from 16.8 to 20.2 mm in "41" reserve ($r = -0.24$; $N = 24$; $P > 0.05$) and from 16.6 to 19.5 mm in "Florestal" reserve ($r = -0.20$; $N = 17$; $P > 0.2$). In "41" reserve, the number of clutches was not statistically related to the SVL of the males, which varied from 16.5 to 19.4 mm ($r = -0.05$; $N = 29$; $P > 0.5$).

In the secondary forest, only eight of the 109 males (7.6%) used one of the constructed nests. The number of eggs per clutch was similar to that found in the primary forest ($x = 3.75$; $SD = 0.71$). Three clutches were located and observed in natural nests. No difference in development or type of predation was observed between the primary and secondary forest clutches.

Clutch survival

In 1995 of 175 clutches recorded, only 165 (of 84 males) were observed since the first day until the development was completed. For those clutches we counted a total of 644 eggs, 281 (43.63%) of which survived until the end of metamorphosis. Each male cared for approximately eight embryos ($\bar{x} = 7.66$; $SD = 4.02$; $N = 84$ males), of which only three or four survived until the end of metamorphosis ($\bar{x} = 3.36$; $SD = 3.16$; $N = 84$ males). There was no relationship between the SVL of males and the proportion of embryos or tadpoles that were preyed upon ($r = 0.10$; $N = 29$; $P > 0.05$). In 1996, 194 eggs were observed ($\bar{x} = 7.18$; $SD = 4.83$; $N = 27$ males) in the primary forest site. Of these, 106 (55%) survived until the end of metamorphosis, giving an average of 3.6 successfully metamorphosed frogs per male ($\bar{x} = 3.59$; $SD = 3.50$; $N = 27$ males). Almost all of the clutches in "41" and Florestal reserves were partially or totally preyed upon (Table I).

Multiple clutches

Nests were not used again after removing the male (F3), and the transferred nests (F2 and SF2) did not

Table I. Variation of the relative frequency of the different degrees (in %) of predation of the clutches of *C. stepheni* according to different experimental treatments. PF: primary forest; SF: secondary forest; F1, F2, F3, SF1 and SF2—different experimental treatments (see Material and methods).

	Degrees of predation (%)				
	0%	17–25%	33–50%	60–75%	80–100%
PF "41" Reserve	0.24	0.12	0.09	0.06	0.47
PF Florestal–F1	0.41	0.12	0.08	0.06	0.33
PF Florestal–F2	0.41	0.07	0.07	0.17	0.34
PF Florestal–F3	0.38	0	0.05	0.05	0.52
SF Florestal–SF1	0.50	0.13	0.25	0.13	–
SF Florestal–SF2	0.50	0.18	0.04	0.11	0.18

present new clutch. On the other hand, the nests where the male remained undisturbed had multiple clutches, indicating that the paternity of these multiple clutches was due to only one male. Forty-four males in "41" reserve had multiple contemporaneous clutches (34 males had two clutches, and 10 males had more than two). A single male may have as many as five contemporaneous clutches. The number of contemporaneous clutches was not related to the male's SVL ($r = -0.02$; $N = 24$; $P > 0.5$). When males were able to acquire a second mate, 39 used a different nest, while five used the same nest in which an earlier clutch was still developing.

Contemporaneous clutches that developed in separate nests (28 pairs of contemporaneous nests) suffered 10% less predation than contemporaneous clutches which developed in shared nests (14 pairs and three triple contemporaneous nests), although this number was not statistically significant (clutches: $\chi^2 = 0.96$; fd = 1; $P > 0.05$; eggs and tadpoles: $\chi^2 = 2.83$; P > 0.05; fd = 1) (Table II). In area A1, 10 males had more than one clutch. Of these, six had two and four had more than two contemporaneous clutches. Among these 10 individuals, nine used the other nest for the second clutch. A significant number of the nests (35% in 1995 and 39% in 1996) harboured more than one clutch (whether contemporaneous or not), indicating that nests were often reused.

Survival of clutches in primary and secondary forests

In the "Florestal" reserve, besides the 75 clutches in area A1 (primary forest) and eight clutches in area A2 (secondary forest), 61 additional clutches (from 43 males) were obtained in B1 and B2 (both primary forest). Of these additional clutches, 29 were transferred to area A1 (F2) and 32 were transferred to area A2 (SF2). No differences were observed in the mean number of days to metamorphosis in clutches from F1 ($\bar{x} = 30.4$ d, SD = 1.3, $n = 16$), F2 ($\bar{x} = 30.8$ d, SD = 1.2, $n = 12$), F3 ($\bar{x} = 31.0$ d, SD = 1.1, $n = 12$) SF1 ($\bar{x} = 30.7$ d, SD = 0.5 $n = 4$) and SF2 ($\bar{x} = 31.0$ d, SD = 0.9, $n = 15$).

Predation was the principal cause of death of eggs and tadpoles of *C. stepheni* in both habitats. Some nests, however, were totally destroyed by heavy rains (three nests constructed in primary forest, one nest transferred to primary forest, two nests constructed in secondary forest, and three nests transferred to secondary forest).

Colostethus stepheni clutches were preyed upon to different degrees in different situations (Table I). A greater number of nests that had 80–100% of their eggs and tadpoles preyed upon were observed in primary forest than in secondary forest. Overall, clutches in secondary forest had greater survival rates than those in primary forest (Table III).

The number of eggs and tadpoles that were preyed upon in primary forest was significantly smaller when under parental care (number of clutches = 49) than when parental care was denied (number of clutches = 21) ($\chi^2 = 4.86$; $P < 0.05$; fd = 1). Besides, the predation of clutches transferred to primary forest was not significantly different from the predation of clutches without parental care, i.e. parental care was denied through removal of the males (occurrence of predation on clutches: $\chi^2 = 0.38$; $P > 0.05$; fd = 1 and

Table II. Differences in predation (%) of contemporaneous clutches (at least in part temporally overlapping clutches of the same male) in 41 Reserve during the breeding season of 1995.

	Contemporaneous clutches different nests ($n = 56$)	same nest ($n = 34$)
Total number of eggs	232	132
Clutches preyed upon	43 (76.8%)	29 (85.3%)
Number of eggs and tadpoles preyed upon	123 (53.0%)	82 (66.7%)

Table III. Number of clutches and eggs/tadpoles that suffered predation, or that survived in primary and secondary forests of the "Florestal" reserve.

	Primary forest		Secondary forest		
	Preyed upon	Survived	Preyed upon	Survived	χ^2 test
Clutches	30	19	4	4	0.36
Eggs/tadpoles	74	106	6	24	4.86*
Transferred clutches	15	13	14	15	0.16
Transferred eggs/clutches	54	67	35	72	3.39

* $p < 0.05$.

total number of eggs and tadpoles preyed upon: $\chi^2 = 2.13$; $P > 0.05$; fd = 1).

Clutches in their initial phases of development were most heavily preyed upon (Figure 2), while predation on tadpoles older than 19 d (stages 36–46, Gosner, 1960) was less than 3% in both forest types. The situation was more complex for eggs and embryos younger than 20 d. In primary forest, eggs and embryos between 1 and 5 days old were subject to less predation than 6–15 days old embryos. On the other hand, in secondary forest, eggs and embryos between 1 and 5 days old were subject to more predation than older embryos.

Reproduction and predation in relation to precipitation

Even though *C. stepheni* reproduces only in the rainy season, there was no significant correlation between rainfall and the number of clutches produced during the 5–6 day periods of observation in 1995 ($r = 0.38$; $P > 0.1$; $N = 17$) and 1996 ($r = 0.04$; $P > 0.5$; $N = 18$). However, greater predation on eggs and tadpoles was observed during periods of heavy rain. This correlation was positive and significant in 1995 ($r = 0.58$; $P < 0.02$; $N = 17$) and in 1996 ($r = 0.70$; $P < 0.001$; $N = 18$) when all clutches in primary and secondary forest were considered, including those transferred to other areas and those denied parental care *in situ*. When considering separately those clutches in the 1996 study that either received or were denied parental care, the correlation between rainfall and predation is not statistically significant for those clutches receiving parental care ($r = 0.42$; $P > 0.05$; $N = 17$), but is strongly significant for clutches without parental care, whether in primary or secondary forest ($r = 0.81$; $P < 0.001$; $N = 18$).

Predators

On only two occasions predation was observed on clutches of *C. stepheni*. An ant, *Pachycondyla apicalis* (Ponerinae), approximately 10 mm long, was found on the upper leaf of a nest eating a one-day-old embryo, and an aquatic dytiscid beetle, about 3 mm long, was eating the vitellus of a 14-day-old tadpole. We regularly found 1–3 specimens of this dytiscid in the water accumulated in the lower leaf of the nests with or without a clutch. Of the total number of eggs and tadpoles eaten, 14.5% (1995) and 19% (1996) showed perforation of the yolk sac.

Discussion

Efficiency of artificial nests

Similarly to the results obtained for some species of birds (see Harvey et al., 1988 for example), the use of artificial nests as a resource to evaluate the reproductive success of *Colostethus stepheni* was highly efficient. It allowed us to observe the number of clutches per male and the first or second amplexus, without having to wait for the female arrival and the complete mating behaviour to know where nests were located. The success of artificial nest occupation and their reutilization suggest that appropriate places for reproduction in nature might be in short supply. On the other hand, the distribution of these artificial nests near male vocalization sites allows easy access to them by males that in turn spend less time searching for nests, instead maximizing their efforts in courting females, territory defence, parental care and foraging time. The much lower acceptance of artificial nest sites in the secondary forest may be

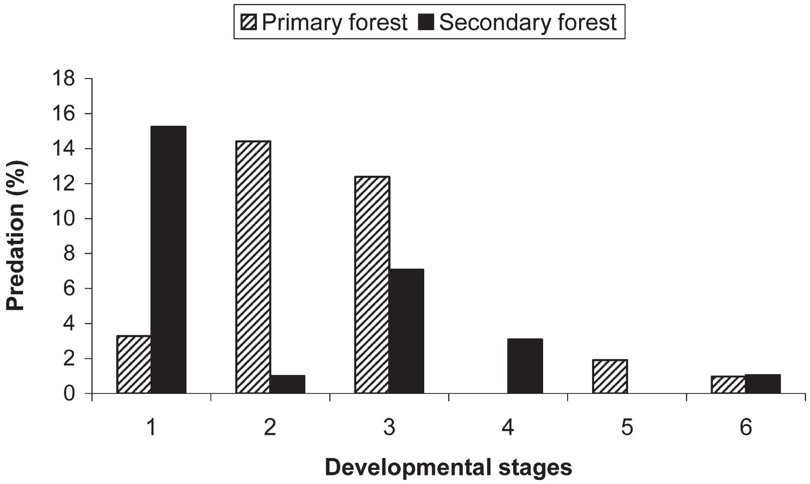

Figure 2. Relative frequency of predation in relation to the total number of eggs and tadpoles available in each development stages (see Material and methods) in clutches which were transferred to primary and secondary forests.

related to habitat differences between the two forest types. *Cecropia* spp. leaves are much more abundant in the secondary forest (Mesquita, 1995), so that there is a greater availability of natural nest sites. This decreases the chances that males in the secondary forest use artificially constructed nests. The same predation observed in clutches without parental care (without transference of site) and in clutches that were transferred indicated that the act of transferring nests did not in itself significantly alter survival rates.

Potential mating success

The high average mating success of *C. stepheni* males compared to data for other anurans that range between 0.2 and 2.5 is, at least in part, explained by the fact that our sample comprised only males that did in fact reproduce and not the whole male population, as in the other studies (Davis & Halliday, 1979; Howard, 1978, 1988; Wells, 1979; Arak, 1983; Ryan, 1983, 1985; Cherry, 1993; Martins, 1993; Bastos & Haddad, 1996). As males of *C. stepheni* do not group at any special reproductive site, it was not possible to determine whether the males that did not use the potential nests did or did not reproduce.

Cherry (1993) observed that among species whose females spawn more than once during the same reproductive period, the average mating success of the males can be two or three times greater than that encountered in species that spawn only once. Additionally, the sex ratio within the population can influence the male's mating success (Arak, 1983; Pough et al., 1998). Previous research during the months of greatest vocal activity resulted in a sex ratio for *C. stepheni* of approximately 1:1.5 (males: females) (Juncá, unpublished data). It was also observed that females could mate two times within a period of about one month during a single reproductive season (Juncá, 1998). From this data, and from the number and the state of development of eggs observed in the ovaries of *C. stepheni*, it seems that females may be capable of spawning up to three times in the same mating season (Juncá, 1998). Roithmair (1992, 1994) observed that only a few males of *Epipedobates femoralis* were able to mate even once during the reproductive season, while *E. trivittatus* males may mate up to three times. Among anurans that exhibit direct terrestrial development, males of *Eleuterodactylus coqui* (Leptodactylidae) mated on average 1.58 times, and a single male might mate up to five times (Townsend, 1989b). Multiple contemporaneous clutches were common in *C. stepheni*. This phenomenon was also recorded in two other dendrobatid species with semi-terrestrial development, *C. marchesianus* (Juncá, 1998) and *Dendrobates pumilio* (McVey et al., 1981), and *E. coqui* (Townsend et al., 1984; Townsend, 1989a).

In *C. stepheni* the male size did not seem to influence the number of matings nor the survival of its clutches as it did in some other anuran species (Woodward, 1982; Howard, 1983; Ritke & Semlitsch, 1991; Cherry, 1993; Roithmair, 1992; Wagner & Sullivan, 1995). However, a possible caveat to this conclusion is the fact that all the males studied received an equal number of potential nests, which could have masked differences in the quality of their territories thereby equalizing their access to mates. Control over territories with safe nesting sites and fewer predators were recognized as a determining factor in male mating success in *Rana catesbeiana* (Howard, 1978, 1983). Such males had more mating opportunities, and the survival of their offspring was greater. When population densities increased, large males were able to better defend their territories, thus increasing their mating frequency.

Possible reasons for clutch mortality

The percentage of clutches preyed upon in primary forest while under parental care (75.67% in 1995 and 63.27% in 1996), as well as the percentage of clutches which had 80 – 100% of their eggs and tadpoles preyed upon (47.56% in 1995 and 32.65% in 1996) were both considerably higher than observed in 1989 (40% and 28%, respectively; Juncá, 1996). The observed increase in predation may have been due to dytiscid beetles frequently observed in the nests. Neither the presence of these beetles nor the indirect evidence of predation by them (eggs or embryos ''perforated'' and with most of the yolk lost) were notified in 1989.

In this study, as well as an earlier one (Juncá, 1996), the absence of parental care significantly increased predation on eggs and tadpoles. In other species, the artificial removal of parental care resulted in even more drastic increases in mortality, sometimes reaching 90% (Simon, 1983; Townsend et al., 1984). Although the predation seen in these studies were very similar to that seen in *C. stepheni*, contamination by fungi and desiccation significantly increased their final mortality rates. These two mortality causes were not recorded with *C. stepheni* with or without parental care.

Egg laying was not directly related to daily precipitation, therefore the higher number of eggs preyed upon during the days of greatest precipitation is not simply the result of a greater availability of egg clutches. Other factors, probably related to the action of predators, must be involved.

The results of the mortality rate of eggs and tadpoles in primary and secondary forest environments are unclear. Although many more clutches were obtained in the primary than the secondary forest, those from secondary forest suffered significantly less predation. However, the nests transferred to secondary forest suffered similar predation rates than nests transferred to primary forest.

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