CEER-T-191 The Adaptive Significance of Male Parental Care in a Neotropical Frog by Daniel S. Townsend A Dissertation Submitted to the State University of New York at Albany in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy Department of Biological Sciences 1984 CENTER FOR ENERGY AND ENVIRONMENT RESEARCH

The Adaptive Significance of Male Parental Care in a Neotropical Frog, by Daniel S. Townsend. A Dissertation Submitted to the State University of New York at Albany for the Requirements of the Degree of Doctor of Philosophy in the College of Science and Mathematics, Department of Biological Sciences, 1984.

Abstract: This study describes the reproductive ecology and parental care of the Neotropical frog, Eleutherodactylus coqui. It measures the benefits and costs of parental care to individual reproductive success, and integrates benefits and costs into a single view of the adaptive significance of parental care for this species. Eleutherodactylus coqui males call from elevated perches at night. Eggs are laid in non-aquatic nest sites and undergo direct development, hatching as tiny frogs in 17-26 days. Clutch size (mean = 26) is correlated with female body size. Parental care is performed exclusively by males, who attend eggs and hatchlings. Males attend their clutches 97.4% of the time by day and 75.8% of the time at night. Most of this time is spent brooding eggs. Males also defend eggs against cannibalistic intruders. Care is provided throughout development; neither nest fidelity nor brooding frequency changes. Parental care significantly increases hatching success. In a field experiment, clutches from which parental males were removed failed 3.4 times as often as control clutches (males not removed). Experimental clutches suffered greater mortality from desiccation and cannibalism than controls. Plotting average hatching success of experimental clutches against the developmental stage at which males were removed yielded a convex second-order function, hence, the benefits

The effects of parental care accelerate throughout development. Parental males do less feeding than non-parental males and suffer small but significant losses in body mass during parental care.

Section 8 also indicates that parental males call less than non-parental males and sacrifice approximately one additional mating during a 20-day period of parental care. A marginal value model of parental care is proposed which integrates the time-dependent benefits of attending eggs and the consequent costs of reduced reproductive activity. Using empirically determined values for E. Coqui, the model indicates that by providing care throughout pre-hatching development, males maximize their lifetime reproductive success. The model also indicates that, starting with no care, either sex would have been favored to evolve care in E. Coqui. Male Coquis may have evolved parental care because of their initial association with eggs at defended retreats.

Dedication: To my children, Christopher and Carissa, may theirs be a better world.

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For her unfailing love, encouragement, and understanding throughout this whole ordeal, Karyn deserves more than I will ever be able to repay.

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INTRODUCTION

Parental care has long been of interest to ethologists, ecologists, and evolutionary biologists. The potential for males or females to allocate post-fertilization time and energy to offspring is a critical factor in sexual selection (Trivers, 1972; Williams, 1975; Maynard Smith, 1978), the evolution of mating systems (Orians, 1969; Eelen, 1973; Balen and Oring, 1977; Kleiman, 1977; Welters, 1982), and the evolution of social behavior in general (Alexander, 1974; Wiley, 1974; Brown, 1975; Wilson, 1975; Wittenberger, 1981). Parental care is an integral part of the reproductive strategies of mammals and birds (Orians, 1969; Kleiman, 1977). In these two vertebrate groups, evolutionary questions revolve around how the allocation of parental time and energy should relate to mating systems, with the central issue being whether one or both parents should be involved.

Favored to care for the young (Orians, 1969). Parental care by at least one parent is essential because of the large input of energy and thermoregulatory buffering required to raise an endothermic offspring. These stringent physiological requirements are often not the case for lower vertebrates, both because of their ectothermic physiology and because immature and adult animals often occupy markedly different habitats. This is the case with most temperate and many tropical amphibians, in which the typical life history involves an aquatic larval stage that is completely different in its physiology, behavior, and trophic niche from the adult. Not surprisingly, parental care is unusual in frogs, known to occur in only about 10% of all species (McDiarmid, 1978). Its rarity raises questions, on one level, about how, when, and why it arose and on a second level provides the ideal situation for investigating the evolution of reproductive strategies in animals within related taxa.

Also, because the sex which provides care may differ among congeners, there exists the opportunity to investigate the relationship between environmental conditions, social systems, allocation of parental effort, and sex-specific reproductive strategies. Parental care has been studied mainly in birds and more recently, the evolution of parental care in lower vertebrates has received attention, especially in fishes and amphibians (McDiarmid, 1978; Perrone and Zaret, 1979; Blumer, 1979; Barlow, 1981; Baylis, 1981; Gross and Shine, 1981; Wells, 1981; Simon, 1982, 1983). In anurans, it should rarely be the case that a second parent can provide much additional effective care (effective in further increasing the survival of the offspring), and since it seems that cooperative behavior is rare in frogs, the dichotomy between whether one parent or both parents should care (as in endothermic vertebrates) is a moot question. The principal issues are whether uniparental care or no parental care should be favored and which sex should perform the care. These

Two questions have been addressed theoretically (Trivers, 197; Maynard Smith, 1977; Grafen and Sibly, 1978). To understand the evolution or maintenance of parental care in any animal, it is necessary to know how reproductive success varies as a function of parental care. More specifically, we need to measure how an increase in offspring survival due to care trades off with the consequences of reduced allocation of time and energy to future offspring. Specification of benefits and costs for each sex is crucial to interpretation of sex-specific parental strategies (Trivers, 1972).

Interspecific differences in cost-benefit relationships, resulting from different breeding systems (Maynard Smith, 1977) or differing degrees of paternal certainty (Werren et al., 1980), may alter predictions about the evolution of parental care. Parental care has been documented in most frog families (McDiarmid, 1978). There is tremendous diversity in the ways that amphibians provide post-fertilization parental care to their offspring (Atte and Mecham, 1974; Lamotte and Lescure, 1977; McDiarmid, 1978). Wells (1981) recognized four major categories of anuran parental care: egg attendance, tadpole attendance, egg transport, and tadpole transport. In addition, viviparity occurs in a few species (Lamotte and Lescure, 1977; Wake, 1978, 1980), and recent evidence indicates that, in a few species, parents may provide nutrition to larvae (Graeff and Schulte, 1980; Heygold, 1980; Zimmermann and Zimmermann, 1981). In anurans, parental care is practiced almost exclusively by species that lay eggs either in terrestrial or in specialized aquatic microhabitats. Many cases of anuran parental care have been suggested to be an adaptive response by parents to the problems of maintaining a vulnerable amphibian egg in a terrestrial environment (Myers, 1969; McDiarmid, 1978; Wells, 1961), either to prevent desiccation of eggs or to protect them from predators and pathogens. There are only a few studies which quantitatively assess the relative

Portoricensis, but Tomas (1956) recognized the existence of two species and named the second one E. coqui. There has been an explosion of work on E. coqui since the mid 1960s. Dery (1970s, 6; Drewry and Rand, 1983) worked on the population biology, life history, and vocal behavior of several Puerto Rican Eleutherodectylus. A great deal of descriptive and detailed experimental work on the vocalization, neurobiology, and calling behavior of E. coqui has been done by Narins and his associates (Narins and Capran, 1976, 1977, 1978, 1980; Narins, 1982a, b, 1983; Warine and Hurley, 1982; Zelick and Narins, 1982, 1983). Aspects of the physiological ecology of E. coqui have been studied by Heatwole et al. (1969), Pough et al. (1983) and Taigen et al. (1984).

The coqui is nocturnal and achieves high densities in the Luquillo Mountains of northeastern Puerto Rico (Stewart and Pough, 1983) and, along with its congeners, has diverse development (Townsend and Stewart, in press). The fieldwork was conducted in the Luquillo Experimental Forest near the El Verde Field Station of the Center for Energy and Environment Research in the Luquillo Mountains of northeastern Puerto Rico. The E. coqui population that is studied inhabits second-growth tabonuco (Dacryodes excelsa) forest at about 250 m elevation. Motillo, Sloanes peterians, and ausubo, Manilkara bidentata, are also prominent species. Three other trees are important to the population ecology of E. coqui: Cecropia peltata, Didymopanax morototoni, and Prestoea montana. Dead leaves of Coccoloba and fallen fronds of Prestoea are used extensively as shelter and nest sites by coquis, and the axils of Prestoea palms are often used as calling sites by males (see below). Cecropia and Didymopanax are both early successional species which take advantage of temporary openings in the forest canopy, while Prestoea is a sub-canopy palm which occurs regularly throughout the forest (Beet and Whitmore, 1973). The forest has a moderately seasonal climate with a cooler, dry season.

Measuring, Sexing, and Marking Frogs: The snout-vent lengths (SVL) of frogs were measured in the field by placing them inside a plastic bag, pressing them against a flat surface and measuring to the nearest 0.5 mm the distance from the tip of the snout to the distal tip of the pubis. In areas where frogs were marked, they could be sexed when recaptured while calling or in amplexus. The following morphological criteria were also used to determine sex. Adult males in the El Verde population range from 29.5 mm to 38.0 mm SVL (see Chapter 2) and have a vocal sac of thin flexible skin beneath the throat. Females range from 35.5 mm to 52.0 mm SVL (see Chapter 2), lack the flexible skin of the vocal sac, and often have ovarian eggs visible through the abdominal wall. Frogs were marked in several ways during the study. This was done by clipping a unique combination of toes; never more than one toe per foot or four toes per frog. Also, the first digit on the hind foot was never clipped. Toes were always clipped proximal to the first joint. This prevented any substantial regrowth of clipped toes, and marked frogs were easily recognized for up to two years following initial marking.

The description of the staging table is given in Appendix 1. For any purposes in what follows, I have divided the 15 pre-hatching stages of my table into three developmental intervals, I-III, each corresponding to about one-third of development. Developmental interval IV includes all post-hatching stages. In addition to clutch parameters, I recorded the nature of the location of the nest site, its height off the ground, and several metric characters of the nest, including its largest dimension, the longest dimension of the actual nest cavity and the perpendicular length (e.g., the length and diameter of a round roll), and the angle from the horizontal of the substrate on which the clutch rested.

Calling surveys were conducted on a regular basis in several areas during the study. These surveys were designed to record the number of males calling and several characteristics of their call sites, in prescribed areas of the habitat. A calling male survey consisted of passing slowly through an area while listening for calls. The identity of calling males (whose frogs were marked) was determined by visual inspection of exposed toes. In the elevated calling posture, it is possible to do so without capturing the frogs. The characteristics and height above the ground of the calling site were also recorded.

All surveys were done between 2000 hours and 2300 hours, and generally lasted for 1-2 hours. To ensure that all calling males had been found, each area was completely traversed at least twice. Some partial surveys were performed in which an area was only partially covered, or traversed only once.

White sampling was done in many areas of the forest at El Verde. One large plot was sampled continuously and intensively throughout the study. Dick's House Plot was a 500 square meter quadrangular area in which 30 bamboo frog houses had been hung. All major topographic features, palms, and trees were noted within Dick's House Plot. Twelve reference stakes placed in the plot allowed pinpointing the horizontal location of each observation.

Location of any frog, nest of other creatures in the plot. Beginning in 1976, all frogs of 24 mm SVL or greater were marked upon initial capture. Marking continued throughout 1979 and 1980 field work. A complete diurnal survey and a complete calling male survey were done during alternate weeks (each done biweekly) throughout 1979 and 1980. In 1982, a series of 5-7 sample calling surveys were done on consecutive nights prior to each competition: means are given ± 1 SE unless otherwise indicated. Statistical tests used are the Student's t-test, Pearson product-moment correlation and One-Way ANOVA when variables are normally distributed and homoscedastic (Sokal and Rohlf, 1969). When those assumptions are violated or for small sample size, non-parametric statistics such as the Mann-Whitney U-test, the Chi-square test, and the Kruskal-Wallis One-Way ANOVA are used (Siegel, 1956). Alpha is set at 0.05 as the level of rejection in all hypothesis testing. Data were analyzed and some statistical procedures performed using the computer statistics package SPSS (Nie et al., 1975).

Chapter 2: THE REPRODUCTIVE ECOLOGY OF E. COQUI Notes Body size. Complete calling surveys of Dick's House Plot were conducted on 21 nights in 1980 (Table 1) and 29 nights in 1982 (Table 2). Calling male SVL was recorded on 9 separate occasions only during 1980 (Table 1). Individual sizes ranged from 29.5 mm to 37.0 mm SVL and nightly means ranged from 32.0 ± 0.57 mm (N=9) to 33.92 ± 0.28 mm (N= 20), with an overall mean of 33.4 ± 0.50 mm (N = 207). There was significant variation among monthly means of calling male SVL (Kruskal-Wallis One-Way ANOVA, H= 8.49, $p < 0.02$). Average body size decreased from dry to wet season, the difference stemming primarily from the increased presence of smaller males in the chorus during April through June (note extension of size range to lower values during those months). During 1980, 134 clutches were deposited in Dick's House Plot. The SVLs of the parental males were noted then

(Table 4). The overall mean

Body size of parental males was 33.4 ±0.12 cm (W = 132). Although there was a decrease in mean SVL from January to June (as with calling males), there was no significant variation in body size among months (Kruskal-Wallis One-Way ANOVA; H = 4.53, df = 5, MS; July not included in analysis). The calling male and parental male body sizes distributions (Tables 1 and 3) in Dick's House Plot during 1980 were not significantly different (Mann-Whitney U with transformation: U = 1114, p = 0.1335).

Table 1. The numbers and mean body sizes of calling males in Dick's House Plot during 21 complete surveys in 1980. Note that the April 30 sample is combined with May for monthly analysis: Number of Snout-Vent Length Night calling males Mean SE Range

Jan. 7 338 0.34 32.0-34.5, 18

Feb. 6 334 0.29 32.5-34.0, 2

Mar. 4 338 0.20 33.0-34.0

Monthly Mean (SE) 4.3 (1.6) 33.4

Apr. 10 32.2 0.5 31.0-36.5,

May 7 4 33.3 0.18 31.0-36.5, 2

June 4 22.0 0.57 29.5-34.8, 7

Grand Mean (SE) 17.9 38.8 0.40 29.5-37.0

Table 2. The numbers of calling males in Dick's House Plot during 29 complete surveys in 1982,

Jan. 7 10 2 4

Monthly Mean(SE) 7.6 (1.0)

Mar. 6 9 14 10

Monthly Mean(SE) 17.3 (2.0)

June 10 16 15 8

Monthly Mean (SE) 14.0(1.5)

Oct. 12 4

Monthly Mean (SE) 14.5(2.55)

Table 3. Mean body sizes of parental males in Dick's House Plot from January to July 1980. Small July sample results from sampling only.

During the first four days of the month, the Snout-Vent Length and Tear Sage for each month was recorded as follows:

- January: 5 measures, Average Length - 34.0, Tear Sage - 9.42, Range - 33.0-35.0
- February: 14 measures, Average Length - 33.8, Tear Sage - 0.37, Range - 32.0-36.0
- March: 2 measures, Average Length - 33.6, Tear Sage - 0.28, Range - 31.0-36.0
- April: 2 measures, Average Length - 33.5, Tear Sage - 0.27, Range - 31.0-36.0
- May: 30 measures, Average Length - 33.4, Tear Sage - 0.27, Range - 31.0-36.5
- June: 30 measures, Average Length - 33.0, Tear Sage - 0.28, Range - 40.0-37.0
- July: 7 measures, Average Length - 33.3, Tear Sage - 0.53, Range - 31.5-38.0

The summary for these months recorded a total of 90 measures, with an average length of 33.4, Tear Sage - 0.12, and a range of 30.0-57.0.

Different microhabitats were observed for calling and nesting. Two variables were measured for both types of sites: height above the ground and relative cover. The height is the vertical distance to the frog's calling position or to a clutch. The relative cover was ranked using a qualitative scale devised by Narins and Hurley (1982; p. 289) to categorize the amount of cover around the calling sites.

Twenty-one calling male surveys in the Dicke House Plot during 1980 (3 partial and 18 complete surveys) yielded a total of 297 calling site observations. The distribution of perch heights showed that most frogs (92.6%) called from sites that were 25 cm or higher, while only 5 males (1.7%) used sites that were less than 10 cm high. Only a few males (2.4%) used perches higher than 3m. The average perch height was 93.5 ± 4.6 cm (n=297). Males employed a wide range of substrates for calling, but the majority of males used... (text cuts off here)

Of them, 252 out of 297 (84.9%) were relatively exposed.

Figure 1: The frequency distributions of height above the ground for calling perches (top) and clutch locations (bottom) in Dicke House Plot from January to June 1980. Means and Medians were computed using raw data. Number of calling perches = 297; Number of clutches = 134. Hatched areas of the lower figure represent clutches in bamboo houses.

The median and mean heights above ground are represented in centimeters (cm) on the horizontal axis from 0 to 300 cm.

The categories 1 to 3 are displayed in Table 4. The majority of these sites were exposed such as axils (96 of 252 = 37.3%), surfaces and crevices of tree trunks and branches (65 of 252 = 25.8%) and open surfaces of leaves (33 of 252 = 13.12%). Thirty-three sites (11-12) used type 4 sites, mainly consisting of doorways of bamboo frog houses (8 of 33 = 24.22), open ends of fallen sierra palm fronds (6 of 33 = 18.28) and hanging clusters of dead leaves or palm leaflets (7 of 33 = 21.22). Only 12 sites (4.02%) were of category 5, including calling from inside the curls of Cecropia leaves (6 of 12 = 50.02) or from inside bamboo frog houses (5 of 12 = 41.73%).

As a single category, palm axils were the most frequently used call sites, comprising 33.0% (98 of 297) of all sites. The height distribution of 134 clutches deposited in Dicks House Plot during 1980 is shown in Figure 1. Note that the peak in clutch height frequency between 125 and 200 cm is due entirely to bamboo houses which were concentrated in that height range. The majority of oviposition sites (92 of 134 = 68.7%) were less than 25 cm high (79.3% of 116 natural sites). The average nest site height was 47.8 cm ± 6.0 cm for all nests; 30.5 cm ± 5.4 cm for natural nests (N= 116).

The height distributions for calling sites and nest sites are significantly different (Mann-Whitney U with s-transformation: 2 * 8.293, $p < 0.0001$). The relative cover distribution of Dicks House Plot nest sites is given in Table 8.

Body size and fecundity: From January to July 1980, 69 females were captured in nest sites immediately following oviposition. Their average SVL was 41.4 + 0.4 cm (Range = 35.5-52.0 cm) and average clutch size was 28.1 + 0.6 eggs (N= 58, Range = 16-41). There was a significant correlation between female body size and clutch size ($x = 0.56725$ $p< 0.01$, Figure 2). In 65 cases, the SVL of the amplexant male was also recorded. The regression of male SVL on female SVL for amplexed pairs was not significant (Figure 3; $F < 1.0$). Hence, there does not appear to be positive assortative mating by body size, at least within the range of male body sizes that were sampled (30.0-35.5 cm SVL).

Break - Female SVL (mm) measurements: 34, 36, 38, 40, 42, 44, 46, 48, 50, 52.

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Female SVL (mm) measurements continued: 34, 36, 38, 40, 42, 44, 46, 48, 50, 52.

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The interclutch interval was 55 days (8 weeks). One clutch was laid on 5 May (the eggs were not counted) and a second clutch of 26 eggs was laid on 3 July, yielding an interclutch interval of 59 days (8.5 weeks). A third female was captured laying a clutch (uncounted) on 11 March and had laid a second clutch by 21 May, yielding a maximum interclutch interval of 71 days (10 weeks).

The seasonality of reproduction study showed calling activity recorded during every month of the study. Nightly densities in Dicks House Plot ranged from 0 to 29 calling males and varied significantly among months in both years (Kruskal-Wallis One-Way ANOVA; 1980: $H= 13.2$, $df = 5$, $p< 0.025$; 1982: $H= 19.9$, $df = 4$, $p< 0.001$). The principal source of the variation was a difference between dry season (Jan-March) and wet season (April-July) densities in the plot.

Clutches were found during every month of the study. There was significant variation among months in the number of clutches deposited in Dicks House Plot when compared to an expected distribution of equal monthly clutch frequency (Chi-Square = 22.99, df = 5, p< 0.001), with the main source of variation being the lower frequency of clutch deposition during the dry season.

Figure 4 illustrates the temporal distribution of deposition of 134 clutches in Dicks House Plot during 1980. No more than four females ever deposited eggs in the plot on a single day. At least one female oviposited on 81 of 186 days (43.62%) with an average of 1.65 clutches per deposition day (134/81).

Calling activity and egg deposition were low during January and most of February.

Page Break

Table 5 outlines the numbers and sizes (number of eggs) of clutches found in Dicks House Plot and in all habitat surveys (including DAP) during 1980.

Dicks House Plot:
- January, 5 clutches
- February, 15 clutches
- March, 26 clutches
- April, 3 clutches

(Numbers for each month are assumed based on the given text. Precise clutch sizes for each month are not provided in the text.)

20th May. A series of surveys from 2nd January to 2nd July, shows the following data: On 2nd January, the value is 129. 5. In February, the value is 127. 2. On 7th March, the value is 25.80.78. On 6th April, the value is 26.3 0.67. In May, the value is 86 2770.78. On 7th June, the value is 2811 0.68. On 2nd July, the value is 216 0.89. The summary shows the average value as 26.7.

Figure 4 shows the temporal distribution of clutch deposition in Dicks House Plot from January 1 to July 4, 1980. Each bar width equals one day.

Study your work; use it to your advantage.

26th February saw a spike in reproductive activity (Figure 4), reproduction increased into March and continued at that level through July 4, the date of the last complete diurnal survey at Dicks House Plot. From March 1 to July 4, 1980, females deposited eggs on 69 of 126 days (56.82%). Both calling activity and oviposition were associated with rainfall (Tables 6 and 7). Calling male densities in Dicks House Plot were significantly greater on nights following 24-hour periods in which there was some rainfall than on nights which followed 24 hours without rain (Table 6). Females deposited clutches significantly more often following 24-hour or 46-hour periods in which there was some rainfall than following similar periods with no rainfall (Table 7).

Courtship and Mating Behavior

Leptodactylus coqui is a nocturnal frog. Frogs generally leave their diurnal retreat sites and become active in the forest within the first hour after dark. Calling activity begins before dark, the chorus is generally at full strength within a half-hour of full darkness, and calling is heaviest before midnight, declining in the early morning hours until dawn (Drewry, 1970; Drewry and Rand, 1983; Wootbright and Townsend, Ms.). I have observed 18 partial or complete courtship sequences. Courtship was always initiated by a female approaching a calling male and making contact. The initial contact by the female often resulted in a sudden pause in the male's calling followed by a switch in the vocalization to a lower amplitude, softer call. Within seconds of the initial contact by the female, the male began to move away from her.

Break--- Table 6. Chorus sizes at Dick's House Plot on 31 complete survey nights during March-June 1980 and March, June-July 1982, as a function of whether or not rainfall occurred during the previous 24-hour period.

A. Complete table of chorus sizes.
B. Reduced table for statistical analysis.

Number of Calling Males Test:
No rainfall - a3, a, a, a, °
Rainfall - 2, 2, 8

Number of Calling Males:
No rainfall - 8,
Rainfall - 2

Exact Tests $p < 0.008$.

Table 7. Frequencies of days when 0, 1, or 2 clutches were deposited on Dick's House Plot from March to July 1980, as a function of immediate past precipitation.

A. When rainfall did or did not occur during the previous 24 hours.
B. During the previous 42 hours.

Number of Clutches per Day:
No rainfall - 2, a, 10
Rainfall - 24, 2, a

$\chi2 = 6.59$, df + 2, $p < 0.02$.

Number of Clutches per Day:
No rainfall - 2, 6
Rainfall - 29

$\chi2 = 16.61$, df = 2, $p < 0.001$.

At the call site, males always continue to call. Typically, a male would move from 10 to 30 cm and stop. The female had to follow the male and either get very close to him or actually make contact in order for the male to move again. The typical courtship involved a long series of these leading-and-stopping moves by the male with following moves by the female. Males always continued to call while leading, although the calls were usually much softer than the advertisement calls that had been given prior to initial contact by the female. No male went more than 50-60 cm in one move before waiting for the female to catch up. On several occasions, when females took too long to follow, the male turned around and went back to the site of his last stop. Female behavior during the leading phase was variable. Some females did little more than follow the male directly. In two other cases, females spent time investigating various curled leaves and cavities along the courtship route. One female did this to such an extent that the male backtracked three times to find the female and initiate leading again.

Without exception, however, the female eventually entered the nest cavity that the male first entered and remained. Once the female had followed the male into the cavity, the female normally initiated amplexus by backing under the male within 15 minutes. The male's calling became progressively softer, with an increase in the number of soft, multiple-note calls (repeated coo notes), and eventually stopped. All courtships were observed before 2300 hours, and most were initiated within the first 1.5 hours of dark. Leading courtship lasted from 15 to 60 minutes, the time varying as a function of the distance between the call site and nest site and of the propensity of the female to follow the male directly.

Once amplexus was initiated, the pair remained in amplexus for the rest of the night and into the following day, when eggs were finally laid. Early in amplexus, the male was atop the female in approximately an axillary position, but was never seen to clasp the female. Prior to oviposition, and often close to dawn (after 5-8 hours of amplexus), the pair assumed a secondary amplexus position, in which the male's hind legs come to rest on top of the male's hind legs. As a result, the male's posterior end is firmly pinned against that of the female and against the substrate. This position is maintained throughout the rest of amplexus and oviposition.

At some point between the initiation of amplexus and oviposition, the female ovulates her full ovarian complement and the male inseminates her, although not necessarily in that order. Two females that were captured two hours after the initiation of amplexus were found to have all mature ova still in their ovaries, so ovulation apparently does not occur prior to amplexus. Also, females were observed to undergo very heavy abdominal pulsations for up to two hours prior to oviposition; these may correspond to ovulation. Fertilization in E. coqui is internal (Townsend et al., 1981) and while I do not know at what point during amplexus the male inseminates the female.

Presume that it occurs after the onset of the secondary amplexus position. Oviposition begins 7-10 hours after the initiation of amplexus, and requires 3-5 hours to complete. Oviposition begins without any visible interruption of the abdominal pulsations that have been interpreted as ovulation. As eggs are laid, the female moves out from under the male, and eventually comes to sit directly in front of him.

When egg-laying is done, the male is then directly over the new clutch in a typical brooding posture (see Chapter 3). The male and female remain in these positions for the majority of the daylight hours. As dusk comes, both parents become more active and, virtually without exception, the new male parent begins giving aggressive calls toward the female and may even make several biting attacks in chasing her out of the nest (see Chapter 3). Females usually return to their regular retreat sites within one or two days of mating.

Males that entered nest sites and initiated amplexus did not always remain and mate with the female. In five courtships witnessed during 1980 and 1982, a female left the nest site after the initiation of amplexus without staying with the male. I did not capture any of these females mating at other sites, so I do not know their subsequent mating history. In two of the five pairs, disturbance by the observer was a probable cause of the aborted mating. However, in the other three pairs, there was negligible interference by the observer, and it seems probable that females were rejecting either the male or the nest site.

In none of the five instances had the pair entered the secondary amplexus position; the latest time that a female was observed to leave the nest was 0209 hours.

Developmental Biology

As with all other known Eleutherodactylus, E. coqui has direct development. At oviposition, eggs are large (3.6 ± 0.1 mm in diameter, N= 21) and unpigmented. Development occurs entirely within the egg and at hatching, a fully pigmented miniature frog emerges bearing a keratinized egg tooth, but no tail.

Remnant, and a yolk reserve (Townsend and Stevart, in press). A staging table describing the development of E. coqui is present in Appendix 1. Hatchlings average 6.1 ± 0.1 SVL. The egg tooth disappears within 36 hours of hatching, the tail is absorbed within 3 days, and the yolk reserve is used up within 6 days, by which time the hatchlings have dispersed from the nest site. Developmental time (oviposition to hatching) ranges from 26.3 days in January and February to 16.8 days in June and is strongly and inversely correlated with ambient temperature (Appendix 1).

Discussion: Reproduction is continuous in E. coqui, with some calling activity and egg depositing every month of the year (this study; Stevart and Pough, 1983). Although continuous, it is seasonal in intensity. Male calling activity (Tables 1 and 2) during the dry season (e.g., January-February) is about 25% of that in the wet season (e.g., June-July), although erratic rainfall patterns within a season can give rise to some variability. For example, January 1982 was unusually wet, and calling male densities were inflated relative to 1980, while a dry June in 1982 resulted in depressed calling male densities (Tables 1 and 2). Rainfall has a significant effect on calling activity, with chorus densities being greater on wet nights (Table 6). Likewise, egg deposition varies significantly with season. There was a significant increase in the number of clutches deposited in Dicks Nose Plot from January to June 1980. Within the wet season, the schedule of egg deposition varies significantly with habitat moisture; females oviposit more frequently when the habitat is moist than when it is dry (Table 7).

There does not appear to be any non-random mating in the population with respect to male body size. The distributions of calling female SVL and parental male SVL were not different, and mean values were identical for the two groups; 33.4 mm (Tables 1 and 2). Large males are not obtaining mates in a higher proportion relative to their size.

The text appears to have multiple errors, including spelling mistakes, typographical errors, and incorrect punctuation. Here's the corrected version:

Females can deposit new eggs about once every two months in the field. In laboratory populations with an ad libitum diet, female coqui frogs can produce eggs every six weeks. These data suggest that E. coqui females could produce at least four clutches per year, if egg production is limited primarily to the wet season (March through October), and may be able to lay as many as six or seven clutches if food is abundant and egg production continues, even at a reduced level, during the dry season. Female coqui frogs maintain a positive energy budget throughout the year and appear to have excess available energy for growth at all body sizes (Lake, Hoots, and personal communication) so that energy limitations to egg production do not appear to be present in this population.

CHAPTER 3 'THE MALE PARENTAL BEHAVIOR OF E. COQUI'

In order to evaluate the net adaptive value of parental care, it is important initially to know the basic care behavior repertoire and to have some idea of the time budget of care provision for a species. This information has been gathered for a number of birds and mammals in which parental care has been studied (Kleiman, 1977; Martindale, 1962; Wolters, 1982), but there exist virtually no data of this kind for amphibians (exceptions include Kluge, 1961; Simon, 1982, 1983). Knowing the temporal pattern of care provision is especially crucial for amphibians which exhibit egg attendance (which comprise the vast majority of species with parental care) because without having the eggs physically attached, the parent is free to pursue activities that are alternative to care behavior. Alternate activities may include maintenance functions (feeding, rehydrating) and behaviors that influence mating success (calling, territorial maintenance). The trade-off between caring for one brood and either survival or additional reproduction will be strongly influenced by the allocations of time to alternative activities. Furthermore, it is important to know the details of care behavior because mere presence at an oviposition site does not imply care.

The site may not constitute functional parental care but only coincidental presence in the same microhabitat epee (Woodratt, 1977). Testing predictions about the evolution of parental care will require gathering such data, particularly when interspecific comparisons are used to make inferences about evolutionary trends.

In this chapter, I describe the major behavioral characteristics and temporal patterns of parental care in E. cogui. The sampling method by which clutches were located was discussed under General Methods. Most clutches were left undisturbed and subsequently checked at various times of day and night. During each nest check, the position and behavior of the parent, and the developmental stage and condition of the eggs were recorded. Nest checks did not appear to disturb the nest or parents greatly (but see Methods of Chapter 4). Aggressive calls (see below) were recorded using a portable cassette recorder (Channel Master Model 6395) and analyzed on a Model 4500 Unigon Uniscan real-time spectrum analyzer and a Tektronix Model 5103N Storage Oscilloscope. Sonograms were made on a Kay Model 60618 Sona-Graph with the band selector set on wide. In all analyses, 'day', 'daytime' and 'diurnal' represent the period 0601-1759 hours and 'night' and 'nocturnal' the period 1800-0600 hours.

Results

Sex of the Attending Parent

On the basis of the behavioral and morphological criteria used to determine the sex of an attending parent (General Methods), I have no evidence that females ever attend eggs in this species.

Frequency of Unattended Clutches and Multiple Clutches

I found only 11 clutches (out of 616) which never had an attending parent. Males do not attend eggs in more than one nest simultaneously. Any pattern of complementary presence and absences at neighboring nest sites would have been suspicious. I never found such a pattern. There were cases of multiple simultaneous clutches per site (29 double clutches and two triple clutches). However, multiple clutches were usually

Continuous inside the nest; only seven of the double clutches had more than one body length separating them. Description of Parental Care: Parental care in E. cogui is characterized by egg attendance beginning at oviposition and lasting throughout development, a period of 17-25 days. Mates often continue to attend hatchlings for 1-6 days after hatching. Males perform two major parental activities: brooding of eggs and defense of the nest and eggs.

Brooding: A parent was considered brooding at any time that a part of its ventral side was in contact with its eggs (Figure 5A). Although males varied with respect to how well they were centered over their eggs, they typically covered most of the clutch. Males that brooded after hatching adopted an elevated posture near or over the egg capsules. Because hatchlings typically grouped together on or near the capsules, they were often clustered beneath the male.

Parental behaviors observed during nest defense included aggressive calling, biting, sustained biting, blocking, and wrestling. Contests usually consisted of long periods (minutes) of inactivity punctuated by short bursts (seconds) of activity. Parents spent 51% of total contest time in active behaviors (calling, biting, wrestling, and chasing) and the remainder in static positions, whether separated from intruders or in contact with them (blocking or sustained biting). Prolonged contact (lasting more than 5 sec) between parent and intruder occurred in five of the six contests. An average of 51% of contest time was spent in contact.

Although the range in the six individual contests was 0 to 982, there were two types of prolonged contact: blocking and sustained biting. In the typical blocking posture (Figure 5B), a parent was on top of the intruder, its front leg and forebody blocking the intruder's head and forebody, and its hind legs partly extended in a bracing position. In sustained biting (Figure 5C), a parent held some part of an intruder's body, usually the head, in its feet. Aggressive calling by parental frogs was heard in 16 out of 15 contests. Although the regular advertisement call of E. coqui has been extensively studied (Drewry, 1970, Narins and Capranica, 1976, 1978, 1980), the aggressive call has never been quantitatively characterized. Therefore, I will describe it briefly. All variance estimates in the following section on aggressive calls are 1 SD. Aggressive calls were composed of 4-37 (mean = 11 + 5 notes per call, N= 88) brief, rapidly repeated notes with dominant frequencies of 1.4-2.7 kHz (Figure 6). The calls always began with a note of 120 ± 15 ms duration (range = 100-160 ms), followed by a sequence of notes.

Figure 6. The aggressive call of E. coqui. A. A sonogram of frog's call recorded during a nest-defense contest. Mean dominant frequencies (bar equals ± 50; sample size below SD bars) of the first 10 notes of aggressive calls by five different males during nest-defense contests. Sample sizes decrease because some calls had fewer than 10 notes.

Each note was 60 ± 5 ms (range = 40-70 ms) in duration. The period between the first and second notes was 250 ± 20 ms (range = 220-300 ms) and that between all subsequent pairs was 160 ± 15 ms (range = 120-200 ms). Individual aggressive calls ranged from 0.6 s (four-note call) to 5.7 s (37-note call) in length. The average dominant frequencies of notes increased from 1.64 ± 0.1 kHz for the first note to an asymptote at 2.5 ± 0.1 kHz by the tenth note.

(Figure 6) Aggressive calls were common in the six contests (mean = 14.9 calls per contest, range = 7-31), occurring in bouts of 2-5 calls. The average overall rate of aggressive calls was 0.8 calls/min (range of average call rate for individual contests was 0.4-1.6 calls/min). Biting by the defending parent was observed in all six contests (mean = 43.3 bites per contest, range = 2-10). The frequency of biting ranged from 0.2-0.4 bites/min in individual contests, with an overall frequency of 0.4 bites/min. Individual bites were rapid lunges, usually at an intruder's head. On five occasions, in four different contests, the parent bit and held on to an intruder's head or body (sustained bite - Figure 5C) for a period of 0.25-22.0 min (mean = 28.8 min). Wrestling occurred during periods of blocking contact. Typically, the parental male grabbed or levered the intruder's head or forebody and pushed the intruder away from the eggs. Wrestling bouts were brief, lasting from 5 to 20s. Nine wrestling bouts were observed during the three contests in which blocking contact occurred. Intruders did not engage in aggressive behavior (although, during one contest, an intruder gave several aggressive calls). Movement by intruders seemed entirely directed at getting around the parent and to the eggs. In four of the 15 occasions when nest defense was observed, the outcome was inconclusive because the frogs were disturbed. In six of the other 11 cases, intruders ate most or all of the clutch. Intruders were chased out of the nest and consumed few or no eggs in five cases. Temporal patterns of parental care analysis of temporal aspects of parental care in E. cogui was based on 4879 nest checks made on 510 clutches during 1980 and 1982. Nest checks were divided between day (44.9%) and night (55.1%), and among the four developmental intervals (1: 22.4%, II: 27.2%, III: 39.5%, IV: 10.9%). I arbitrarily established four categories of male position with respect to eggs: brooding, in the nest not brooding, at the nest entrance.

Occupying retreat sites that happened to contain clutches comes from a consideration of the parental male's position in the nest. When in the nest, a male could either sit on the eggs or somewhere else inside the nest. The circular area, whose radius is defined by a clutch plus one male body length, is the area where a male could sit and be considered brooding. This area was usually much less than 25% of the interior surface area of a nest. Hence, on a random basis, males should have been found brooding eggs about 25% of the time that they were present in their nests. In fact, when found in their nests, parental males were brooding eggs in 93.1% of all daytime checks and 81.9% of all nocturnal checks. To test the hypothesis that the high level of nest presence at night (~5.82) represents a departure from nocturnal activity.

Figure 8: The frequency histogram of nocturnal nest attendance levels for parental males at nests during 1980 and 1982. Attendance level is represented as the percentage of net checks in which a male was present in the nest or at its entrance. Only nests with at least four nocturnal checks were included. Arrow indicates the estimate.

44 See sequence of 40 60 80 percent attendance.

In terms of adult couples, two sets of observations were made during 1982 (June 27-28 and July 7-8). During the afternoon of the first day, the bamboo frog houses in each of two plots were surveyed and the numbers of parental males and non-parental adults were recorded. During the following night, all houses were resampled at 2-hour intervals, starting at least 1 hour after sunset and continuing until 1 hour before dawn (see Figure 9 for nocturnal survey time intervals). All houses were checked a final time during the afternoon of the second day. On June 27-28, 99 houses were checked, five parental males and 16 non-parental adults were found during the first afternoon survey. On July 7-8, 187 houses were checked; the initial count was 17 parental males and 54 non-parental adults.

Adults. The results of the two nights were combined and the initial counts of parental and non-parental frogs during the first afternoon survey were designated as 100% (Figure 9). During the first nocturnal check, parental male presence dropped to 59%, while that of non-parental adults dropped to 42%. During the second check, parental presence rose to 86% and subsequently remained at that level. The presence of non-parental adults dropped to about 10% and remained there until the last check, when it rose to 22% as frogs returned to their retreats prior to dawn. The average presence for all nocturnal checks was 82% for parental males and 12% for non-parental adults. The difference was significant (Chi-square = 193.5, p= 0.001).

Differentiate daytime and nighttime attendance, nor did he provide sample sizes for evaluating attendance data. Stomach contents of brooding parents indicate markedly lower foraging rates, suggesting that attendance levels are high enough to preclude normal foraging activities at night. Kluge (1981) found that the Myla rosenbergi exhibited high nest attendance during pre-hatching development but that once eggs hatched, attendance was lower (although in a second year pre-hatching attendance levels were much lower). In this species, eggs are aquatic and pre-hatching development lasts only 1.5-3 days, so the temporal and behavioral constraints on parental care provision are quite different from those operating in terrestrial species with long pre-hatching periods. Brooding is probably the most common type of parental behavior in amphibians (Salthe and Mechan, 1974; McDairmid, 1978; Wells, 1981). This is not terribly surprising. Brooding is generally a simple behavior which would require relatively little innovation in motor patterns or neural pathways in order to evolve. Also, since eggs are often deposited in the regular retreat site of the parent, there may be no need for a microhabitat shift in order to provide care.

There should be no added energetic cost of brooding, at least initially. Finally, brooding may have a relatively large effect on increasing offspring survival. The benefits and costs of brooding behavior in E. cogui will be addressed in the next two chapters. The evolution of nest defense behavior probably represents the redirection of territorial behavior to a parental care function. In B. cogui, both males and females will defend retreat sites from conspecifics (personal observation; M.M. Stewart, personal communication). Nest defense by parental males may be more intense and prolonged than retreat site defense, during which now serves a function more directly related to fitness. That nest defense is more intense than defense and constitutes somewhat separate category as a parental care behavior is.

Supported by several observations. First, intruder males were never observed to engage in aggressive behavior, but rather appeared intent on approaching and ingesting the eggs. Second, parental males never pursued intruders beyond the entrance of the nest. Third, nest defense contests lasted longer and generally involved higher levels of wrestling, biting, and sustained biting than did retreat rite defense.

82 CHAPTER & THE BENEFITS OF MALE PARENTAL CARE

Methods: During April-June 1980 and June-July 1982, attendant males were removed from their clutches in some nests and the fate of these experimental clutches was compared to that of control clutches which had attendant males throughout development. Parental males were removed over the whole range of pre-hatching developmental stages, from immediately post-oviposition to Stage 13. Experimental and control clutches were monitored daily until they hatched or failed. There were two major causes of clutch failure: desiccation and predation. I observed two types of egg predators: invertebrates and coquies. In cases where the predator was not evident, I used criteria based on field and laboratory observations of predation to identify the predator. All invertebrate predators left a residue from their feeding activity, whether empty egg capsules or partially chewed eggs. Coquies always ate eggs whole. Hence, when eggs had been chewed or others partly consumed, invertebrate predation was inferred; when entire eggs disappeared, cannibalism was presumed to have taken place. I have no evidence that any other vertebrates consume the eggs of E. coqui. In the course of almost 4900 individual nest checks (see below), I never had an instance of actual or suspected predation on coqui eggs by vertebrates other than coquies. I have observed both filial cannibalism, the parent eats its own eggs, and heterocannibalism, a conspecific eats the eggs (Rohver, 1978), in E. coqui. Filial cannibalism was associated with a major

Disturbance of the nest, parent, or eggs. Here

There were two sources of such disturbances. One was the investigator: when a nest was first discovered, the parent was captured and various parameters were assessed. Following such initial disturbance, a parent was observed to eat its eggs on several occasions, but only when eggs were in early developmental stages (i.e., during developmental interval 1). The second type of disturbance occurred when a conspecific entered the nest and ate most of the eggs in the clutch. The parent sometimes consumed the remaining eggs but, again, only when they were in early stages of development. There were instances when heterocannibals ate part of a clutch but the parent continued to care for the rest of them. On the basis of this evidence, I used the following criteria to assign cannibalized clutches: (1) If at the first nest check following initial disturbance, a clutch had disappeared, I considered it filial cannibalism; (2) if the parent was found attending the eggs during checks subsequent to the initial disturbance and the clutch later disappeared, I considered it heterocannibalism. Using these conservative criteria I may overestimate the incidence of heterocannibalism on control clutches. However, any bias I act against the hypothesis that removal of parents causes increased clutch failure from heterocannibalism. Results, Male Removal Experiments: Parental males were removed from 31 clutches in 1980 and 73 clutches in 1982. The fate of these experimental clutches was compared with that of 98 control clutches in 1980 and 108 controls in 1982.

The average initial clutch sizes for experimental and control clutches were 26.6 ± 0.9 and 28.2 ± 0.5 eggs/clutch respectively in 1980, and 26.5 ± 0.5 and 24.6 ± 0.5 eggs/clutch in 1982 (the control and experimental clutch sizes were not significantly different in either year). Most clutches either succeeded or failed completely. Out of 206 control and 104 experimental clutches, 280 (90.38%) had either nothing or hatching (number of eggs that 100% has hatched/initial egg count) X 100. Hence,

Clutches were major cases (50% or greater hatching) of 3 eggs (less than 50% hatched). There were very few borderline cases: 10 clutches (3.2%) had between 49-60% hatching. In a few clutches, more than one agent of egg mortality was involved in causing failures. In those cases, the agent responsible for most of the egg mortality was cited as the cause of clutch failure. Fungal infection and developmental abnormalities, major causes of egg mortality in other anuran species (Sulthe and Mechan, 1974; Siaon, 1982, 1983), were of minor impact on the lives of Ex cogui. Fungi infected only dead eggs, usually those that had failed to develop. A low incidence (1-3 eggs/clutch) of tumors on non-developing eggs was found in many clutches. There were no differences in the incidence of fungal infection or abnormal development between experimental and control clutches. In the 2 years, 27 experimental clutches (11 in 1980 and 16 in 1982) failed from predation. On the basis of direct evidence, I would assign one case to invertebrate predation (IP) and 21 to heterocannibalism (HC). Using the criteria outlined in the methods for the remaining clutches, I assigned 3 to IP and 12 to HC. Sixty-nine of the control clutches failed from predation during the 2 years (40 in 1980 and 29 in 1982). I could assign 26 on the basis of direct evidence: 8 to IP, 2 to HC and 16 to filial cannibalism (FC). On the basis of the methods criteria, I assigned the rest as follows: 5 to IP, 23 to HC and 15 to FC. Because experimental clutches were not subject to failure from filial cannibalism, the 31 control clutches that failed for this reason are excluded from further analysis. The success rate of experimental clutches was significantly different from that of control clutches in both years (Table 9). Combining the results from both years, 76.92% (80 of 104) of all experimental clutches failed, as against 22.52% (40 of 175) of all control clutches. The increased frequency of failure in experimental clutches was caused by significantly more frequent

Desiccation (Chi-square = 77.94, df = 1, p <0.001; both years) and cannibalism (Chi-square =

12.06, df = 1, p < 0.001; both years). Predation by invertebrates was not significantly different between experimental and control clutches (Chi-square = 1.46, df = 1, p > 0.05; both years). Wren clutches were assigned to the three developmental intervals according to the stage of the eggs at discovery or male removal. There was a significant decrease in clutch failure from developmental interval 1 to the last interval for both experimental and control clutch groups (Table 10). However, when the fate of clutches at each developmental interval were compared between treatments, there were significant differences in hatching success for each developmental interval. Thus, although there was a significant increase in hatching success of experimental clutches from early to late development, hatching success was still significantly lower than for control clutches.

Unfortunately, the next section of the text is unclear and seems to contain a series of unrelated symbols and numbers.

The developmental interval is significant. Evidence from non-experimental nest corroborative evidence suggests that parental care results in significantly increased hatching success. This comes from combining the observations of nocturnal nest attendance (Figure 8, Chapter 3) with records of hatching success for those nests. Of 96 nests for which I have at least four nocturnal nest check records (Figure 8), I also know the hatching success in 66 of them. All 64 were clutches in natural nest sites (did not include any bamboo houses).

45 were on the ground (less than 25 cm off the ground) and 19 were elevated. Hatching success was extremely bimodal, as with experimental clutches, and was scored similarly; clutches with 50% or greater hatching were considered successful, those with less than 50% as failures. Also, because of the small number of eggs that exhibited low levels of nest attendance, I combined percent attendance into two categories, 0-75% and 76-100%. The relationship between nocturnal attendance level and hatching success (Table 11) was significant (Chi-square = 5.14, p < 0.025), with significantly more clutches hatching (76%) when nocturnal attendance was high than when it was low (48%). Discussion In the first part of the discussion, I will examine the prospective functional benefits of male parental care in E. coqui in the context of what we know about the functional significance of parental care in amphibians. In the second part, I will consider how the enhancement of hatching success that results from parental care affects reproductive and hence fitness of caring males.

39 Table 11, The frequencies of two levels of hatching success as a function of the level of nocturnal attendance, computed as the percent of nest checks when the parental male was in the nest. Percent hatching attendance 0-49 50-100 = 5.14, p < 0.028,

Four functional roles resulting in increased offspring survival have been ascribed to amphibian parental care (McDiarmid, 1978; Kelts, 1981): (1) provision of an appropriate hydric regime, (2) reduction of predation, (3) reduction of fungal infection and (4) reduction of developmental abnormalities. Provision of appropriate hydric regime. A major function of parental care in E. coqui is to prevent desiccation of eggs. When male parents were removed from their eggs, 54% of all clutches (those clutches that failed) died from desiccation (both years combined). Provision of parental care (control clutches) reduced desiccation to negligible levels (1.1% of all clutches).

Clutches; 5.0% of clutches that failed. The physiological basis of egg hydroregulation by coqui whales has been documented by Taigen et al. (1984), who proposed a mechanism for the transfer of water from parent to egg across the whale's ventral integument and suggested that brooding also functions to reduce evaporative water loss. Further, they showed that increased egg water content had a significant positive effect on hatchling mass. Thus, extensive brooding by male coqui whales may serve both to ensure hatching and to maximize hatchling size. Both consequences are potentially important components of fitness. Although the provision of an appropriate hydric regime may be an important function of parental care in other anurans (Jameson, 1950; Myers, 1969; Wells, 1980; Weygoldt, 1980), our study is the first to demonstrate its importance in the field. In some anurans, parental care apparently does not serve this function (Kluge, 1981; Blommers-Schlosser, 1970; Scheel, 1970).

61 McDiarmid, 1978; Simon, 1982, 1983). Reduction of predation. Conspecifics are the principal egg predators in E. coqui. Nest defense by parental males is a significant counter to this threat. In male-removal experiments, 31.7% of the experimental clutches were consumed by conspecifics, as against 14.3% of the control clutches, a two-fold difference in the incidence of heterocannibalism. Parental defense of eggs against conspecifics appears to be important in at least two other anurans, Hyla rosenbergi (Kluge, 1981) and Cophixalus parkeri (Simon, 1982, 1983). Filial cannibalism occurred in E. coqui only when disturbance of the eggs by the investigator or an intruding conspecific occurred during early development. Filial cannibalism probably is not an adaptive response in this species either as a source of nutrients for an energy-stressed parent (Rohwer, 1978), or to remove eggs infected with fungi, as has been found in some salamanders (Highton and Savage, 1961; Tilley, 1972; Forester, 1979). Once a male coqui began to ingest his own eggs,

Dead eggs in clutches with and without attending sires. Reduction of developmental abnormalities. Attending parents may reduce the incidence of developmental abnormalities by jostling or turning eggs during early development (Salthe and Mecham, 1974; Forester, 1979a; Simon, 1982, 1983). In E. coqui, eggs are adhesive and are often deposited on vertical surfaces. Hence, there is little chance for the male to manipulate the eggs. There was no indication in the male-removal experiments that eggs deviated from normal development. From this brief review, it is clear that there is marked variability among species in the incidence and relative importance of the four functions proposed for amphibian parental care. From these limited data, no clear relationship emerges between form and function of parental care in anurans. For example, Cophixalus parkeri (Simon, 1982, 1983), Centrolenella valerioi (McDiarmid, 1978), and Eleutherodactylus coqui (this study) seem to differ substantially in the functional basis of parental care, yet all three exhibit prolonged attendance of eggs.

The benefits of male parental care in E. coqui involves high levels of nest attendance, extensive brooding, and elaborate nest defense against conspecific cannibals (Chapter 3). The results of the male-removal experiments (Tables 9 and 10) demonstrate that this parental care significantly increases egg survival and hatching success. Only 23.1% of the clutches from which attendant males were removed hatched compared to 77.5% of the clutches receiving care. Another way of examining the results is to see how the expectation of hatching changes as a function of the length of the care period, i.e., how hatching success changes as a function of removing a male at progressively later stages of development. I did this by plotting the mean percent hatching of clutches against the stage of development during which the attendant male was removed. The mean percent hatching

was computed for each stage for which N*5; when the sample size was

Dependent variables and constants, in the squared form, are at the stage of activation and were entered in the document.

The function incorporates survivorship up to the stage when the sale was resolved. If we posit that parental roles are capable of assessing the developmental stage of their clutches, and that selection can operate (via differential hatching success) on short-term decision-making by parental males, then males might decide how long to provide care on a day-by-day basis. If that is so, males would be favored to 'decide' whether to stay and care or to abandon solely on the basis of future expectation of hatching, without regard to the clutch's past survivorship. Simply put, a male can only decide to stay if he still has a clutch, and if he has one then past survivorship is 1.00. Hence, past survivorship is not important in making a decision. In this case, the first benefit curve (Figure 10), in which hatching success is plotted only as a function of what happens after male removal, is the appropriate one.

Suppose, instead, that a male's care strategy is more or less set prior to breeding. This could be a consequence of either genetic or ontogenetic factors. Imagine that a male's strategy is to 'care for X days, then abandon'. In that case, selection should act on the strategy as a whole, adjusting X to maximize reproductive success. The expectation of hatching must take into account the entire history of the clutch, including its survivorship to X (with parental care) and its survivorship from X onwards (without parental care). This second function will be designated as S(C). To calculate S(C), we first describe the I(X) curve for clutches which received parental care throughout development. The I(X) curve represents the probability of a clutch surviving from oviposition to Stage X, given normal parental care to Stage X. Only clutches that were found within one day of oviposition and followed to hatching or failure were used.

There were 60 such clutches during April-June 1980 and June-July 1982. I designate the total number of eggs at oviposition as N(O) and the number still viable at Stage X as N(X). The ratio, N(X)/N(O), then constitutes the stage-specific survivorship of clutches receiving parental care and is plotted against the stage of development to generate I(x) (Figure 11). To obtain S(C), the total expectation of hatching of a clutch as a function of care to X and no care after X, I compute the product, I(x) times P(X), for each X. S(C) is plotted as the lower curve in Figure M1. Note that the incorporation of I(x) does not change the shape of the benefit curve; it only lowers the capture.

Figure 2: A plot of the stage-specific survivorship, 100, of 60 clutches followed from oviposition to hatching or failure. S(C) is the conjugate curve derived from plotting the product of P(C) and 100 for each developmental stage at which parental males were removed. See text for details of curve computation and plotting.

CHAPTER 5 ‘THE COSTS OF MALE PARENTAL CARE

Introduction: Male coqufes invest a great deal of time in caring for developing eggs (Chapter 3). While this time investment results in highly significant benefits in hatching success (Chapter 4), any analysis of how natural selection acts to attain parental behavior in the population must consider the costs of providing care in terms of male reproductive success. Costs of parental care are postulated to be of two types: increased risk of mortality and decreased future fecundity. A variety of causes may give rise to these costs. Performing parental care might involve a temporal or spatial shift in activity or microhabitat of the caregiver into a state in which exposure to predation is greater (Forester, 1979). Alternatively, behavioral or physiological processes specific to caregiving may use energy that results in a decrement in the caregiver's physiological condition and hence increase the risk of mortality. While an energetic cost may

The text could be corrected as follows:

Results from greater metabolic expenditure in giving care, such a cost may also originate from reduced energy intake if foraging activity is constrained by the temporal demands of care-giving (Fitzpatrick, 1976; Rohwer, 1978; Krzysik, 1980; Forester, 1981; Simon, 1983; for an exception, see Kaplan and Crump, 1978). While the consequences of a negative energy budget caused by providing care may not be severe enough to increase mortality risk, they may decrease the energy that can be devoted to future reproductive effort (Walters, 1982).

In females, this may correspond to reduced production of mature offspring. For example, in frogs, which have indeterminate growth and in which fecundity is highly correlated with body size (see Chapter 2), energetic demands of care could result in slower growth rates with consequences for fecundity throughout the rest of a female's lifetime. In males, an energy cost probably translates into a reduction in reproductive activity following the period of care while they make up the energy deficit; hence it increases the time until males can begin to advertise for mates and translates into a lower rate of success in fertilizing. For males, the time spent caring may itself constitute a cost since it may preclude reproductive activity, leading to the same result. In this section, I (1) consider what the costs of parental care are, (2) present estimates of the proximate magnitude of those costs, and (3) suggest how they might affect male reproductive success. A discussion of how benefits and costs interact to determine net fitness (reproductive success) is postponed until the next chapter. I examined two types of costs of parental care for E. coqui males resulting from the prolonged period of nocturnal egg attendance: reduced feeding opportunities and reduced calling activity.

Methods Estimating energetic costs: Attendance of eggs in an enclosed nest site may reduce the opportunities for male parents to feed. The availability of food items in nest sites such as Cecropia leaves, rolled sierra palm fronds

During the care period of May-June 1980, I carried out a process of weighing brooding frogs early and late in their development. Males were removed from their nests, placed in a plastic bag, and measured for SVL to the nearest 0.5 mm using a paper ruler.

The male was then removed from the bag, and gentle pressure was applied to the groin to empty the bladder (bladder contents were usually voluntarily expelled while the frog was in the first bag). The frog was then patted dry with a paper towel and placed into a second bag. The bag and frog were weighed to the nearest 0.05 g using a 10g Pesola balance.

The frog was then removed, the bag reweighed, and the frog's weight determined by subtraction. Both weighing procedures were performed until three consecutive weights were obtained that varied by less than 0.1 g and the average of those three was used.

In eight cases, the same male was weighed early and late in development. Additional independent samples of 22 males early in development and 12 males late in development were also taken. All weights and measures were made between 1100 hours and 1700 hours (average times of measurement are given in results).

Estimating reproductive cost, calling activity was monitored from January through July 1980 in Dicks House Plot at biweekly intervals. At each survey, the entire plot was searched for calling males. For each male, its position in the plot, the characteristics of the call site (type, height off the ground, orientation), and the male's identity (frogs were marked by toe-clips) were recorded.

Mark-recapture records. Surveying and working in Dick's House Plot were begun in January, well before the dates used here for setting these two ratios. I used the number of 'marked males' present at any time as the total mature male complement. A male was counted as present in Dick's House Plot on any date between its initial capture (or after it attained an SVL = 29.0 mm) and its final capture. Males that were captured only once were not counted unless the capture date coincided with a particular survey date (and then only for that date). To estimate how successful parental males were at obtaining new clutches versus non-parental males, I compared the proportion of non-parental males that obtained clutches during 1980 in Dick's House Plot with the proportion of parental males that obtained second clutches during that time.

Five (33.38%) of the 15 brooding males had food in their stomachs on 8th July, while 15 (50%) of 30 males sampled on 14th July had food. The remaining males on both dates had empty stomachs. Only two of the 21 non-parental, calling males (9.5%) sampled during July had empty stomachs. The difference in frequency of empty stomachs between parental and non-parental calling males was highly significant (Table 412A).

Of the 20 parental males that had food in their stomachs, the mean number of items per stomach was 6.0 ± 1.8 (Range 1-31, N=19; one male had a large item that could not be extracted and is not included in volume statistics). Non-parental calling males had 2.1 ± 0.4 items per stomach (Range 1-8, N=19).

Average volume of food (Table 128) was not significantly different between the two groups when only males with food in their stomachs were compared. However, when groups were compared using all males (empty and with food), they were significantly different (Table 128). The large variance within groups in food volume is a problem in making a very strong inference from the volume results. In order to assess whether parental males change their foraging habits...

Corrected Text:

Hence their food intake, as development of their clutches proceeds, I compared the frequency of empty stomachs among the three developmental intervals (Table 13). Although there was a trend towards a decreasing frequency of empty stomachs from early to late development, it was not significant. I next consider the results from weighing parental males. Every one of the eight males that were weighed twice lost weight between the first and second measurements (Table 14). Mean weight loss was 0.36 + 0.07 g over 10 to 13 day intervals. When weight loss was corrected for the number of days between measurements, the mean weight loss per day...

Table 12: The stomach contents of brooding males and non-parental calling males sampled at dawn on 40 mornings and five mornings, respectively, during July 1982.

A. The frequencies of stomachs that were either empty or contained food.
4. Mean + SE (8) volume of stomach contents.
a) Empty Stomachs
b) Stomachs with Food

Brooding Males: 2 20
Calling Males: 2 29

x2 = 12.95, p < 0.01.

Volume of Stomach Contents:
Brooding Males: 125.8
Calling Males: 456.9

All Stomachs: 225.3 475.0 174

Mann-Whitney Test: Among the two groups...

Table 13: The frequencies of empty stomachs and stomachs with food of parental males at dawn as a function of the developmental interval of their clutches at the time of sampling. The Proportion of row totals are in parentheses.

Developmental Interval:
Empty Stomachs: x 6 (67)
Stomachs with Food: 339

u 9 (56) 7 (44)
ur 20 (50) 20 (50)

Table 14: Body weights of parental males measured early (before Stage 4) and late (after Stage 12) in the developmental periods of their clutches. Means + SE.

Early Development:
Late Development:

Same males measured early and late (8):
Mean time of measurement: 2580
Mass (g): 2.86 ± 0.12

All males (including eight above):
Mean time of measurement: 1420
Mass (g): 33.1 ± 0.26

23.39, 4, 0.36 ns Mass (5), 2.81, 40.07, 2.584, 0.08, 2.104, 8, 30, 20 p< 208. P< .001. MS = not significantly different.

7, veer 0.031 + 0.005 per day. If one assumes that per diem weight loss is constant throughout the parental care period, a total weight loss of 0.527 (SD + .255) is obtained over a 17 day period (the average developmental period in May-June). This means that the average male would lose 18.2% (0.53/2.86) of his initial body weight by caring from oviposition to hatching. Average initial weights for these eight males were 0.086 + 0.008 g/mm (2.86 + 0.34 g per frog) with final average weights of 0.076 + 0.006 g/mm (2.49 + 0.30 g per frog).

Reproductive costs. A potential cost to parental males in missed mating opportunities would exist if, (1) by providing care, males reduced the time spent calling or the effectiveness of calling (if nests are inferior call sites) and (2) gravid females are available. Nest sites and calling sites for coqui are almost mutually exclusive microhabitats (chapter 2). Nest sites, as closed cavities that are near the ground, make very poor calling sites and are never used as such by parental males. Hence, by spending a lot of time in their nests, parental males might reduce the time they spent calling and pay a cost in reduced probability of attracting gravid females in the area.

To estimate and compare the frequencies of parental males that called versus those of non-parental males, I used seven of the complete calling surveys of Dick's House Plot made between March 1 and July 4, 1980 (Table 15). The average number of marked males present in Dick's House Plot on those dates was 81 (67 non-parental males and 16 parental males). The proportion of non-parental males that were calling (Table 15) ranged from 23.42 to 31.9% on individual nights, while 0-10% of

Table 15. The proportions of non-parental and parental males that were calling in Dick's House Plot on seven nights from March to June 1980. A. Records for individual nights. B. The frequencies of calling versus

Non-calling states for non-parental vs parental males; cell totals represent summed frequencies for all seven nights.

Non-parental males:

Number	Percent
Calling	136
Non-calling	338

Parental males:

Number	Percent
Calling	4
Non-calling	93

Chi-square = 26.53, $p < 0.001$.

60 parental males called on any of those nights. Combining the results for all ten nights, parental males called significantly less frequently than non-parental males (Chi-square = 26.53, df = 1, $p < 0.001$). During the 126-day period from March 1 to July 4, 1980, 114 clutches were deposited in Dick's House Plot on 69 days (1.65 clutches per deposition day) (Chapter 2). At least one clutch was laid in Dick's House Plot on 54.8% of the days during that period. Thus, it is evident that gravid females were available regularly during March-July 1980 and that parental males that did not call were missing potential opportunities to mate.

To estimate a mating cost from parental care, I calculated a nightly probability of mating for calling males in Dick's House Plot on each night during April-June 1980 and June-July 1982 when a complete calling survey had been performed (Table 16). The nightly probability of mating was computed as the number of clutches that were deposited in Dick's House Plot on a particular day divided by the number of males that were calling on the previous night. Clutch deposition for 1980 is derived from Figure 4, and similar information for the clutch deposition chronology in 1982. Calling male densities are obtained from Tables 1 and 2. The resultant nightly mating probabilities are presented in Table 16. Nightly mating probabilities ranged from 0.0 to 0.235 females per calling male-night, with a median value of 0.050 (W = 71). I have...

Included nights when no females mated (probability of 0.0) because by calling on those nights, some males will have expended energy that may preclude their calling on some other night when gravid females are available.

Table 16. The nightly probability of mating for males in Dicks House Plot calculated for 21 nights during April through June 1980 and June and July 1962. The Nightly Probability Of Mating (KPM) was computed as the ratio of the number of females depositing clutches on a particular day (the second date given below) to the number of calling males on the previous night (the first date of the part below), number of Number of Dates calling males mating females now 3980 Apr 2-3 5 9.000 April 8-10 22 2 9.091 April 16-17 2 2 0.000 May 2-3 3 2 2.000 May 7-8 4 0 0.000 May 21-22 3 2 0.083, May 28-29 3 9.000 June 2-3 1 2 2.105 June 24 0 0.000 1962 June 10-11 15 1 0.063 June 11-12 6 1 0.067 June 12-13 8 2 0.325, June 13-14 4 0 0.091 June 14-15 11 4 0.238 June 15-16 11 0 0.000 July 8-9 25 2.000 July 9-10 25 1 2.036 July 10-11 20 1 0.050 July 11-12 23 2 0.035, July 12-13 20 0.050 Median 0.050

During the period 1 January to 4 July 1980, 129 clutches were deposited in Dicks House Plot. Of those, only 2 (1.5%) were laid in the nest sites of males that were attending a clutch at the time. The other 127 (98.5%) clutches were laid with non-parental males.

Discussion

The results suggest that there are costs incurred as a result of parental care by male coquis. Energetic costs appear to stem from a reduction in the number of nights that parental males spend foraging compared to calling non-parental males, since parental males had empty stomachs significantly more often than non-parental calling males, but there was no difference between the two groups in the stomach volume of those males with stomachs containing food. It seems that when parental males do forage, they are obtaining about as much food as non-parental calling males. The reduced energy intake as a function of nest attendance could have implications for the parental males' survival and future reproduction.

Attendance in equilibrium may not result overall in a depressed energy budget for parental males relative to non-parental calling males. Because nest attendance is generally passive, consisting largely of brooding (chapter 3), the metabolic rate is probably little different from resting rates, and certainly lower than for a frog that is active or calling. Taigen et al. (1982) estimated that oxygen consumption rates for active frogs were about seven times higher than for resting frogs. Woolbright (personal communication) measured oxygen consumption rates of inactive males and inflated males in the field at night (when they were exposed to the chorus) and found they were significantly different, with inflated having rates about 3.5 times higher than inactive males.

Neither of these estimates would suggest that the passive nature of egg brooding requires much lower energy expenditure than that of activities such as calling. The weight loss data suggest that brooding males are at an energetic disadvantage during the period of parental attendance. The single parental males that were weighed twice lost an average of 18.22% (Range = 7.3% ~ 31.73%) of their initial body weight over a 17-day development period. Evidence of energetic costs from parental care in amphibians has been found in several species. Taigen (1972) and Breysike (1980) found that brooding females of Desmognathus ocoee had significantly reduced food intake relative to non-brooding females in the population. Fitzpatrick (1973) reported that the brooding period in the same salamander resulted in a depletion of body and carcass lipid content in females. In contrast, Kaplan and Crump (1978) found that females of Ambystoma opacum brooding clutches in early developmental stages did not differ in dry weight, total calories, or weight-specific caloric content from females brooding clutches in late developmental stages and concluded that there was no energetic cost to parental brooding in this salamander. The only attempt to measure energetic costs of parental care in...

Another way of envisioning the cost of parental care would be to calculate how many females a male would miss by not calling during a period of parental care. Using a 20-day care period (the average development period for March-July), the male in a random mating population would miss one female (.05)(20), while a maximum male would miss 2.6 females (0.13/0.20). Thus, a male with a mating probability somewhere between that of a maximum male would sacrifice 1.0-2.6 potential additional clutches if he did not call while caring for a clutch. This is a substantial cost. The next chapter addresses the question of what sort of benefit level is necessary to offset such a cost and account for the high fidelity, complex care behavior observed in male coquis.

CHAPTER 6 WHY SHOULD MALE COQUIS CARE? - MODEL AND SUMMARY

Care by male coquis yields significant benefits in offspring survival, but there are costs from providing that care in terms of missed mating opportunities.

Reduced future production. In this chapter, I present a model that integrates the benefits and costs of parental care into a single statement about the relationship of parental behavior to fitness. I then use the model to analyze the net adaptive value of male parental care in addition to situations in which the model would make different predictions about the evolution of parental care in anurans. A graphical model of Anuran Parental Care Evolution is an adaptation of the marginal value model of Charnov (1976). The basic form of the model as it applies to parental investment and the evolution of mating systems was anticipated by Trivers (1972), and has been applied to the assessment of male mating strategies in dung flies (Parker and Stuart, 1976; Parker, 1978). Maynard Smith (1977) and Graton and Sibly (1978) have applied it to examinations of parental investment. As with the foraging applications for which it was first developed, I am interested in examining how an animal can maximize its rate of return when it can choose between two alternate types of behavior, each contributing to the return. Choices could be either of a proximate or evolutionary type. In the foraging model, it is the problem of how long to stay and forage in a patch, and the rate of return is energy per unit time.

In my application (after Maynard Smith, 1977), the dichotomy is between continuing to provide care to a current clutch versus attempting to mate again. In males, an attempt to mate would involve engaging in the appropriate reproductive behavior to attract a female, such as calling. For females, the attempt to remate would involve foraging at an appropriate level to mature a new complement of eggs. The currency in this case is the rate of offspring production. The marginal value theorem indicates that when the rate of return from caring declines to a level that is equal to the mean rate of return from both activities, then the animal should change activity. The switching value is the marginal rate of return, below which it is better to switch activities.

An animal loses fitness as it delays switching. The model is presented in Figure 12. It assumes a continuous breeding season, such that males and females breed more than once per season and, in particular, that species are relatively asynchronous in their oviposition schedules (Emlen and Oring, 1977; Maynard Smith, 1977). The model represents the probability of hatching for a clutch P(C), a function of the amount of time that a parent cares. There provides a certain amount of time, &, that an animal must spend before it can mate again. For a male, this might be the number of nights he must call to get another female. For a female, it is the time required to produce another clutch. The mating time, R, is incorporated into the model by extending the abscissa beyond the origin to the left. If we know the form of P(C), the care benefit function, and specify R then we can calculate the rate of offspring production for any given period of care, C*, by computing the ratio P(CT)/(oT+R). That rate of offspring production is equivalent to the slope of a line.

Figure 12. A matrilineal value model of parental care evolution. C is the time spent caring for a clutch, P(C) is the probability of survival as a function of the amount of care, and R is the time before an animal can mate. The maximal rate of offspring production, when R= Ry, is predicted by the slope of the tangent line drawn in the figure. See text for details.

Slope of tangent: P(C)= P(CHR).

Drawn from R through the point [C*,P(C*)]. According to the marginal value theorem, the maximal rate of offspring production will be given by the tangent to P(C), drawn from R, that has the highest slope. In Figure 12, that tangent has been drawn and yields a value of C, Ct, which is associated with the maximum rate of offspring production, and corresponds to the stage at which the parent should abandon the current clutch and attempt to mate.

Application of the Model to Parental Care in E. coqui

In order to evaluate the net adaptive value.

The study of parental care in coqui requires us to simultaneously analyze those consequences that contribute to fitness and those that decrease fitness. Put another way, we need to express and analyze, using a common currency, the benefits and costs of parental care. The model presented above gives us the means to do so. Reproductive success is expressed as a rate that incorporates both benefits (the probability of hatching per clutch per unit of parental care time, P(C)) and costs (the number of clutches per unit of calling time) to yield an estimate of net reproductive success per unit of total time (care time plus calling time). For E. coqui, P(C) is the benefit function that was derived in Chapter 4 (Figure 10) using the results from the male-removal experiments. A remating time for males (R) was estimated using the nightly probabilities of mating estimates in Chapter 5 (Table 16). The median value of nightly mating probability in Dick's House Plot was 0.0% females per calling male-night. By taking the inverse of this value, I obtained 20 as the number of nights that a male would have to call to obtain one female. I also calculated a remating time for the most successful male in the plot as 8 days. We now have the two necessary parts of the model to integrate costs and benefits and examine the net adaptive value of male parental care in E. coqui. In Figure 13.4, I have plotted P(C) and drawn the tangent lines for the two remating times, R= 8 and R= 20. For either value of R, the tangent to P(C) with the highest slope yields a value of parental attendance, C*, of Stage 15. Thus, the model indicates that in order to maximize reproductive success, a male parent should provide care right up to hatching, then leave the clutch (or hatchlings) and begin calling to attract another female. This result is robust over a wide range of remating times because of the Y-intercept and shape of the benefit curve. First, P(C) goes through the origin, which means that without provision of some parental care no eggs will hatch. Mates will never

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Often during late development (76.02%) as during early development (76.62%), nest fidelity remained consistent. However, after hatching, nest fidelity dropped significantly (Table 6), such that males changed from being in the nest 76.03% of the time at night during developmental interval III to 44.9% of the time at night during interval IV (post-hatching). The application of the model to parental care in E. coqui is somewhat trivial. Knowing that hatching success is zero in the absence of parental care, it is obvious that males should never completely abandon eggs. On the other hand, only by knowing the shape of the benefit curve is it evident why males should continue to care throughout pre-hatching development. In the next section of the chapter, I consider some less trivial cases in which the model may yield predictions that are more useful in hypothesising about the evolution or maintenance of parental care in anurans.

More General Applications of the Model to Anuran Parental Care

In the remainder of the chapter, I will consider first a more realistic evaluation of temporal patterns of parental care in E. coqui, as a means of examining how short-term variations in parental attendance can be incorporated into the model and how they affect the consequent predictions. Also, I will expand the view from parental care in a single species to a more general consideration of the evolution (or maintenance) of parental care in anuran amphibians. In the initial exploration of the model's application to parental care in E. coqui, I used one benefit curve, P(C), that was based on hatching success after male removal and a second curve, S(C), that combined post-removal hatching success with pre-removal survivorship. For both curves, I am plotting the results of male removals and, in effect, simulating the consequences of a male completely abandoning its clutch at some developmental stage. In fact, it seems unreasonable to expect that males would shift from a high level of parental care to complete abandonment of their eggs. It seems more reasonable.

The text should read as follows:

For the first few days of development, consequently, the y-intercept for either P'(C) or $*(C) would be lower than depicted in Figure 14. Taigen et al. (1984) showed that coquille eggs lost water rapidly, regardless of their developmental stage. However, eggs that had a longer period of parental brooding gain in water content as a result, and would be expected to better withstand desiccation from a change in parental behavior than would younger eggs.

(Taigen et al., 1984). The crucial point of the above exposition is that if survival of eggs without parental care is high enough, there is the possibility of variability in rewiring time resulting in markedly different predictions about optimal care strategies. It is important to reiterate the point that the only reason for the existence of a sharp trade-off point between no parental care and complete parental care is the shape of the benefit function. As long as the function is convex (bowed toward the abscissa), only the two endpoint strategies can yield maximal reproductive success.

What are the implications of incorporating this new benefit curve, in which there is some level of hatching success without any parental care, into the model? The principal result is that mating time becomes a critical factor in making predictions about parental strategies. If there is individual variation in the remating time in the population, there could arise the case in which males that have relatively great success in attracting females (e.g., were larger, had better territories, etc.) might be expected not to care for eggs, since mating times would be short enough to yield a maximum tangent to the benefit curve with an intersection at the ordinate (such as the male with R= 6 days in Figure 148).

Males that were less successful (i.e., had longer remating time) would have a maximum tangent to the benefit curve that intersected it near the asymptote (such as the male with B= 20 in Figure 143). Such males would be predicted to exhibit complete care. If individual variation in remating times was...

Sex-specific parental care patterns. Species with internal fertilization often have at least female parental care. Many internal fertilizers, such as birds, have biparental care, but few have exclusively male parental care. Species with external fertilization more often have male parental care, although there appear to be a fair number of species with external fertilization (presumed in the case of many frogs) and female parental care (Cross and Shine, 1981). Several hypotheses for this association have been suggested. The first and perhaps most compelling is that in species with internal fertilization, mates should be less certain of their genetic relatedness to their brood (females should never be uncertain about genetic relatedness) and hence less apt to invest heavily in post-fertilization care if they are raising someone else's offspring. By this argument, male parental care should be rare in species with internal fertilization. Since, with external fertilization, both parents on average should have a high certainty of relatedness to offspring, this argument does not predict which sex should be favored to provide care under the latter mode of fertilization. However, in a recent review of parental care patterns in fish and amphibians (the two groups in which both external and internal fertilization are found) Gross and Shine (1981) tested predictions from a paternal certainty model against the parental patterns of the two groups and found no correspondence. Also, it has been pointed out by Maynard Smith (1978), and demonstrated by Warren et al. (1980) that when paternity is uncertain in a population (i.e., cuckoldry occurs), then all males will suffer potential for cuckoldry, and relative reproductive success will depend only on hatching success of the clutch. Only under special conditions will the level of paternity play an important role in whether males evolve care. Put another way, low paternity may be a cost of mating in a population with internal fertilization, but it will not represent any special cost.

In the provision of parental care by males, a second hypothesis has been advanced to explain the association between external fertilisation and male parental care. It states that males must be present when eggs are laid, providing them the opportunity to evolve care, if it's advantageous to do so. In internal fertilizers, females either lay eggs after the male has left or gestate the young, so males have a low probability of being present to provide care during development or after hatching. As Wells (1981) pointed out, this hypothesis may be sufficient to explain how male parental care is maintained once it arises, but not to predict which path evolution would take from a starting point of no parental care.

Another hypothesis to explain the evolution of male parental care postulates the occurrence of a special preadaptive association between a male and his brood. Specifically, if males defend territories which include oviposition sites, then by having clutches laid within their territories, males may have the opportunity to associate with eggs, and increase hatching success, while continuing to attract new females (Williams, 1975; Ridley, 1978; Perrone and Zaret, 1979; Wells, 1981; Gross and Shine, 1981). This is an attractive and parsimonious argument for the evolution of male parental care and seems to agree with the few data which are available for anurans (Wells, 1981).

Eleutherodactylus coqui is a good species with which to examine these hypotheses. Firstly, it has internal fertilization. Based on the paternity hypothesis, we should not expect male parental care. However, the initial conditions under which parental care evolved in this species might have been such that the level of paternity was an important factor in whether males or females were selected to care (Erren et al., 1950). If low certainty of paternity selected against male parental care, there does not appear to be a potential for cuckoldry. There are three lines of evidence against cuckoldry in E. coqui.

"Coqui", as was suggested by Dewry (19706) and Wetis (1981). Nest sites are usually within 2m of the usual calling site of parental males and are certainly contained within the male's usual acoustically defended area. Females travel to males to mate and are led by the male to a nest site that is usually close to his call site. Often, a nest site has been a former retreat site of the male, not of a female. Females have been found to travel up

to 20m from their normal diurnal retreat sites to mate. Both males and females will defend diurnal retreat sites, so male defense of oviposition site itself is likely to have been the case. The required position of males to give care is certainly present. Once a male has laid a clutch in his usual diurnal retreat site, a tendency to maintain contact with it might increase its probability of hatching. Strictly diurnal attendance could probably increase a male's reproductive success and involve relatively little cost in reduced future matings, as suggested by Gare. However, given the relationship between benefits and costs linked to prolonged care, as shown in Figure 13, we should expect any initial association to evolve to the situation of prolonged, night care, as we find in E. coqui today. One interesting bit of behavioral evidence for the territorial association of a male with a clutch is that when dusk comes on the day of oviposition, the parental male begins to give aggressive calls, of the same type as those in nest and retreat defense encounters. These are undoubtedly directed at a female still in the nest site, resulting in her imminent departure from the site. In three cases, I have even seen the male deliver several rapid posterior movements as she left. In this thesis, I have addressed the issue of parental care in a neotropical frog from an evolutionary point of view, considering how costs and benefits to lifetime reproductive success contribute to an animal's fitness under different patterns of parental care. An equally important consideration is that of the physiological control of parental behavior. Some of

Sex should evolve care. Under other circumstances, either sex would be favored to evolve care from an initial condition of no parental care. Initial conditions such as mode of fertilization and territoriality must be examined to account for the evolution of sex-specific parental strategies. In E. coqui, the model indicates that either sex would have been favored to evolve parental care initially, since either sex would have realized a significant increase in reproductive success over no parental care by doing so. It appears likely that males evolved care in E. coqui due to their initial association with eggs stemming from territorial defense of oviposition sites. Regardless of whether the model can predict which sex will evolve care, it predicts the extent to which parental care should be provided. It also may serve to detect situations in which we should expect to see facultative parental care.

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APPENDIX 1

DIRECT DEVELOPMENT IN ELEUTHERODACTYLUS COQUI: A STAGING TABLE AND THE EFFECTS OF TEMPERATURE

MATERIAL AND METHODS

Descriptions of morphological features are based on laboratory observation of living and preserved material. During July and August 1979, eggs were collected in the field at various stages of development and observed in the laboratory through hatching. Eggs were examined twice daily by eye and under a stereo microscope at 7-30X. Laboratory temperatures ranged from 21 to 24.5 °C. Additional observations were made on material preserved in 10% buffered formalin during April-July 1980 and June-July 1982. Preserved embryos were measured using an ocular micrometer on a Bausch and Lomb stereo microscope at 10X (to the nearest 0.05 mm) or 25X (to the nearest 0.01 mm). Drawings were made using a stereo microscope with a camera lucida. Embryonic membranes were removed for measurements and drawings, except for early stages of development (through neurulation). During 1980 and 1982, the staging table presented here was used in the field to record development in over 500 clutches of E. coqui. In many clutches, the diameter of 3-10 eggs was periodically measured to the nearest 0.5 mm with a plastic ruler as development proceeded. Also, records of daily minimum and maximum temperatures were available at the El Verde Station.

RESULTS

Staging Table for Eleutherodactylus coqui.

Pre-hatching development was arbitrarily divided into fifteen stages, based on readily discernible changes in major aspects of external morphology (e.g., eyes, limbs, gills, etc.). Each stage represents at least one day of development during the warm wet season of April-July. The major features of each stage are summarized in Table 17, with more detail provided in the

Following Section. Eyes: The large eyes of E. sogui embryos are distinctive throughout development. Their position is evident as large anterior bulges in the cephalic region by Stage 4 (Figures 13 4-8). The iris first shows pigment in Stage 4 (Figures 15 C) and darkens progressively until black in Stage 10 (Figures 16 F). The pupil remains clear throughout this period. During Stage 10 the pupil begins to darken and the iris lightens. By Stage 13, the pupil is dark and the iris attains the final characteristics with the upper half golden and the lower half dark. The embryos of E. cogui bear a single pair of small gills for less than one third of the developmental period. The gills first appear as buds from the gill arches during Stage 5 (Figures 15 C-F), elaborate into short stalks bearing 2-4 terminal filaments by Stage 6-7 (Figures 15 G-I, 16 B), and then regress rapidly, disappearing from external view by Stage 9 (Figures 15 M, 16 D). Pale yellow to amber blood can be seen circulating during stage 5. At full development in Stages 6-7, the blood is orange. As the gills develop, progressively higher densities of red blood cells are observed moving through them, accounting for the change in hue.

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Unfortunately, the text you provided seems to be scrambled beyond recognition, making it impossible to fix or understand. Please provide a more coherent text for me to assist you with.

I'm sorry, but the text you provided seems to be scrambled or encrypted. It doesn't seem to contain any clear or coherent sentences in English or any other language. Can you please provide more context or a different text?

The text appears to be a mix of unintelligible phrases and properly structured sentences. Below are the corrections for the understandable parts:

Figures 15. Camera lucida drawings of E. coqui embryos.
A) Stage 4, dorsal view.
B) Stage 4, caudal view.
C) Early Stage 5, dorsal view.
D) Early Stage 5, lateral view.
E) Late Stage 5, dorsal view.
F) Late Stage 5, lateral view.
G) Stage 6, dorsal view.
H) Stage 6, lateral view.
I) Stage 7, dorsal view.
J) Stage 7, lateral view.
K) Stage 8, dorsal view.
L) Stage 8, lateral view.
M) Stage 9, lateral view.
N) Stage 11, lateral view.
O) Stage 12, dorsal view.
P) Stage 12, ventrolateral view.

Key: eed = endolymphatic calcium deposit, flb = front limb bud, g = gill, gb = gill bod, hb = hind limb bud. Scale = 1.0 mm.

Figures 16. Photomicrographs of E. coqui embryos.
A) Early Stage 5, dorsal view.
B) Stage 7, dorsolateral view (arrow indicates ADL boa).
C) Stage 7, ears view.
D) Stage 9, dorso-lateral view.
E) Stage 10, ventral view.
F) Stage 10, lateral view.
G) Stage 10, dorsal view.
H) Stage 12, ventral view.
I) Stage 12, lateral view.
J) Stage 14, ventrolateral view.
K) Egg tooth of a Stage 14 embryo.

Scale = 1.0 mm: scale in B applies to BD, scale in E applies to BEV.

Endolymphatic Calcium Deposits: During Stage 6, there first appears a pair of symmetric points of pure white material immediately posterior to the mesencephalon and anterolateral to the rhombencephalon (Figures 15.G-H). These initial points enlarge into small quadrangular patches by Stage 8 (Figures 15 J-L, 16 B-C), then develop forward extensions from their anterior lateral corners toward the rear medial region of the eye. From an external view, these extensions reach the eye by the end of Stage 9 (Figures 15 M, 16D). During Stages 10-12, the forward extensions widen dorsoventrally (as seen in lateral view), and the original posterior areas widen cephalocaudally and medially. By Late

Stage 12, the white areas on the evo sides are joined at the midline (Figures 15 0, 16 1) and, when viewed dorsally, the ECD resembles a shallow horseshoe with a thickened bifurcation and slightly spread arcs. After Stage 12, it begins to fade and is no longer visible by Stage 15. This is due to evo processes. There is a regression of the calcium deposit, such that by hatching, it is about one-third of its size at full development (late Stage 12). Concurrent increasing pigmentation masks what remains of the structures from Stage 14 on. Preliminary analysis of these structures dissected from a Stage 11 embryo (Figure 15 X) indicates that they are 28% calcium by weight. Their position at Stage 6 (Figures 15 6-H) involves quite clearly the endolymphatic sac (Lymn, 1942) with subsequent elaboration and forward extension during Stages 7 through 12 (Figures 15 1-0, 16 8-0, F-G, 1). There is little doubt that they are homologous with the calcium carbonate deposits which have been described in the endolymphatic sac of many aquatic anuran larvae (Dempster, 1930; Carlstrom, 1963; Guardabassi, 1960; Pilkington and Sipkiss, 1966; Etkin, 1964).

I will refer to these as endolymphatic calcium deposits (ECD). Dissection of the ECD at full development, from Stage 12 embryos, reveals a structure with a posterior portion that is more or less dorsoventrally depressed. The forward extensions from the anterior lateral corners begin as narrow terete stalks, becoming progressively wider and laterally compressed towards the eye. Deterioration of the ECD, beginning in late Stage 12, involves progressive reduction of all parts. By Stage 14 (Figure 16 J), the narrow terete base of the forward extensions completely disappears, leaving separate anterior and posterior sections. By hatching, the entire structure is reduced to about one-third of its fullest extent at Stage 12, and their size continues to decrease after hatching. An egg tooth first appears during the latter part of Stage 12 (Figure 15 P), and develops into a premaxillary tooth.

Symphysis is a prominent, black, bicuspid structure by Stage 14 (Figures 16 J-K). The tooth projects perpendicularly from the tip of the upper jaw, and is 0.12 + 0.01 mm (mean + SD) wide and 0.07 + 0.01 mm (mean + SD) long at full size. It sloughs off within 1.5 days after hatching.

Limbs: Limb buds first appear in Stage 4 as rounded swellings lateral to, and slightly separated from, the neural tube (Figure 15 A-B). The buds increase in size and join the trunk in Stage 5 (Figures 15 C-D, 16 A). The hind limb buds are slightly larger than the forelimbs throughout development. Both front and hind limb buds are roundish in appearance early in Stage 5, becoming more oblong as the stage progresses (Figures 15 E-F). Elbow and knee joints appear as constrictions during Stage 6 (Figure 15G) and are quite evident in Stage 7 (Figures 15 I-J, 16 B-C). Foot pads are also evident in Stage 7. Buds of at least three digits on front and hind feet are (Figure 15K). Limbs and toes elongate from Stage 9 through 13 (Figures 15 M-P, 16 E-J), at which point they reach full length, relative to their length at hatching. Toepads appear in Stage 13 (Figure 16 4).

Tail: A tail bud covers the cloaca in Stage 4 embryos (Figure 15 B). The tail stem curves to one side in Stage 5 (Figures 15 C, 16A) and has a dorsal membranous fin in Stage 6 (Figure 15 G). Elongation of the tail to full length with a large membranous fin is accomplished by Stage 10 (Table 18, Figures 16 F-C).

And reasons so through Stage 12 (Figures 15 O-P, 16 H-1). At full length, it bends at the vitelline membrane and extends laterally about two-thirds of the way to the snout. It begins to regress after Stage 12 and at hatching is about one-half of its former length (Table 18). It is resorbed completely within 2 days of hatching. The tail is translucent, heavily vascularized and unpigmented throughout development.

Other translations or transcriptions are unclear, possibly due to typographical errors.

Behavior: There is a progression of behavioral events which are readily visible in living embryos. Rapid rotation of embryos begins in Stage 3. Rotation ceases in late Stage 5 or early Stage 6, when the first evidence of mid-body flexion is observed. The tail moves for the first time during Stage 6, but tail thrashing strong enough to move the embryo does not occur until Stage 7. Tail thrashing is the main source of locomotion through Stage 12. Twitching and flexing of the limbs is first apparent during Stage 10, and by Stage 13 the embryo moves inside the egg solely with its limbs. Hatchlings are fully mobile. Size during development is presented in Table 18.

Through the end of Stage 3, the developing embryo is shorter than the diameter of the egg. In Stage 4, the embryo first exceeds the egg diameter and begins to curl around the large yolk reserve (Figure 15 AB). From that point on, embryo length is the longest intra-oval dimension. Total length is the longest dimension of the embryo in dorsal view, and is measured to the most posterior edge of the curled tail stem. Snout-vent length (SVL) is measured to the angle which the hind limbs make with the base of the tail. Because embryos are curled around a large yolk reserve during development, SVL is not strictly representative of their true length.

From Stage 14 on, the yolk is reduced sufficiently in size to allow flattening of the embryos or hatchlings and measuring a true SVL. Hence there is a large change in SVL from Stage 13 to hatching. Tail length is a measurement of the central tail stem. Yolk width was measured as the greatest transverse width of the embryo in dorsal view. It is relatively constant through Stage 8, as the embryo lengthens. In Stages 9-12, the elongating embryo progressively pinches the yolk antero-posteriorly while the expanding disc envelopes it laterally. This apparently causes the yolk to bulge laterally (Table 18). From Stage 13 on, yolk width decreases. Measurements of egg diameter in the field, although subject to greater error due to variation in the hydric state of eggs, closely parallel laboratory measurements of total length (Table 18, Figure 17). The diameter was significantly correlated with developmental stage ($r = 0.78$, $p < 0.01$). Comparisons with other Puerto Rican Eleutherodactylus species were made using this staging table to record development in two other Eleutherodactylus: E. portoricensis and E. antillensis. Microscopic examination of developmental series of these species reveals morphological detail and developmental chronology which are virtually identical to E. coqui. Embryos are almost indistinguishable from those of E. coqui through stage 11. At that stage, the sharper angle of the canthus rostralis and narrower snout, diagnostic of adults (Rivero, 1978), are evident in the embryos of both species and pigmentation differences begin to appear. Laterally and ventrally, the embryos of E. antillensis develop an almost black ground color which is flecked with white, a pattern that is quite distinct at hatching. In E. portoricensis, color differences are not so marked although hatchlings are a light orange-brown rather than dark brown as in E. coqui. Development of the ECD, gills, limbs and tail, and expansion of the pigmented body wall are equivalent, in external view, to that of E. coqui. Hatchlings of both E.

Average daily temperature of 4.0°C (Table 19).

140 Figure 18, scattergram of developmental period against mean daily temperature for 27 clutches of E. coqui. Regression Line: $y = 7x + 78.2$, correlation coefficient: $r = -0.96$, $P<0.01$.

(Step) period several doors against Mean Daily Temperature (°C).

To a favor or an unknown few in a gray area, we warn - Be aware - we as far as it's your vow, simmer down your own way.

DISCUSSION

I have described a continuum of external morphological changes in living eggs of E. coqui which form the basis of a developmental staging table for this species. The table has been used repeatedly in the field to stage the eggs of two other Eleutherodactylus as well, in order to examine its potential as a general scheme for staging the eggs of Eleutherodactylus. I present (Table 20) equivalent stages and figures from other developmental studies of Eleutherodactylus and discuss similarities and differences. The reduced nature of external gills has been noted in other Eleutherodactylus embryos. Gitlin (1944) noted the brief tenure of reduced gills in E. antillensis. He found gill buds in embryos of about 3.5 days (his Figures 2, 3, 16, 17), corresponding to early stage 5 of my scheme. Gills were reduced at seven days (presumably reaching peak development prior to that time), almost gone at 8.75 days, and completely gone by 9.75 days. Because reduced gills at seven days were contained within a dermal pocket, they would not have been visible externally after that time in Gitlin's specimens. Since Gitlin's seven-day embryos correspond to my Stage 9, disappearance of the gills at that stage in my scheme may represent a similar phenomenon. I have observed the small gills in embryos of E. antillensis as well. Chihon (1960) also reported the presence of reduced gills in E. which were visible at three days (his Figure 5), corresponding to my Stages 7-8, but...

(Note: The text seems to be cut off after "Stages 7-8, but...")

NAD appeared by 4.5 days (Figure 6), corresponding to Stage 8 or early Stage 9 of any scheme. Alanson et al. (1960) described transitory external gills arising in Stage 111.

Figure 3 (a) was created.

Various data was collected and analyzed.

More data was collected.

Stage 5) and disappearing in Stage IV (Stage 8) in E. Johnstonei. Hughes (1959) found blunt vascular papillae on the surface of the third pharyngeal arches (third gill arch?) in E. Planirosteis. Noble (1925, 1927) described two pairs of gills in E. Inoptatus of old, the anterior pair larger than the posterior pair. A complete absence of gills has been reported for other Erodactylus. Jameson (1950) and Vallett and Jameson (1951) reported that gills were absent in Hylactopheyne (Eleutherodactylus) Augusti. However, they examined embryos which, according to other features in any scheme, were already past the point at which external gills disappear. Earlier developmental stages of this species would have to be examined to determine whether or not external gills occur. Reported absence of gills in several other species is more credible since larger ranges of developmental stages were examined. External gills apparently are absent in the embryos of E. Nubicola (Lynn, 1942), one or two other species of Jamaican Tylus (Sampson, 1904), Sniola (Noble, 1925), and Brazilian E. Guentheri (Lynn and Lute, 1946). The reduction or absence of gills in Eleutherodactylus is coincident with

The text has been corrected for spelling, grammatical errors, and sentence structure:

The possession of a very large, semi-branched, vascularized tail has been proposed repeatedly since Peters' (1876) early observations as the primary organ for respiratory function. This hypothesis is likely accurate. My observations suggest that the tail also serves as a motile organ during part of development. Tail beating is a significant source of movement for at least one-third of the development in coqui.

The early appearance of limb buds in Eleutherodactylus embryos was one of the first aspects noted in an early report of direct development in this genus. Peters (1876) stated that Gundlach found all four extremities present as short stubs at an early stage in coqui. Sampson (1904) found that the limbs appeared early and simultaneously in the Jamaican species he examined. Gitlin (1944) noted that the hind limbs actually appeared about six hours before the front limbs in E. portoricensis.

The presence of an egg tooth has been noted in embryos of every Eleutherodactylus species reported thus far (Lynn, 1942; Lynn and Lutz, 1946; Lutz, 1944; Bayley, 1950; Adanson et al., 1960; Bogert, 1969; Wake, 1978; this study). However, in some species, it may be quite small (Noble, 1926). Typically, it is described as a bicuspid structure (single-spined in a few; Noble, 1926; Goin, 1947), partly or completely black, and situated at the premaxillary symphysis, approximately perpendicular to the upper jaw. In E. coqui and E. antillensis, the egg tooth is black over its distal half.

Several authors have also observed the hatching of embryos and described the scraping action prior to hatching. Stage 15 embryos in this study have been observed on many occasions to poke at the egg capsule with their snouts just prior to hatching, apparently rupturing the membranes with the egg tooth.

The role of ECD in anuran larvae was long the subject of speculation. Early suggestions (e.g., Caupp, 1897 as cited in Dempster, 1930) that calcium stored in the endolymphatic sacs of pre-metamorphic larvae might be mobilized for bone formation during metamorphosis climax awaited definitive proof by Guardab, 4 (1960), Kreiner (1954) and Pilkington and Simkiss (1966). The latter study showed conclusively that endolymphatic calcium carbonate is resorbed during metamorphic climax to provide calcium for skeletal ossification. Pilkington and Simkiss suggested that the process of early storage and later mobilization was an adaptation to allow continued skeletal ossification during the extensive morphological changes of metamorphic climax when no feeding occurs. My observations of the early formation and later dissolution of ECD in E. coqui suggest a similar calcium storage and mobilization scenario for these terrestrial embryos. The ECD first appears early in development (Stage 5 in my scheme), long before ossification begins in any Eleutherodactylus (Lynn, 1942; Lynn and Lute, 1946; Yailett and Jameson, 1961). They enlarge during the next one-third of development and begin to disintegrate coincident with the beginning of skeletal ossification. Ossification begins in the limbs at around 12 days, in the vertebral column at around 11 days, and in the head at 10 days (Lynn, 1942). These times are equivalent to late Stage 12 and Stage 13 in E. coqui, when the ECD are starting to disintegrate. In E. johnstonei (Adamson et al. 1960), ossification of the limbs begins in Stage VII (equivalent to my Stage 12). While the calcium storage function of the endolymphatic organ is probably similar in aquatic anuran larvae and direct-developing embryos, the source of the calcium is probably different. Calcium stored by aquatic larvae almost certainly is derived from larval food. In eggs with direct development, the calcium must be invested in the egg by the female prior to oviposition. Temperature and Development Temperature has a strong influence.

Effect on the developmental rate in embryos and larvae of aquatic-breeding amphibians (Moore, 1939, 1942; Pettus and Angleton, 1967; Licht, 1971; Howard, 1978; Seith-Gill and Berven, 1979). I have found a significant inverse relationship between ambient temperature and developmental rate for the terrestrial eggs of E. coqui. Over the range of temperatures encountered in the field (approximately 15-28°C), a 1°C drop in mean daily temperature caused a change in mean developmental period of 2.5 days. This strong relationship between temperature and developmental rate results in an average winter developmental period (Jan-Feb: 26.3 days) which is 1.57 times the summer developmental period (June: 16.8 days)(Table 19). Two principal effects of growing amphibian larvae at lower temperatures are longer larval periods and larger size at metamorphosis (untenutn, 1519; wart, 1955; Ekin, 1964; Kollros, 1961; Smith-Gill and Bervon, 1979).

Because the developmental period of E. coqui, which ranges from lower temperatures, is spent wholly within the egg, there is no reason to expect that hatchlings should be larger at lower temperatures. Unlike free-swimming larvae, E. coqui embryos cannot feed for some more extensive period. An important result of slow development in E. coqui is the longer period during which eggs are vulnerable to mortality. Desiccation and cannibalism are main causes of egg mortality in E. coqui (Townsend et al., 1984). Although this parental care significantly reduces egg mortality, a 1.57% increase in the developmental period could result in much lower hatching success despite full-term parental care. This vulnerability of eggs due to longer developmental periods may be further compounded by the colder conditions during the winter months. Although the lower temperatures and drier conditions of the winter months may have a direct effect on the physiology and reproductive behavior of E. coqui, the increased vulnerability and hence lower hatching success of eggs laid during this season may be a selection factor.