

SEXUAL DIMORPHISM IN BODY SIZE
OF THE SUBTROPICAL FROG,
ELEUTHERODACTYLUS COQUI

by

Lawrence L. Woolbright

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

College of Sciences and Mathematics

Department of Biology

1985



CENTER FOR ENERGY AND ENVIRONMENT RESEARCH
UNIVERSITY OF PUERTO RICO -- U.S. DEPARTMENT OF ENERGY

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ABSTRACT

Sexual dimorphism in vertebrate body size has been traditionally seen as the result of sexual selection on male size. In spite of documented selection favoring large males of many frog and toad species, 90% of anuran amphibians have females that are larger than males. Two major explanations have been proposed for such situations: natural selection favors large female size, and differential predation on calling males reduces average male size. In addition I propose that the energetic costs of advertising for mates may limit male growth.

I examine these hypotheses using the prolonged breeding subtropical frog, Eleutherodactylus coqui. Female coquies are 29% larger than males. Sexual selection favors large male size because of an increase in mating success. Natural selection favors large female size because of increased fecundity. However, the number of eggs fertilized increases with male body size six times faster than clutch size does with female body size. Thus selection pressures predict that male coquies should be larger than females.

In the field, male coquies stop growing shortly after beginning reproductive activity. However when males are denied access to calling sites and females, growth resumes at rates similar to those of females. These observations are consistent with an energetic interpretation of size dimorphism but not with the differential predation

hypothesis.

Male coquies do not forage while calling. Resultant food intake of calling males is reduced by 20 - 35%. In addition, metabolic rates increase significantly when males are exposed to the nocturnal chorus and even more when they are calling. Energy budget analysis indicates that for about 75% of the year females take in more energy than they use for maintenance and egg production. Males take in excess energy only 33% of the year and appear to use more energy than they take in when they call during the dry season. Energy analysis predicts that male growth should stop at body sizes much smaller than those predicted for females. I suggest that coqui size dimorphism is maintained by the energetic constraints of male reproductive activity.

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Chapter I

Introduction

Sexual dimorphism in body size is common in many vertebrate taxa. Among anuran amphibians, males are typically the smaller sex. The purpose of this study is to examine ecological mechanisms and selection pressures that have the potential to explain this phenomenon and to measure their impact on body size in a single species. I chose the subtropical arboreal frog, Eleutherodactylus coqui Thomas (Anura: Leptodactylidae), as a study species for two reasons: 1) its extremely prolonged breeding season leads to clear-cut predictions and easy data collection and 2) mating systems of tropical anurans are not as well studied as those of temperate species. I assumed throughout the study that body size has a heritable component and that current ecological conditions adequately mirror historical ones.

The body of this work is divided into five chapters, each written as a separate manuscript. Thus each chapter contains the necessary background information for the material included in it, as well as its own methods, literature cited, acknowledgments, etc. Chapter 2 was published in the American Naturalist in January, 1983 and Chapter 5 in Herpetologica in March, 1985. The remaining chapters are to be submitted to various journals. This method of organization is efficient in terms of writing effort and ensures that all data sets are associated with a publishable unit. However, the method detracts from the cohesion possible in

a unified format. Therefore I include this chapter primarily as a summary of how the following chapters fit together in the overall work.

The theoretical background of anuran size dimorphism is developed in Chapter 2. The traditional view for other vertebrates has been that size dimorphism results from differential selection pressure on body size between the sexes. Sexual selection may favor large males through competition for mates, and natural selection may favor large females through higher fecundity or better parental ability. I refer to the view that anuran size dimorphism results from an imbalance between these selection pressures as the hypothesis of the large female advantage because its acceptance would require that the reproductive advantage of large size to females outweigh that to males in the majority of anuran species. On the basis of theoretical arguments, I suggest that this hypothesis alone is not capable of predicting size relations of anurans in general.

A second mechanism proposed to explain anuran size relations is the hypothesis of differential predation. This view suggests that male calling behavior attracts predators that differentially crop reproductive (= large) males while allowing greater average longevity of females. Predation related differences in age, combined with indeterminate growth, could result in larger average female body size. Differential predation appears a likely explanation of size dimorphism for certain species, but a review of the literature suggests that it is not a universal explanation. An easily testable prediction is that size-specific

male and female growth rates should be equal if differential predation is the only factor maintaining a species' size dimorphism.

I conclude Chapter 2 by proposing a third model of anuran size dimorphism. This model includes consideration of selection pressures on male and female body size but also suggests that energetic constraints on male growth may occur in species in which male reproductive behavior extends over a prolonged period of time. These male energetic costs are suggested by recent studies showing that metabolic rates of calling males are extremely high and by anecdotal evidence that males do not feed while calling. The predictions of the "selection - energetics" model for extremely prolonged breeders are that natural selection should favor large female size because of increased fecundity, sexual selection should favor large male size even more because of increased reproductive success, and that male growth should be constrained by the lower energy intake and higher energy expenditure experienced by calling males.

In the final four chapters I examine various aspects of the three major models of size dimorphism using the coqui. In Chapter 3 I test the predictions of the large female hypothesis and the differential predation hypothesis. Reproductive success data do not support the large female hypothesis. Although clutch size does increase with female body size, the number of eggs fertilized increases even faster with male body size. These results suggest that, based only on selection pressures, male coquies should be larger than females. In fact, female coquies

are about 30% larger than males.

Likewise, data on size-specific growth rates do not support the differential predation hypothesis. Male coquies actually stop growing shortly after beginning reproductive activity. However, when males are kept in the laboratory and not allowed access to calling sites or females, they resume growth at rates not different from those of females. Thus the results in Chapter 3 suggest that neither of the standard models of size dimorphism is capable of explaining sexual size relations of the coqui. However all results are consistent with the predictions of the selection - energetics model developed in Chapter 2. Therefore I proceed to test that model.

One aspect of the selection - energetics model for which no previous data existed was the prediction that calling male anurans forfeit feeding opportunity and therefore energy intake. I test this prediction in Chapter 4 by measuring the early morning stomach contents of coquies known to have called or not to have called during the preceding night. Results show that males do not forage while calling and that they take in less prey on those nights than similar sized frogs that do not call. I use the magnitude of this difference later in the calculation of energy budgets for calling and non-calling frogs.

A conclusive test of the selection - energetics model of size dimorphism requires energetic analyses to determine whether the energetic costs of calling activity are sufficient to limit male growth. Before constructing energy budgets, it was necessary to know how much time male coquies spend calling and

whether coqui movement during the night is extensive enough to represent a significant energy expenditure. I examine these questions in Chapter 5 by following individual coquies throughout the night and measuring movement and time spent calling. Results indicate that coquies are extremely sedentary and probably do not use a significant portion of their energy intake for movement. Estimates of the time per night and number of nights spent calling by male coquies are used later in calculating energy budgets. Thus Chapter 5 does not actually test hypotheses of size dimorphism, but rather presents data necessary for future tests.

Energy budgets are calculated in Chapter 6. By comparing estimates of energy intake with independent measurements of energy expended for metabolic costs, egg production and growth, I conclude that male coquies are frequently on negative energy budgets while females never are. The extension of these energy analyses to larger body sizes suggests that male coquies should stop growing at body sizes much smaller than those predicted for females.

The results reported in these studies add greatly to our understanding of anuran size dimorphism. They stress the importance of considering both selection pressures and ecological constraints in modelling observed trends. The model presented in Chapter 2 considers both and appears to have valid predictive ability at least in the case of the coqui. I suggest that this model, when adjusted for special circumstances such as differential predation, may be capable of explaining size

dimorphism across a broad range of anuran species.

Chapter II

Sexual selection and size dimorphism in Anuran Amphibia

Darwin's (1871) concept of sexual selection has been generally accepted as the explanation of sexual size differences in higher vertebrates (e.g., Amadon 1959; Clutton-Brock et al. 1977; Crook 1972; Selander 1972; Trivers 1972). Mechanisms of sexual selection include competition between males (intrasexual selection) and female choice (intersexual selection).

Evidence of male-male competition in anurans abounds. In explosive breeders (those with breeding periods of a few days to a few weeks - Wells 1977a) large males have been shown to defeat small males in aggressive encounters (Davies and Halliday 1979) and to displace small males from amplexus (Berven 1981; Davies and Halliday 1977; Wells 1979). In prolonged breeders (those with breeding periods of more than a month - Wells 1977a) large males have been shown to defeat small males in aggressive encounters and to displace them from territories (Emlen 1976; Howard 1978a, b; Ryan 1980b; Wells 1977b, 1978). Large males have been shown to have higher reproductive success in several species of both explosive and prolonged breeders (Berven 1981; Davies and Halliday 1979; Fairchild 1981; Gatz 1981a, b; Howard 1978a, 1980; Wells 1979).

Female choice is more difficult to demonstrate, but it has been suggested for several species (Davies and Halliday 1977, 1978; Emlen 1968; Gatz 1981b; Greer and Wells 1980; Howard 1978a;

Ryan 1980b; Wells 1977b; Wilbur et al. 1978). Ryan (1980a) has shown that female Physalaemus pustulosus preferentially choose mating calls with lower fundamental frequencies and that this is significantly associated with large male size. Fairchild (1981) found that female Bufo woodhousei fowleri consistently chose the taped call of a large male over that of a smaller male.

Thus it is apparent that sexual selection, through male-male competition, female choice, or both, favors large males in a wide variety of anuran species. Based on this information it would be reasonable to expect the majority of anuran species to have large males and small females; yet Shine (1979) found that 90% of 589 species studied have females that are larger than males. Not surprisingly, sexual selection alone is inadequate to explain observed trends in anuran body size.

LARGE SIZE IN FEMALES

Sexual dimorphism in body size may also be influenced by selection pressures affecting female body size (Ralls 1976, 1977). Large size in female anurans is adaptive because of increased clutch size in larger frogs. This trend has been demonstrated for a wide variety of species (e.g., Collins 1975; Crump 1974; Crump and Kaplan 1979; Davies and Halliday 1977; Howard 1978a; Hulse 1979; Oplinger 1966; Salthe and Duellman 1973) and may well be a universal phenomenon in anurans. Although this undoubtedly explains why females should be large, it does not explain why males should not be equally large. Ralls (1976) suggested that sexual selection may be operating on males

even when they are smaller. However, given that this is true, what factor keeps most males from reaching the biological potential attained by females?

SMALL SIZE IN MALES

Is small size adaptive in males? Ghiselin (1974) proposed that small male size may be adaptive in increased motility and ability to locate females. This explanation does not seem appropriate for anurans, in which males of many species advertise from stationary positions. Another possibility is that small male size allows for differential niche use, adaptive in the avoidance of intraspecific competition (Selander 1966; Schoener 1967). This hypothesis may confuse cause and effect relationships and has not achieved sufficient support to be considered a general phenomenon.

Licht (1976) proposed for Bufo americanus that small male size increases insemination efficiency via close apposition of male and female cloacae. However, his proposal suggests the presence of size assortative mating which does not occur in B. americanus (Gatz 1981b; Wilbur et al. 1978).

Since anurans have indeterminate growth, differential mortality rates between the sexes have the potential to influence size dimorphisms. Mortality of males is higher than that of females in some populations (Howard 1981) but not in others (Berven 1981; Briggs and Storm 1970; Turner 1960). I suggest that although differential mortality may well influence specific populations, it probably is not a universal explanation of small

male size.

I propose that one factor with the potential to explain the general phenomenon of small male size in anurans is the suite of energetic constraints associated with reproduction in males. Previous preoccupation with investment in gametes has largely overlooked other costs to males during the breeding season. Territorial defense, agonistic behavior and advertising behavior may require energy that would otherwise be used for growth. The diversion of time from foraging to these reproductive behaviors may result in a considerable loss of energy intake during the breeding season. A combination of these factors could well impose serious energetic constraints on reproductive males in species with prolonged breeding periods.

Evidence exists that there are energetic costs associated with male reproductive behavior. Wells (1978) describes agonistic interactions between male Rana clamitans that leave participants exhausted, "breathing heavily for 30 to 40 min." In Physalaemus pustulosus calling males have significantly higher rates of oxygen consumption than do non-calling individuals (Bucher et al. 1982). Rabb (1973) noted that feeding behavior is often seemingly suppressed by reproductive behavior. Both Martof (1956) and Wells (1978) noted limited feeding by reproductive male Rana clamitans, and Martof suggested that this might partially explain why more males do not reach large body sizes in that species. Jenssen and Klimstra (1966) found a higher proportion of empty stomachs and lower stomach content volumes for male than female Rana clamitans during the breeding season.

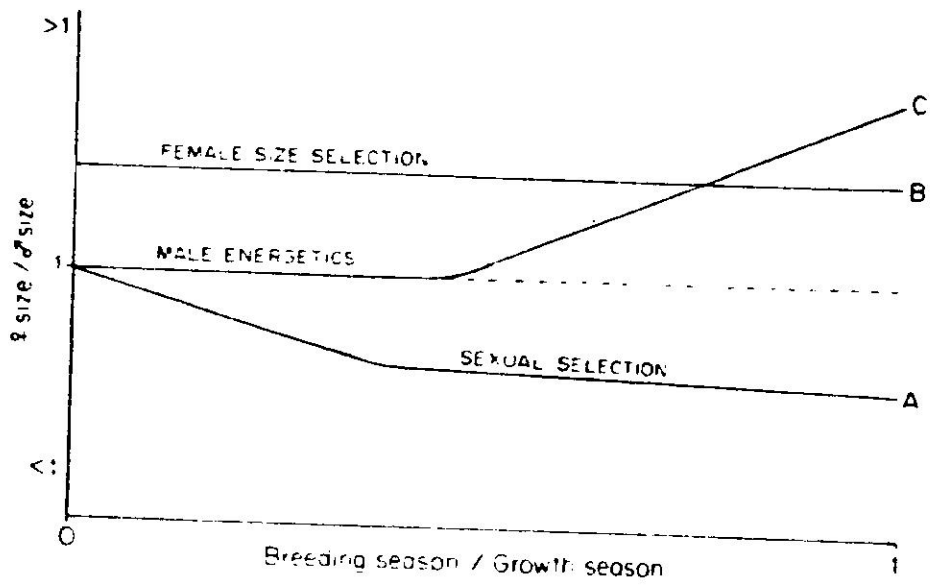
It appears that a combination of these phenomena may impose serious constraints on male growth. Morton (1981) found significantly lower fat body weight in male than in female Bufo canorus during the breeding season (see also Jenssen 1972). Wells (1978) found weight losses of up to 30% in male Rana clamitans during the breeding season, and Fellers (1976) reported significant weight loss in Hyla versicolor after only a few nights of calling.

It is obvious that more data are needed to elucidate the nature and importance of energetic constraints on reproductive males. Nevertheless, the available information suggests that males of species with prolonged breeding periods face potentially severe energy deficits.

THE MODEL

Figure 1 shows qualitative predictions of the effects of each of three major factors (sexual selection, selection for female size, and male energetic constraints) on the magnitude of size dimorphism in anurans. The abscissa of the graph represents the proportion of available growth period spent by the population in reproductive behavior. The inclusion of a growth season factor is necessary to relate populations from different latitudes. Breeding season is actually an estimate of two separate phenomena. In terms of sexual selection pressure on males, the important parameter is the temporal availability of receptive females. For male energetic constraints, the appropriate measure is how many nights the average male calls.

Fig. 2.1. Predicted magnitude of size dimorphism in anuran amphibians as a function of the relative length of the breeding season and growth season. On the x-axis, 0 = explosive breeding, 1 = year-round breeding. The dashed line at $y = 1$ is equality of male and female size. See text for discussion.



In extremely prolonged breeders an individual male may not call every night (Kluge 1981; M. Ryan, pers. comm.). I suggest that for most populations the number of nights of full chorusing will serve as a realistic estimate of breeding season for both purposes.

The ordinate of the graph is the magnitude of size dimorphism. Since this measure may vary between years (Howard 1981, Table 1), the best estimate for a given population is probably the mean value over several seasons.

Line A represents the predictions of the male sexual selection model. The opportunity for sexual selection to operate is least (but not 0, Wells 1977a) for explosive breeders and increases as the breeding season gets longer and receptive females become more asynchronous (Emlen and Oring 1977). At some point, however, further lengthening of the breeding season probably has little additional effect. In some prolonged breeders, females lay more than one clutch per breeding season (Howard 1978b; Wells 1976), thereby decreasing the operational sex ratio. Even if females breed only once, potential variance in male reproductive success is still limited by the area from which a given male can effectively obtain a mate. Thus the slope of the line is less extreme for longer breeding periods.

Line B represents the predictions of selection for large size in females. Since this relation is based on increased female fecundity, breeding type probably makes little difference. Large females in an explosively breeding population, as well as large females in a prolonged breeding population, experience

higher reproductive success. Therefore, this relationship is represented as constant.

Line C represents the predictions of male energetic constraints. These constraints should have little effect on male size as long as the breeding period is short enough for the male to make up for his energetic losses during the balance of the growth season. At some point, however, the energetic loss becomes too great to be counteracted, and from that point any increase in breeding period should be associated with steadily decreasing male size.

The combined effects of the three curves in figure 1 generate three basic predictions, as follows: 1) For explosive breeders the effects of male sexual selection and male energetic constraints should be small. For these species females should be larger than males, and the magnitude of the dimorphism should be roughly proportional to the selection pressure for large females. 2) As breeding period increases, the strength of male sexual selection increases relative to the strength of pressure for large females, and the magnitude of the dimorphism decreases. The point at which male sexual selection is greatest, but energetic constraints on males are not yet a significant factor, should be the point at which males are largest relative to females. Species in which males are larger than females should lie in this region. 3) As breeding season increases further, the effect of male energetic constraints becomes greater and the effect of sexual selection remains fairly constant. Males again become smaller with respect to females and the line is roughly

monotonic from that point on.

TEST OF THE MODEL

As a preliminary test of the model, I have collected from the literature size data on a variety of species (Figure 2 and Table 1). Explosive breeders, whether temperate or tropical, are depicted at the far left of the graph. Prolonged temperate breeders are placed next. They have growth seasons that extend from early spring to late fall (Jenssen 1972; Martof 1956) and breeding seasons that range from one to three months (Wells 1977a). Thus ratios of breeding season to growth season for these species are probably less than or equal to 0.5. Tropical prolonged breeders that are extremely seasonal should have ratios comparable to those of temperate prolonged breeders. However, those for which I have data probably grow all year long (Woolbright unpub.) and have breeding seasons of six months and more. Therefore, their ratios of breeding season to growth season are probably greater than 0.5, and they are placed on the right side of the graph.

Within each group, species are ordered by increasing length of breeding period. This is necessary because comprehensive data on growth season are not available for most populations, so it is assumed that growth seasons within each group are relatively constant. Therefore the exact position of each species along the x-axis is only an approximation.

DISCUSSION

The model presented here attempts to explain size dimorphism

Fig. 2.2. Magnitude of size dimorphism as a function of relative length of breeding season for populations of anurans reported in the literature. Circles are group means ± 1 S.E. See table 1 for data and sources. See text for discussion. Dotted line is fit by eye. (' = points noted in text).

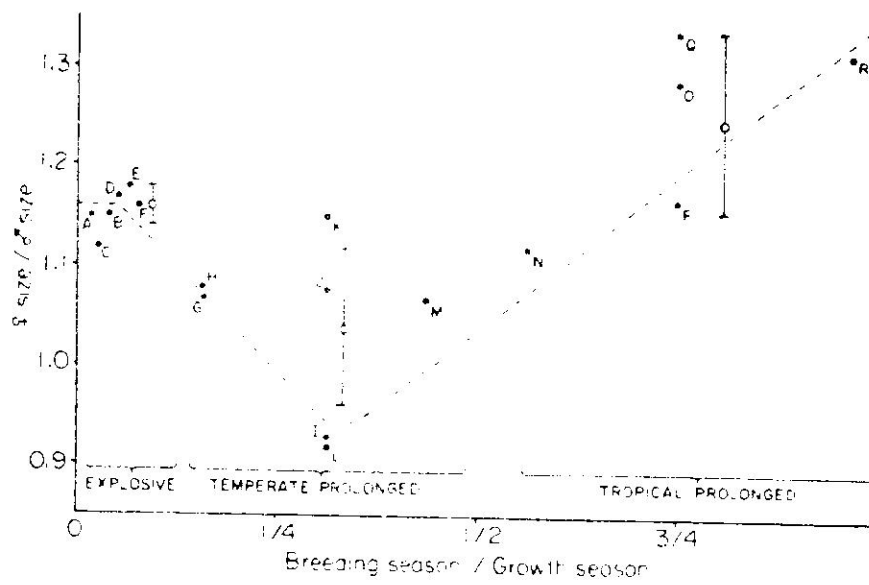


Table 2.1. Degree of size dimorphism for a variety of anuran populations reported in the literature. Point designations refer to Fig. 2.2. Genera listed: B = Bufo, E = Eleutherodactylus, H = Hyla, R = Rana. Alternate sources for breeding season estimates: 1 = Wells 1977a, 2 = Briggs and Storm 1970, 3 = Stebbins 1951. Body sizes are given in mm.

Point	Species	Locality	Female	Male
A	<u>R. sylvatica</u>	Virginia	(15% > male)	
B	<u>B. americanus</u>	Ontario	75.0	67.0
C	<u>R. sylvatica</u>	Michigan	44.0	38.3
D	<u>B. bufo</u>	England	69.4	59.4
E	<u>R. cascadae</u>	Washington	63.0	53.3
F	<u>B. typhonius</u>	Panama	44.4	38.3
G	<u>H. crucifer</u>	Ohio	30.1	28.2
H	<u>R. boylei</u>	California	60.0	55.5
I	<u>R. catesbeiana</u>	N. Jersey	140.3	151.2
J	<u>R. catesbeiana</u>	Michigan	136.9	126.9
K	<u>H. versicolor</u>	Ohio	51.1	44.5
L	<u>H. cinerea</u>	Illinois	48.9	53.1
M	<u>R. clamitans</u>	Illinois	58.0	54.1
N	<u>E. gossei</u>	Jamaica	28.0	24.9
O	<u>E. coqui</u>	Puerto Rico	46.1	35.6
P	<u>E. johnstonei</u>	Jamaica	24.7	21.1
Q	<u>E. cundalli</u>	Jamaica	31.6	23.5
R	<u>E. planirostris</u>	Jamaica	23.4	17.7

(Table 2.1, con't.)

Point	Female/Male	Breed	Source
A	1.15	1 day	Berven 1981
B	1.12	3-6 days(1)	Licht 1976
C	1.15	10 days	Howard 1980
D	1.17	6-14 days(1)	Davies & Halliday 1979
E	1.18	2-4 wks(2)	Wright & Wright 1949
F	1.16	expl. trop.	Wells 1979
G	1.07	1-2 mos(1)	Gatz 1981
H	1.08	1-2 mos(3)	Wright & Wright 1949
I	0.93	2 mos	Ryan 1980b
J	1.08		Howard 1981
K	1.15	1-3 mos(1)	Gatz 1981
L	0.92	1-3 mos	Garton & Brandon 1975
M	1.07	3 mos	Jenssen 1972, ___ & Klimstra 1966
N	1.12	1/2 yr	Stewart & Martin 1980
O	1.29	3/4 yr	Woolbright unpub.
P	1.17	3/4 yr	Stewart & Martin 1980
Q	1.34	3/4 yr	Stewart & Martin 1980
R	1.32	yr-round	Stewart & Martin 1980

for a diverse variety of anuran species. In the interest of generality I have ignored many factors that could be included in a specific model of a more limited taxonomic group.

Territoriality, parental care, life span, differential energy allocation, differential growth rates, and delayed maturity are among the factors that merit consideration. Some of these are probably mechanisms derived from selection pressures considered here and are therefore indirectly included in my model. Others may be useful in explaining deviations of populations from the predictions of this model. Ultimately some may prove common and predictable enough to be included in a general model.

There are several assumptions inherent in my model. One of the most basic is that the intensity of sexual selection varies with its expected potential. This has yet to be shown (Gatz 1981b, Table VI; Kluge 1981, Table 15). I also assume that sexual selection in all groups favors large male size. While there is much support for this idea, it is possible that other characters may be favored in some groups. Searching and grasping ability may be important in explosive breeders as may choice of call site by prolonged breeders (Fellers 1979). Crump (1974) found that large females of some species did not produce larger clutches than did small females. Thus my assumption of a constant effect of selection for large female size may not be valid. It is hoped that further research will better define the shapes of all three of the model's curves.

In spite of my various omissions and assumptions, those data available fit the model quite well. Temperate prolonged breeders

have degrees of size dimorphism significantly lower than both explosive breeders (Mann-Whitney $U = 2$; $p = 0.002$) and tropical prolonged breeding species ($U = 1$; $p = 0.003$). This information is not adequate to specify the low point in the curve (that point at which male sexual selection, in the absence of energetic constraints, gives rise to the largest males). It suggests, however, that this condition is approached by those populations that spend approximately one fourth to one half of their available growth periods in reproductive activity.

The right tail of the data curve seems to increase to a point well above the left tail. The difference in size dimorphism between explosive breeders and prolonged tropical breeders is not statistically significant (Mann-Whitney $U = 7$; $p = 0.089$). However, the trend suggests that male energetic constraints may outweigh the effects of sexual selection in extremely prolonged breeders. This prediction may be complicated by the fact that the five prolonged tropical species shown in Figure 2 are all terrestrial breeders. Because such species do not breed in dense aggregations, there may be reduced opportunity for sexual selection to act on male body size. It is possible that curve A in Figure 1 should actually bifurcate at the right side of the graph, allowing for reduced sexual selection in terrestrial breeders.

Two populations (Figure 2, points J and K) are clearly out of line with the predictions of the model. In the case of Hyla versicolor (point K) the assumption of sexual selection for large male size may be violated since large males were found to have no

higher mating success than small males in one of the two ponds studied (Gatz 1981a). Fellers (1979) also reported that there was no selective advantage to large male size in a Maryland population of H. versicolor and concluded that residence at a "good perch" was the key to mating success in this species.

In the case of point J (Rana catesbeiana), disagreement with the model may result from a local ecological factor. Howard (1981) reported that large territorial males of this population suffer from intense predation by snapping turtles. Another population of R. catesbeiana (point I, Ryan 1980b) fits the predictions of the model quite well.

The model is potentially applicable to intraspecific comparisons of local populations in species that occur over wide latitudinal or altitudinal ranges. If growth season and breeding season covary equally we might expect an equal degree of size dimorphism to result. However, if one varies while the other remains constant, we should be able to predict differences in dimorphism.

Any attempt to describe sexual differences in anuran body size based on only one factor is probably unrealistic. By considering three seemingly important factors simultaneously, I have developed a model that appears capable of predicting major trends. Thorough testing of the hypotheses developed here will determine the extent of the model's validity.

SUMMARY

Evidence for the presence of sexual selection in anurans

suggests that large males should be favored in many species, yet the vast majority of species have females that are larger than males. This is explained in part by the well documented fact that large females in many species have higher fecundity than do small females. In addition, I argue that energetic constraints on reproductive males, caused by the costs of advertising, maintaining territories, and lowering food intake, can affect body size in species with prolonged breeding periods. A model is proposed that considers all three factors simultaneously. Predictions of the model are: 1) large females in species that breed explosively, 2) relatively larger males in species that breed for intermediate periods, and 3) females that are again larger relative to males in species that breed for extremely prolonged periods. A preliminary test of this model, based on published studies, shows general agreement with the predictions.

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Chapter III

Sexual dimorphism in Eleutherodactylus coqui:
selection pressures and growth rates

Abstract. Snout-urostyle length of female Eleutherodactylus coqui averages 29% longer than that of males. Data on the relationship between body size and reproductive success do not support the hypothesis that this size dimorphism is explained by sexual differences in selection pressures. Although large females lay more eggs than small females do, large males obtain more clutches than small males do. The reproductive advantage of large size in males appears to exceed that of females. Growth data do not support the hypothesis that size dimorphism is maintained by predation on adult males. Regardless of predation, males stop growing shortly after reaching reproductive maturity. However, when males are kept in the laboratory under conditions not conducive to reproductive behavior, growth continues at rates not different from females in the field. I suggest that size dimorphism in this species is maintained by energetic constraints resulting from male reproductive behavior.

Key words: Amphibia, Anura, Leptodactylidae,
Eleutherodactylus coqui, size dimorphism, reproductive success,
growth rates.

INTRODUCTION

Darwin's (1872) principle of sexual selection is generally accepted as the explanation for sexual dimorphism in vertebrate body size (e.g., Amadon 1959, Clutton-Brock et al. 1977, Crook 1972, Selander 1972, Trivers 1972). Although there is considerable evidence that sexual selection favors large male size in anuran amphibians (reviewed in Woolbright 1983), females are larger than males in about 90% of frog and toad species (Shine 1979). Here I examine size dimorphism in the Puerto Rican coqui, Eleutherodactylus coqui (Anura: Leptodactylidae). The coqui has a prolonged, year-round, breeding season. Male coquies are therefore potentially subjected to intense sexual selection pressure (Emlen and Oring 1977). In addition, the coqui exhibits male-male combat in defense of retreat sites and egg clutches (Townsend et al. 1984) and thus would be predicted by Shine (1979) to have larger males than females. Nevertheless, female coquies are significantly larger than males. I test two alternate hypotheses that have been advanced to explain such situations: the hypothesis of the large female advantage and that of differential predation.

Ralls (1976, 1977) suggested that even when sexual selection favors large males, females may be larger than males because of stronger natural selection pressure for large female size. Natural selection frequently favors large female anurans because of a positive relationship between female body size and clutch size (e.g., Collins 1975, Crump 1974, Crump and Kaplan 1979, Davies and Halliday 1977, Howard 1978, Hulse 1979, Oplinger 1966,

Salthe and Duellman 1973), and Townsend (1984) reported that such a relationship exists for the coqui. I tested the hypothesis that natural selection pressure for large female size is greater than sexual selection pressure for large male size by measuring the relationship between male body size and reproductive success and comparing it to the female relationship reported by Townsend (1984).

Howard (1981) reported that females in a population of Rana catesbeiana were larger than males because of differential predation on large males. This hypothesis leads to the prediction that males should continue to grow until they are removed from the population. I tested this prediction by measuring growth rates of male and female coquies in the field. I also measured growth rates of coquies kept segregated by sex in the laboratory to test the possibility that the size dimorphism results from determinate growth.

METHODS

Study species and site

Eleutherodactylus coqui Thomas is an arboreal leptodactylid common throughout Puerto Rico (Rivero 1978). It is nocturnally active with males vocalizing during all months of the year (Woolbright 1985). Fertilization is internal (Townsend et al. 1981) and males brood the eggs in terrestrial oviposition sites during the 2 - 3 wk period of direct development (Townsend et al. 1984).

The study was performed in the Luquillo Experimental Division of the Caribbean National Forest in northeastern Puerto Rico. The study site, adjacent to the El Verde Field Station, has been previously described (Woolbright 1985).

Body size

Snout-to-urostyle length (SVL) was used as the basic measure of coqui body size throughout this study. I measured SVL of living coquies by placing the frog inside a plastic bag and flattening the animal against a rigid surface. Body size was measured to the nearest 0.5 mm using dial calipers and measurements were repeatable to ± 1.0 mm.

Only reproductively mature animals were used for estimates of male and female body sizes. I judged animals to be mature when males were observed calling and when females had ova in any stage of development visible through the semi-transparent body wall. Measurements were taken during the mark-recapture study described under "growth rates". Because animals were individually marked, it was possible to ensure that only one measurement per frog was included in the data set.

Male reproductive success

To circumvent the problem of locating frogs in the forest, I measured male reproductive success in plots established for studies of population density (Stewart and Pough 1983). Because coquies in these plots preferentially use artificial cavities made of bamboo for both nest sites and diurnal retreats, it was possible to census plots during the daytime with confidence that

all frogs in the local population would be located. I searched each of four house plots in August, 1982. During plot checks I examined each retreat and captured and measured all frogs located. Males were distinguished by the presence of either an enlarged vocal sac or vocal slits in the floor of the mouth. I noted whether an egg clutch was present in the retreat with each male. To avoid disrupting ongoing population studies, I did not collect egg clutches to count the number of eggs. Clutch frequency data were analyzed by chi square (Sokal and Rohlf 1969).

Growth rates

Growth rates were measured in the field by mark-recapture in a 250 m² plot. The plot was censused on several nights each January and July from July 1981 to January 1984. I marked frogs by clipping a unique combination of toes. Frogs were measured on the first night of each field season that the frog was captured. I calculated growth rate as change in SVL divided by the number of days since the frog was last measured. The relationship between growth rate and frog body size was estimated by least squares regression (Sokal and Rohlf 1969).

To determine growth rates in the laboratory, I transported 20 male and 10 female coqui to Albany and housed 10 frogs of the same sex in each of three 50 gallon terraria. Frogs were given retreat sites (lengths of PVC pipe) but no additional structure that might have served as calling sites. Frogs were given food (crickets) and water ad libitum. Temperature was

maintained between 24.5 - 28 C with a 14:10 LD cycle. I measured SVL at the beginning of the experiment and again four months later, and calculated growth rates as above. The Pearson product moment correlation coefficient (Sokal and Rohlf 1969) was used to test for a relationship between body size and laboratory growth rates. I used the Mann-Whitney U test (Siegel 1956) to compare growth rates that were independent of body size.

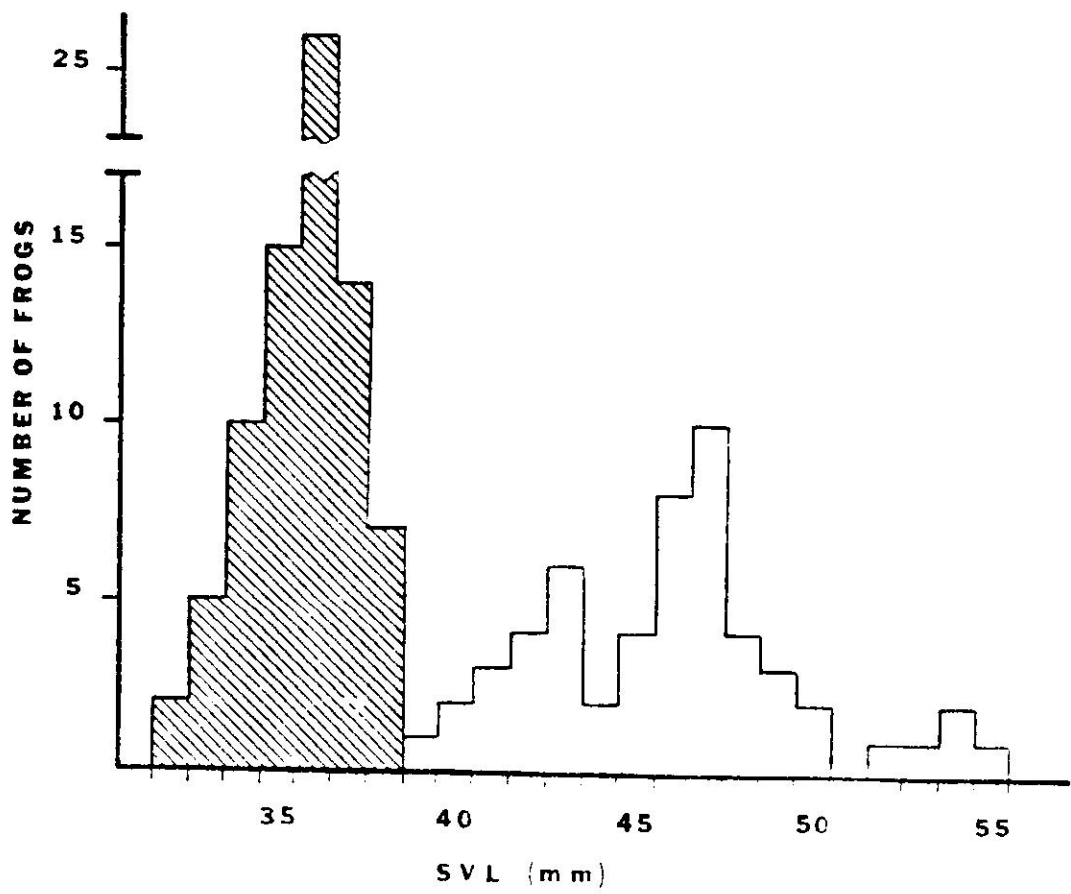
Confidence intervals of regression equations were calculated by methods given in Sokal and Rohlf (1969). A significance level of $\alpha = 0.05$ was used throughout.

RESULTS

Body size

Mean SVL of reproductively active females (eggs visible through the body wall) was 45.9 mm (SE = 0.50, n = 54). Reproductively active males (observed calling) averaged 35.6 mm SVL (SE = 0.16, n = 79). Thus females were 29% larger than males in this population. Distribution of male and female body sizes (Fig. 1) indicates that females delay reproductive activity relative to males. Males were found calling at body sizes as small as 32 mm SVL, but the smallest female with visible eggs was 39 mm SVL. When combined with growth rates (see below), these estimates suggest that females postpone reproductive activity for about 101 days past the body size at which the first males start to call.

Fig. 3.1. Body sizes of reproductively mature male (shaded bars) and female (open bars) E. coqui found during the mark-recapture study.

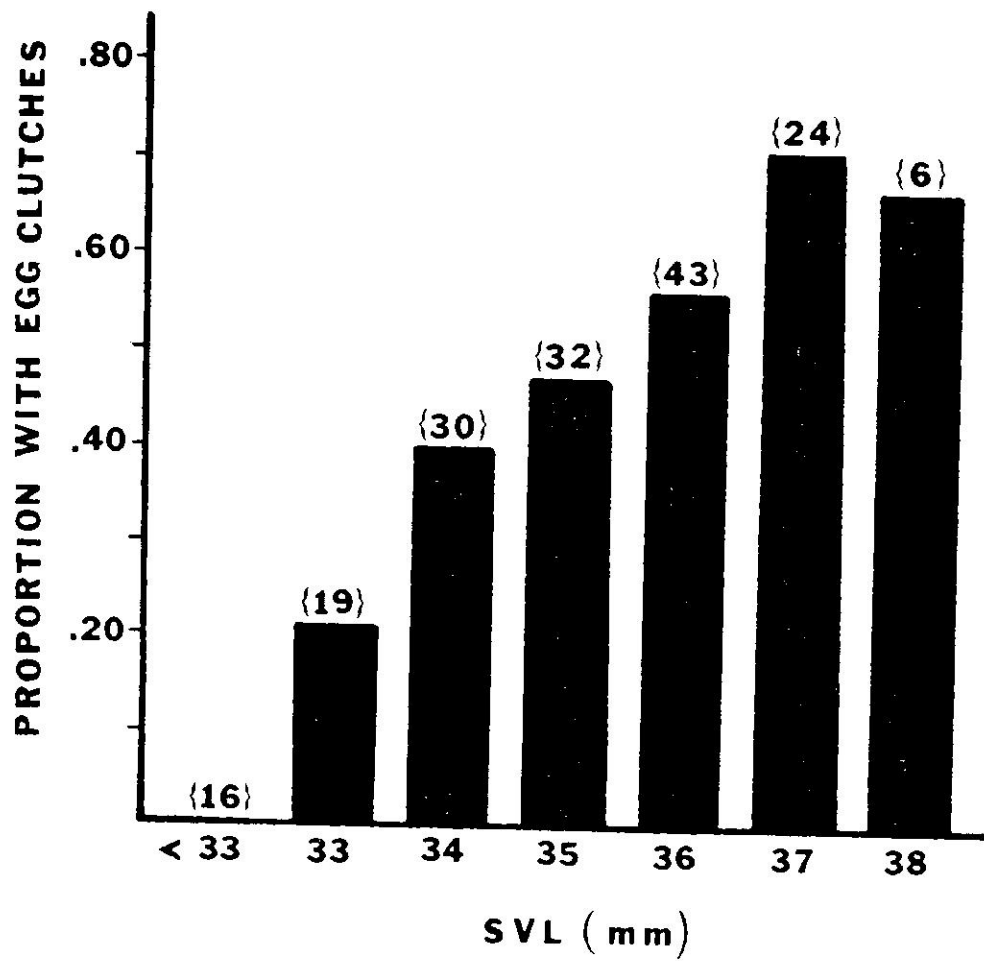


Male reproductive success

Plot surveys showed that large males were more likely to have egg clutches than were small males ($\chi^2 = 27.48$, $p < 0.005$, 4 df; Fig. 2). To transform these data to an index of reproductive success comparable to the relationship between female body size and clutch size, I assumed that the proportion of males that had eggs in each size class was equivalent to the probability of mating for that size class during a period of time equal to the average development time of eggs. For example, since 50% of the 35 mm males had clutches, each 35 mm male had a probability of 50% of obtaining a mate at some time during the 19.4 day incubation period (mean calculated from data in Townsend 1984). I also assumed that clutch size did not vary with male size (i.e. that all clutches were equal to the population mean of 28.1 eggs reported by Townsend 1984). Since females lay eggs about every six weeks (D. S. Townsend, personal communication) I multiplied the proportion of males with eggs in each size class by 2.16 to give the expected number of clutches per male per six weeks. I then multiplied expected number of clutches by the mean clutch size to give the expected number of eggs per male per six weeks.

The resulting estimates were significantly related to body size (least squares regression equation: $\text{eggs} = 6.26 \text{ SVL} - 192.3$, $r^2 = 0.9365$, $p < 0.01$). I calculated the 95% confidence intervals of the slope of clutch size as a function of female body size (from data in Townsend 1984) to be $0.514 - 1.106$. The slope of the expected number of eggs per six weeks for males

Fig. 3.2. The proportion of male coquies of various sizes found in attendance on egg clutches during daytime checks of house plots. Sample sizes for each size class are shown above the bars.



(6.26) is much greater than that for females (Fig. 3).

Growth rates

Field growth rates were significantly related to body size for both males (rate = -0.002 SVL + 0.08 , $F = 8.99$, $p < 0.01$, $n = 31$) and females (rate = -0.004 SVL + 0.21 , $F = 513.67$, $p < 0.001$, $n = 18$). Growth rates of both sexes declined with increasing body size, but adult females grew at much faster rates than adult males at all body sizes (Fig. 4). Male growth stopped at about 38 mm SVL but females continued to grow to sizes greater than 50 mm SVL.

When kept isolated by sex in the laboratory, growth rates were no longer correlated with body size for either males (Pearson $r = 0.03$, $p > 0.05$, $n = 14$) or females ($r = 0.18$, $p > 0.05$, $n = 9$). Male growth rates were greater than those of females kept in the laboratory (Mann-Whitney $U = 20$, 2-tailed $p < 0.05$, $n = 23$) but similar to field growth rates for females of similar body sizes (Fig. 4). After only four months in the laboratory, male body size averaged 42.0 mm SVL (SE = 0.38), and all experimental males had attained body sizes larger than males found in the forest.

DISCUSSION

My results suggest that models including only simple indices of sexual selection pressure, such as the presence of male combat (Shine 1979), are not likely to be successful in predicting anuran size relations. Even by including consideration of a

Fig. 3.3. Estimated relationship between reproductive success (number of eggs per 6 wk) and body size for E. coqui. Solid line is females (from Townsend 1984). Dotted line is males (see Results for calculation).

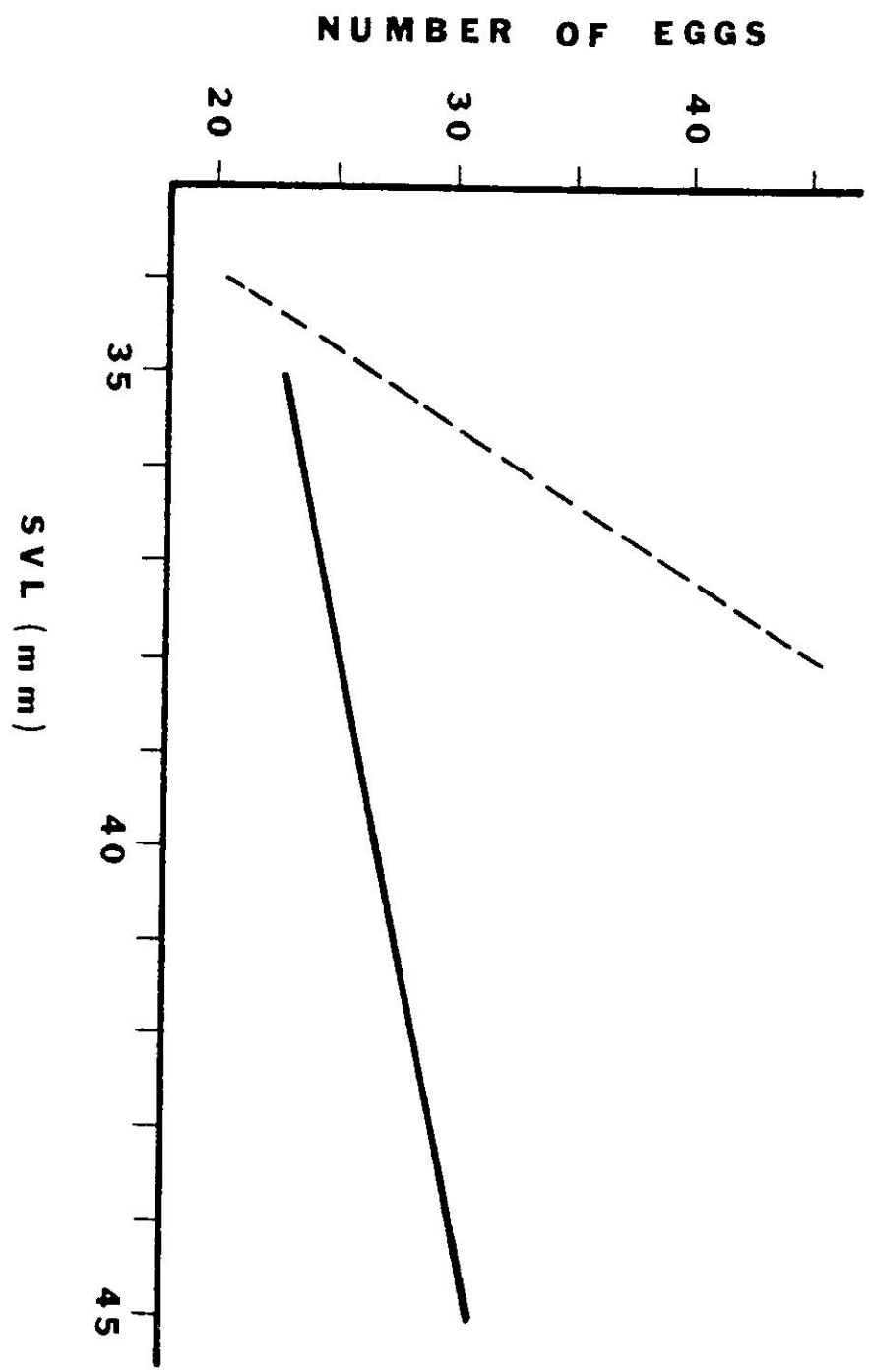
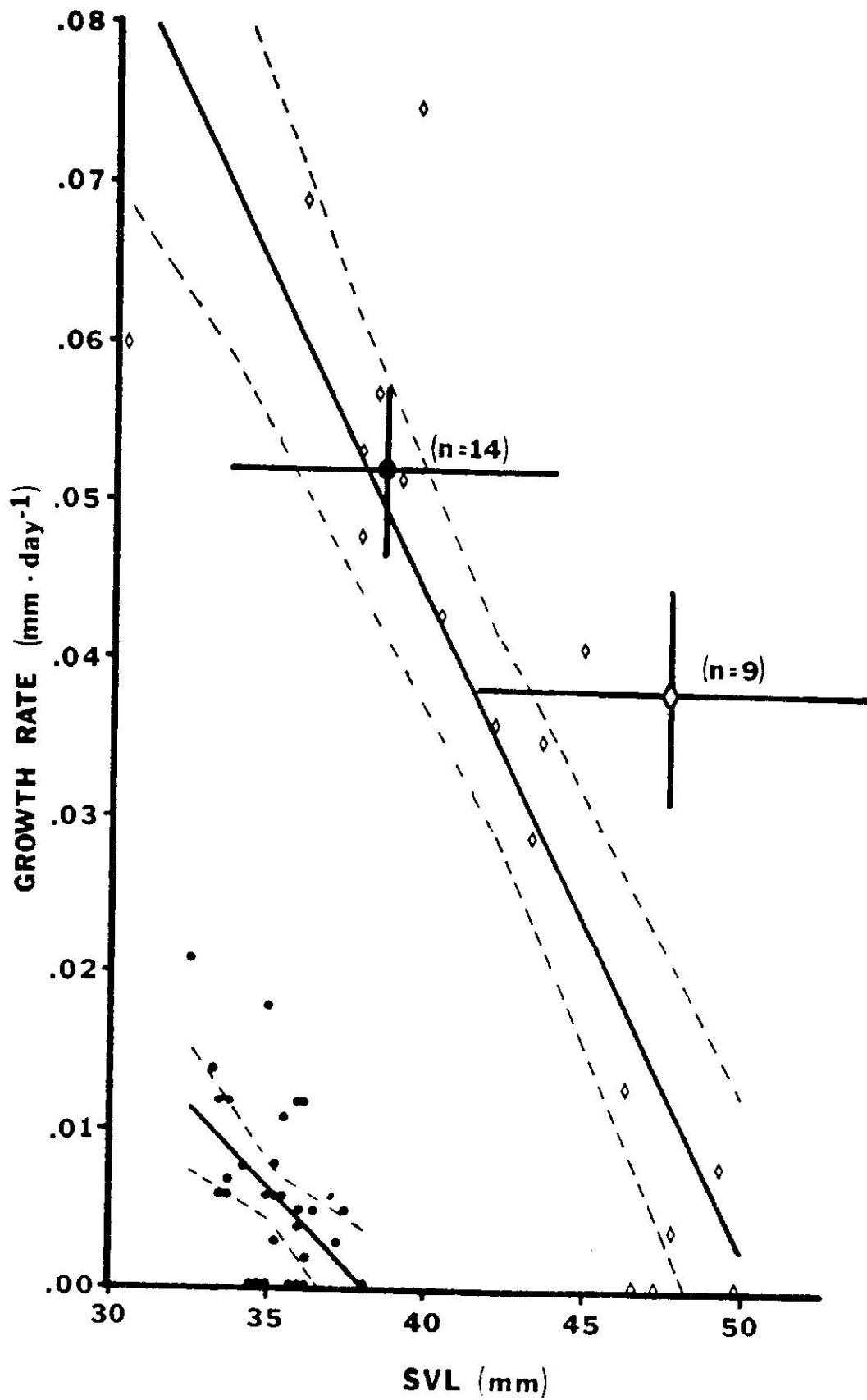


Fig. 3.4. Growth rates of male (circles) and female (diamonds) E. coqui. Small symbols are growth rates in the field, shown with least squares regression lines and 95% confidence intervals. Large symbols are means of laboratory growth rates, shown with sample sizes (n), 2 SE (vertical bars), and SVL ranges (horizontal bars).



large female advantage, I have still been unable to predict that female coquies should be larger than males. Nevertheless, they are. The selective advantage of large female size may explain why females appear to delay the onset of reproductive activity, but it does not explain why males should be smaller than females.

The most numerous coqui predators are invertebrates that appear to be more successful eating small frogs than large ones (Formanowicz et al. 1981). Known vertebrate predators include the snake, Alsophis portoricensis, (personal observation) and three birds, the pearly-eyed thrasher, the red legged thrush, and the Puerto Rican screech owl (M. M. Stewart, personal communication). Two of the birds are diurnal and not likely to distinguish between male and female coquies as they scratch through the leaf litter. The owl is nocturnal and could potentially specialize on calling males. However I have not observed them foraging in the understory and females are the sex most likely to be found in the canopy (Stewart in press). Caged Alsophis readily take adult coquies of all sizes (unpublished data). Thus it seems reasonable to conclude that predators on the coqui do not prefer one sex over the other or large frogs over small ones.

Other selection pressures are possible. Larger females may produce more, as well as bigger, clutches. Although we have no data on frequency of oviposition by females, my estimates indicate that increasing male size by 1 mm increases reproductive success by a factor of 6. It seems unlikely that increasing female size would result in a six-fold increase in the number of

clutches laid.

Other aspects of the male selective regime may also be important. By using plots with a high density of retreats, I have eliminated many of the possible effects of male competition for nest sites. Males are also likely to be subjected to natural selection pressure on their parental care abilities including the ability to protect their eggs from desiccation and from potential predators (Taigen et al. 1984, Townsend et al. 1984). It seems that large size should be favored by all of these selection components; thus my estimates of the large male size advantage may actually be conservative.

It is also possible that the observed size dimorphism is a result of historical rather than current selective regimes or that there is no phenotypic expression of male selection pressures. However, growth data suggest an ecological rather than an evolutionary mechanism. Male coquies stop growing at about the same size they start reproducing. I have recaptured nine mature males a year or more after they were initially marked without observing additional growth. Further, the cessation of growth appears facultative because growth resumes when males are kept in the laboratory and not allowed access to females.

These data are consistent with the hypothesis that size dimorphism in the coqui results from the constraint of male growth by the energetic demands of male reproductive behavior (Woolbright 1983). Recent evidence suggests that acoustic advertisement by male anurans may be the most energetically demanding activity regularly undertaken by ectothermic

vertebrates (Bucher et al. 1982, Taigen and Wells in press). In addition, male coquies do not feed while calling (Woolbright 1985) thus reducing their total foraging success (Woolbright in prep.). Townsend (1984) reported that parental males may lose up to 20% of their body weight during the period of parental care. It seems likely that the sum of all these effects may pre-empt a considerable amount of energy that would otherwise be available for growth. A definitive test of this hypothesis will require measurement of the cost of calling to male foraging success and a comparison of the energetic requirements of male reproductive activities to the cost of egg production for females.

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Chapter IV

Foraging success of a tropical frog:

The cost of calling

ABSTRACT

Foraging success of Eleutherodactylus coqui was estimated from stomach contents. Stomach content volume increased with frog body size as a result of the selection of larger prey by larger frogs. Number of prey per stomach was inversely related to body size. Non-calling frogs had eaten most of their night's food by 2400 h. Males called mainly before midnight and did not forage while calling. Calling males had eaten only 18% of their night's food by 2400 h. Calling males ate prey that did not differ in size from those of non-calling animals. However, they ate fewer prey items and ended the night with less food volume in their stomachs than expected for their body sizes. Foraging success was lower during the dry season than the wet season, but calling males had higher success relative to non-calling frogs because they called for shorter periods of time. On a yearly basis, I estimated that males lose 16% of their potential food intake because of calling activity.

Key words: Amphibia; Anura; Leptodactylidae; Eleutherodactylus coqui; foraging success; prey selection; calling; seasonality; Puerto Rico

INTRODUCTION

Sexual advertisement by male anurans is an important part of mate attraction in most species. However, it may also be a very costly activity, increasing the risk of predation (Jaeger 1976, Ryan et al. 1982, Tuttle and Ryan 1981, Tuttle et al. 1981) and elevating metabolic rates (Bucher et al. 1982, Taigen and Wells In press). In addition, Woolbright (1983) suggested that the act of calling may limit foraging opportunity, thereby reducing energy intake as well as increasing energy expenditure. However, evidence that male anurans do not feed while calling (reviewed in Woolbright 1983) is largely circumstantial, and no previous study has attempted to determine whether calling reduces the total foraging success of males. I examine early morning stomach contents of Eleutherodactylus coqui Thomas (Anura: Leptodactylidae) and test the hypothesis that males consume less food on nights that they call than would be expected if they did not call.

Prey size (and therefore, potentially, foraging success) increases with body size in several species of anurans (Brooks 1964, Houston 1973, Labanick 1976, Strussman et al. 1984). I examined the relationship between body size and prey size, number of prey, and total volume of stomach contents for non-calling coquies. I then compared to these relationships the stomach contents of males known to have been calling the previous night. Because rainfall in the Luquillo mountains is weakly seasonal (Odum et al. 1970), all comparisons were made in both the wet season (April - December) and the dry season (January - March).

METHODS

Study species and site

Eleutherodactylus coqui Thomas is an arboreal leptodactylid frog common throughout Puerto Rico (Rivero 1978). The coqui is active from dusk to dawn with most calling activity occurring before midnight (Woolbright 1985). Males call from stationary locations in the forest understory during all months of the year although less calling occurs during the dry season (Woolbright 1985). Coquies have internal fertilization (Townsend et al. 1981) and male parental care of eggs (Townsend et al. 1984). Growth occurs all year round and juveniles reach reproductive maturity in approximately one year (Woolbright, unpublished data). Male coquies stop growing soon after reaching maturity while females continue growth and reach much larger body sizes (Woolbright, in prep).

The study was performed in 1981 and 1982 in the Luquillo Experimental Division of the Caribbean National Forest in northeastern Puerto Rico. The study area is located at 370 m elevation adjacent to the El Verde Field Station in a second growth forest predominated by tabanuco (Dacryodes excelsior), Cecropia peltata, and sierra palm (Prestoea montana). Rainfall data were obtained from instruments at the field station.

Stomach contents

Whole night foraging success was estimated from frogs collected at 0600 h. To distinguish males that had been calling earlier in the evening, I marked calling and non-calling frogs at

2100 h on the evening before collection by sprinkling them with different colored fluorescent pigments (Scientific Marking Materials, Seattle). As frogs returned to their diurnal retreats the following morning they were relocated with a portable ultraviolet light that caused the pigments to glow. Because practically no males start calling later than 2100 h (Woolbright 1985), non-calling samples should contain few, if any, animals that had called during the night. Stomach contents were taken from calling males and from obvious females (eggs visible through body wall) using a stomach pump (Legler and Sullivan 1979) and these animals were released the following night. Because it is difficult to determine the sex of small frogs, non-calling adults that were not obviously female were killed and dissected. Stomachs were removed and sex was determined by inspection of the gonads. Wet season 0600 h samples were collected on five nights during July and August (range = 8 - 15 frogs/night) and dry season samples on four nights in January (range = 6 - 14 frogs/night).

I measured the temporal pattern of foraging success by collecting additional samples at 2100 h and 2400 h. These samples were taken on six nights during July and August (range = 14 - 18 frogs/night) and on four nights in January (range = 18 - 25 frogs/night). Non-calling adults collected at 2100 h in the dry season were killed and dissected to identify non-calling males. All other samples included only calling males and obvious females which were released after stomach pumping.

To determine the time that prey remain in frog stomachs and

to evaluate the effectiveness of the stomach pumping technique, I held 53 frogs of various sizes in the laboratory without food for two days and then fed each frog from one to six arthropods. I pumped the stomachs of a sample of these frogs every two hours from 2 - 14 h after feeding. Any frog that did not yield its full complement of prey was dissected to see whether missing prey were in the stomach or the intestine.

Frog body size was determined by measuring the snout to urostyle length (SVL) of each frog to the nearest 0.5 mm using dial calipers. During measurement, frogs were held flat against a rigid surface, and measurements were repeatable to within 1 mm.

Stomach contents were preserved in 70% ethanol for later examination. The length and width of each prey item were measured to the nearest 0.1 mm using an ocular micrometer. The volume of each prey item was calculated using the formula for a cylinder. Total volume per stomach was calculated as the sum of individual prey volumes.

Behavioral observations

To relate trends in foraging success to frog behavior, I observed 22 coquies in the field for continuous periods of 15 min each. Observations were made using a flashlight covered with a red filter. During observations, I noted the number of arthropods that passed within 5 cm of the frog and whether each was pursued. The number of prey observed per unit time with this method was greater than that ordinarily available to the frogs because flying insects were attracted to the flashlight. However

there is no reason to suspect that this altered the frogs' reaction to these prey.

Data analysis

Regression equations were estimated using the method of least squares. Regressions were compared using an F test for slopes (Sokal and Rohlf 1981) and a t-test for adjusted means (Dixon and Massey 1969). Relative success of calling males was evaluated by using the sign test (Siegel 1956) to compare observed values to size-specific predictions based on regression equations for non-calling animals. Data not dependent on body size were compared by analysis of variance if parametric assumptions were likely to be met. Otherwise I used non-parametric Mann-Whitney U-tests (Siegel 1956) for two groups or Kruskal-Wallis one-way ANOVA by Ranks (Siegel 1956) for three groups. Correlation was by Pearson product-moment coefficients and frequency data were analyzed by Chi square. A significance level of $\alpha = 0.05$ was used throughout.

RESULTS

Stomach passage time

In the laboratory, stomach pumping within 6 h after feeding produced all prey items intact. After 8 hours, some recovered prey items were fragmented and after 14 hours most were not recovered (Fig. 1). Dissection revealed no prey items left in the stomachs of frogs after pumping.

Effect of body size

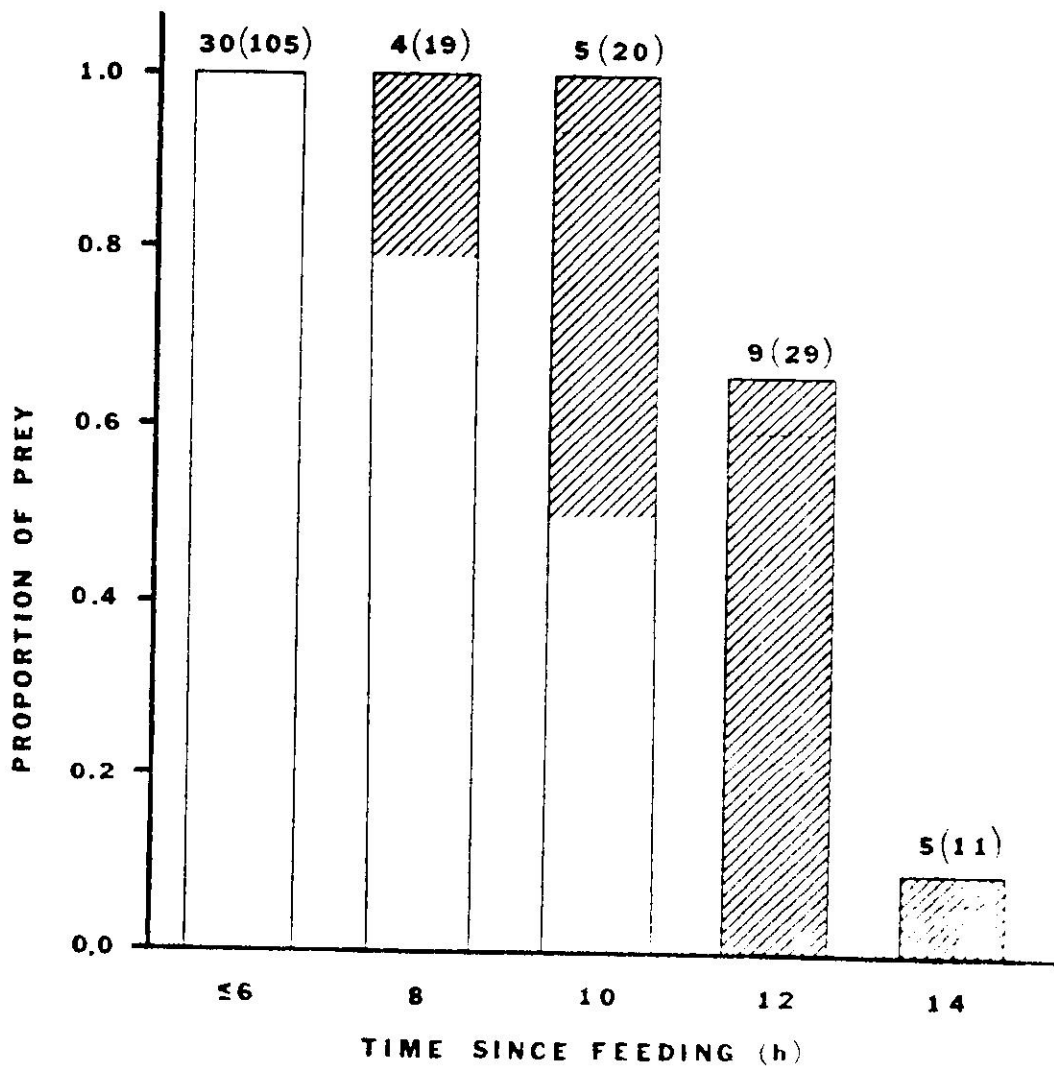


Fig. 4.1. Stomach passage time in E. coqui. The proportion of prey fed to coquies that were recovered by stomach pump from 8 - 14 h after feeding. Open bars represent prey that were recovered intact. Closed bars are prey that were fragmented but still identifiable. Sample sizes shown above each bar are number of frogs (number of prey).

For females and non-calling males taken at 0600 h, body size was a good predictor of mean prey size as well as size of largest and smallest prey items (Fig. 2). In the wet season, body size also predicted the number of prey found in a frog's stomach ($\text{No. prey} = 18.4 - 0.36 \text{ SVL}$, $F = 19.1938$, $p < 0.001$). Large coquies eat one or two large prey while small frogs eat several smaller prey. In the dry season, however, this correlation was not significant (Pearson $r = -0.0989$, $p > 0.05$).

Total volume of stomach contents was highly dependent on body size in both the wet season ($\text{Vol.} = 59.5 \text{ SVL} - 1874.5$, $F = 10.4822$, $p < 0.005$) and the dry season ($\text{Vol.} = 34.0 \text{ SVL} - 1080.8$, $F = 14.7629$, $p < 0.001$).

Seasonality

The slopes of the wet and dry season regressions of total volume on body size did not differ seasonally ($F = 0.7945$, $0.25 < p < 0.50$). The common slope was 45.8. However, adjusted mean volume was significantly higher in the wet season than in the dry season ($t = 2.11$, $p < 0.05$).

The size of prey taken in the two seasons did not differ (Mann-Whitney $U = 7872.5$, $z = 0.817$, 2 tailed $p = 0.41$). However, frog stomachs contained more prey in the wet season (median = 3) than in the dry season (median = 2; Mann-Whitney $U = 386$, $z = 2.23$, 2 tailed $p = 0.026$).

By 0600 h, most frogs (90%) had food in their stomachs regardless of weather conditions. However, 10 of 50 frogs (20%) still had empty stomachs in January as opposed to 1 of 57 frogs

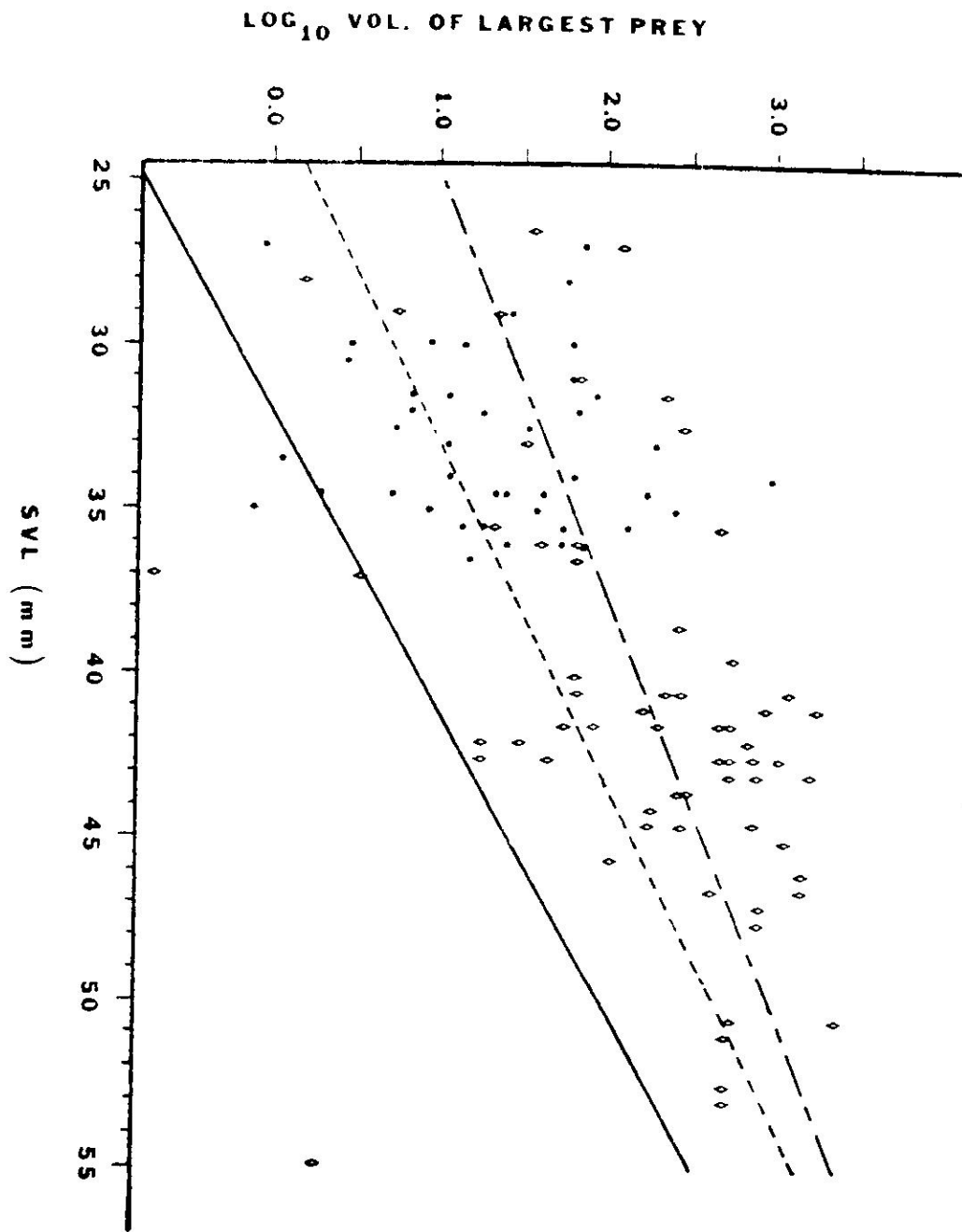


Fig. 4.2. Relationship between body size and prey size for non-calling adult E. coqui. Points are volume of the largest prey item in each frog's stomach. Top line is volume of largest prey ($\log \text{Vol.} = 0.09 \text{ SVL} - 1.50$, $F = 33.2409$, $P < 0.001$). Middle line is mean prey volume per stomach ($\log \text{Vol.} = 0.10 \text{ SVL} - 2.23$, $F = 42.9170$, $P < 0.001$). Bottom line is volume of smallest prey ($\log \text{Vol.} = 0.11 \text{ SVL} - 3.55$, $F = 20.8896$, $P < 0.001$). Seasons are combined because prey size did not vary seasonally.

(2%) in July. Frogs were more likely to have empty stomachs at 0600 in January than in July ($\chi^2 = 9.614$, $P < 0.005$). For samples collected at 2100 and 2400 h, the proportion of empty stomachs in a sample was directly related to the previous three days rainfall (Fig. 3).

Behavioral observations showed that frogs in the water-conserving posture, most common during the dry season (Pough et al. 1983), were less likely than frogs in active postures to pursue potential prey items ($\chi^2 = 14.505$, $P < 0.005$, Table 1).

The cost of calling

In the wet season, stomach content volume of calling males collected at 0600 h was not correlated with body size (Pearson $r = 0.0759$, $P > 0.05$). Comparison of volumes with values generated from the regression for non-calling animals showed that 17 of 21 calling males had less food than expected for their body sizes (sign test: 1-tailed $P = 0.004$). The sum of stomach content volumes for the sample of calling males (4031.6 mm^3) was 65% of the sum of expected values (6194.6 mm^3). Prey size did not differ from values generated from the regression for non-calling frogs: 10 of 21 calling males had mean prey volumes smaller than expected while 11 had mean prey volumes larger than expected (sign test: 1-tailed $P = 0.50$). However, 19 of the 21 calling males had fewer prey items in their stomachs than expected for their body sizes (sign test: 1-tailed $P < 0.001$).

Behavioral observations indicated that calling males were

Fig. 4.3. Relationship between the previous 3 days rainfall and percent of empty stomachs in samples of E. coqui collected at 2100 h and 2400 h. ($Y = 41.4 - 3.9 X$, $r = 0.63$, $P < 0.05$)

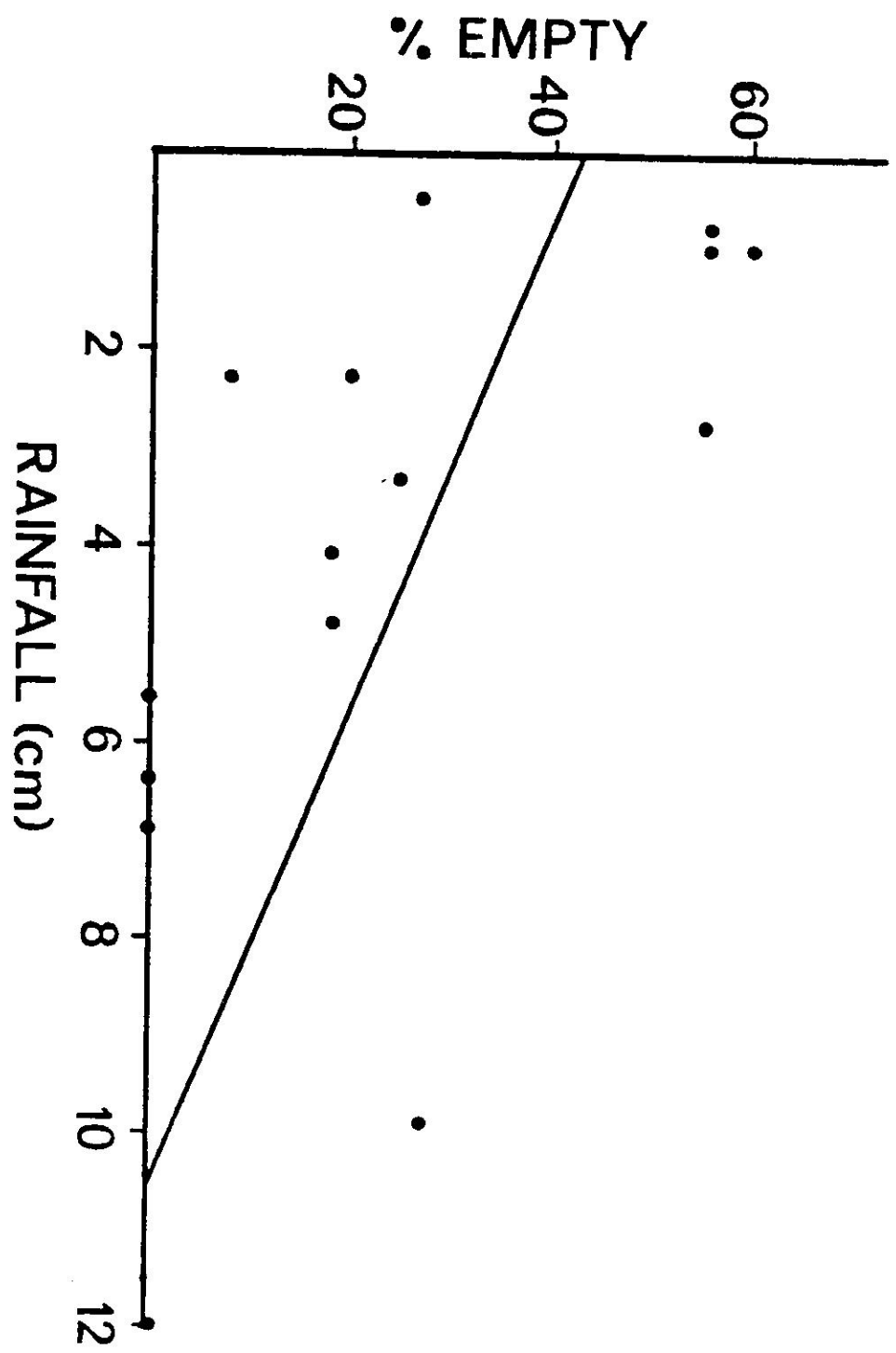


Table 4.1. The effect of calling and the water-conserving posture on the probability of pursuit of 26 potential prey items by Eleutherodactylus coqui.

	prey pursued	prey ignored
active postures	11	3
calling	1	11
water-conserving postures	0	10

significantly less likely to pursue potential prey than were non-calling frogs ($\chi^2 = 12.827$, $p < 0.005$, Table 1).

Comparisons of stomach contents of calling males collected in the dry season could not be performed as they were for wet season data because a large portion of the sample was inadvertently released without being measured. However 7 of 10 calling males had stomach content volumes less than expected for a body size of 34 mm, the smallest male in the other calling male samples. Therefore it is likely that the dry season pattern is the same. Assuming that the mean body size of this sample was the same as that of the other calling male samples (see below), the sum of dry season calling male stomach contents (1373.4 mm³) was 81% of the expected total (1699.1 mm³).

Temporal trends

There was no significant difference in body size between samples collected at different times of night or in different seasons for either calling males (one-way ANOVA: $F = 1.1952$, $p > 0.25$) or non-calling males ($F = 0.8380$, $p > 0.25$). Therefore temporal comparisons for these groups were made without adjustment for body size. Female body size did differ among groups ($F = 3.4546$, $p < 0.01$). I therefore adjusted total volume for each female to a standard body size of 40 mm before making temporal comparisons.

Total prey volumes in stomachs of females collected at 2100 h and 2400 h did not differ from those collected at 0600 h either in the wet season (Kruskal-Wallis $H = 1.145$, $p > 0.30$) or in the

dry season ($\underline{H} = 0.095$, $\underline{P} > 0.95$). The single available comparison for non-calling males (2100 h and 0600 h, dry season) also showed no difference in total volume (Mann-Whitney $\underline{U} = 119$, $\underline{P} > 0.05$). Stomach content volume of calling males increased significantly during the night in the wet season ($\underline{H} = 9.067$, $0.01 < \underline{P} < 0.02$) but not in the dry season ($\underline{H} = 0.348$, $\underline{P} > 0.80$). Mean stomach content volumes for all groups are shown in Table 2.

DISCUSSION

Results indicate that prey items pass out of a coqui's stomach 10 - 14 h after being ingested. Since the coqui's active period ranges from about 10 h in July to 12 h in January (Woolbright 1985), samples collected at 0600 h should contain essentially all prey eaten during the preceding night. Thus these samples should be reasonable estimates of total nightly foraging success. Results also suggest that stomach contents obtained by stomach pump are directly comparable to those obtained by dissection.

The coqui is an extreme sit-and-wait predator. It moves very little during the night and prey capture attempts usually involve movements of less than 5 cm (Woolbright 1985). Ecologically it fits well with Toft's (1980, 1981) characterization of sit-and-wait predators among the diurnal anuran litter communities in Peru and Panama: it eats few large, soft-bodied prey, and is cryptic and palatable. The coqui's exercise physiology is also consistent with the view that sit-and-wait anurans have high anaerobic capacities, low aerobic

Table 4.2. Stomach content volumes (mm³) of female, calling male and non-calling male *E. coqui* collected at three times of night in both wet and dry seasons. Entries are mean \pm 1 SE (n). * denotes the omission of a frog with an abnormally large prey item.

	Calling males	Females	Non-calling males
Wet Season:			
2100 h	25.9 \pm 10.8 (10)	328.2 \pm 175.8 (5)*	-----
2400 h	34.3 \pm 16.1 (19)	522.4 \pm 130.8 (13)	-----
0600 h	191.9 \pm 64.6 (21)	520.8 \pm 122.7 (20)	246.2 \pm 102.1 (16)
Dry Season:			
2100 h	102.0 \pm 56.8 (18)	180.7 \pm 119.3 (7)	62.2 \pm 38.0 (14)
2400 h	73.3 \pm 44.3 (6)	351.5 \pm 95.2 (14)*	-----
0600 h	137.3 \pm 67.0 (10)	269.7 \pm 75.1 (20)	97.6 \pm 33.6 (20)

capacities, and low resting metabolisms (Taigen and Pough 1983).

Body size is a major determinant of foraging success in the coqui, with amount of food taken in during the night directly proportional to the size of the frog. The reason appears to be that large frogs eat larger prey rather than that they eat more prey items. Evidence suggests that large frogs actually take fewer prey than do small frogs. This probably explains why large females are able to fill up so early in the evening while smaller males cannot get their full night's complement of food even in the several hours after they stop calling. Because prey are eaten whole, it seems likely that limitations in handling ability (Schoener 1969) explain why small coquies do not eat larger prey. I have observed hatchling coquies in the laboratory attempt unsuccessfully to eat Drosophila and subsequently starve, apparently from lack of sufficiently small prey. Mouth width (= head width) has been shown to correlate with prey size in other groups of frogs (Toft 1980).

Foraging success is markedly seasonal. Although prey size does not differ seasonally, lower stomach content volumes in the dry season result from the consumption of fewer prey. A likely cause for the reduction in the number of prey is the water-conserving posture which interferes with active foraging. Frogs are more likely to be found in the water-conserving posture in the dry season when they are more subject to desiccation (Pough et al. 1983). Dry conditions have also been shown to limit foraging opportunity for terrestrial salamanders (Jaeger 1980). Our results showing the relationship between rainfall and

early evening foraging success are consistent with such an interpretation.

Male calling activity results in a considerable cost to foraging success. In the wet season, calling males forfeit about one-third of their expected nightly food intake, primarily because they end the night with fewer prey items than non-calling frogs. In the dry season, calling males take in about 80% of the food of similar sized non-calling frogs. This reduction in the cost of calling probably results from the fact that males call for shorter periods of time during the dry season (Woolbright 1985) and therefore have relatively more time left to forage.

Nevertheless, the total impact of calling on male foraging success is rather large. Assuming that males call on 56% of wet season nights and 29% of dry season nights (Woolbright 1985), a reproductively active male forfeits an average of about 16% of the food intake of a similar sized female on a yearly basis. For comparison, females use about 10% of their average daily intake for egg production (Woolbright unpublished data). When combined with the increased metabolic expenditures of calling, reduced energy intake may represent a large reduction in energy available for male growth and therefore help to explain why male coquies do not grow after reaching reproductive maturity.

Because the size of the smallest, as well as the largest, prey eaten increases with body size, there is very little overlap in prey eaten by frogs that differ by more than about 10 mm in body length. Because female coquies are about 30% larger than males (Woolbright unpublished data), the sexes overlap little in

prey eaten. However, the mechanism appears to be a continuous function of body size rather than strictly a function of sex as seen in other taxa (e.g. Amadon 1959, Selander 1972). In addition, we have evidence of temporal partitioning of the food niche. Calling males do most of their foraging after midnight while non-calling animals tend to feed early in the evening. This observation is consistent with differences in the timing of movements by the two groups and may result from a higher availability of receptive females early in the evening which has selected males that call (and therefore do not feed) during that time (Woolbright 1985).

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Chapter V

Patterns of nocturnal movement and calling
by the tropical frog, Eleutherodactylus coqui

ABSTRACT. Individuals of the terrestrial frog Eleutherodactylus coqui were followed throughout the night to determine patterns of movement and male calling activity. Individual male frogs were checked nightly for long-term calling patterns. Studies were performed in both January (dry season) and July (wet season). Total nightly movements averaged 3.0-4.5 m. Movement was most frequent shortly after dusk and shortly before dawn. Frogs were more likely to move when foliage was wet. Males and females did not differ in amount of movement, but calling males differed from non-calling animals in the timing of their movements. Males were unlikely to move or forage while calling. Males spent more time calling in the wet season than in the dry season. Movement patterns were only slightly seasonal. Timing of male calling activity agreed qualitatively but not quantitatively with predictions of female availability.

Key words: Anura; Leptodactylidae; Eleutherodactylus coqui;
Movement; Calling; Seasonality; Puerto Rico

Studies of anuran movements are important in understanding population dynamics. Daily movements are related to problems of obtaining food, shelter and mates and regulating body moisture. Studies of anuran movement patterns are common (e.g., Bellis, 1959, 1962, 1965; Beshkov and Jameson, 1980; Clarke, 1974; Dole, 1965, 1967; Dole and Durant, 1974; Harris, 1975; Ingram and Raney, 1943; Jameson, 1955; Kramer, 1973; Martof, 1953a; Pearson, 1955; Raney, 1940; Stille, 1952). However, most workers have estimated movement by the distance between recapture points. Few have monitored the movement of individual animals throughout the activity period (but see Dole, 1965; Higginbotham, 1939; Kramer, 1973). Most work has been done on North American species, many of which hibernate during the winter and migrate to or from breeding grounds during the spring and summer. I report the timing and distance of movements of individual Eleutherodactylus coqui Thomas (Leptodactylidae) throughout the night. I examine responses to environmental conditions and sexual differences in movement patterns.

In addition, I report the timing of calling throughout the night by male coquies. The diel pattern of chorusing is one aspect of anuran mating strategies that has received very little attention. Calling is important to males of most species in attracting mates but may also increase the risk of predation (Jaeger, 1976; Ryan et al., 1982; Tuttle and Ryan, 1981; Tuttle et al., 1981) and is an energetically costly activity (Bucher et al., 1982; MacNally, 1981). Thus one might expect natural selection to favor males that call only during times when they

are most likely to attract mates.

Walker (1983) proposed a model of diel calling times for chorusing Orthoptera that is a temporal analog of Fretwell's (1972) ideal free distribution. Walker suggested that males should time their calling to maximize the probability of mate attraction and minimize acoustical interference from other males. His prediction is that the number of males calling at a given time should be proportional to the number of females available at that time. I compare the observed diel calling pattern of male coquies to a predicted frequency distribution of female availability. I also examine patterns of calling by individual males for several nights.

The Luquillo Mountains of Puerto Rico are weakly seasonal, with average rainfall from January through March about one third less per month than the rest of the year (Odum et al., 1970). I compare both calling activity and movement patterns in January (hereafter called the dry season) to those of July (wet season) to examine the effect of seasonality on coqui activity.

METHODS

The coqui is a terrestrial frog common throughout Puerto Rico (Rivero, 1978). Frogs emerge from their diurnal retreats at dusk and are found on trees and shrubs until dawn. Males call from a stationary location until they are approached by receptive females. After mating, males brood the eggs until hatching and actively defend their nests against other frogs (Townsend et al., 1981, 1984).

The study was performed during January and July 1982 and January 1983 at the El Verde Field Station, located at 350 m elevation in the Luquillo Mountains of northeastern Puerto Rico. Mean daily minimum and maximum temperatures (± 1 SE) were 19.3 C (± 0.1) and 23.3 C (± 0.1) in January 1982; 21.9 C (± 0.1) and 26.3 C (± 0.1) in July 1982; and 19.4 C (± 0.1) and 22.8 C (± 0.1) in January 1983. Total rainfall was 139.7 mm in January 1982, 439.4 mm in July 1982, and 161.3 mm in January 1983.

All Night Movement and Calling Checks

On six nights in January and July 1982, I marked 12 - 20 adult coquies with fluorescent pigment (Scientific Marking Materials, Seattle, Washington) as they appeared shortly after dusk. Because of differences in the time of dusk, observations began between 1900 and 1930 h in January and between 2000 and 2030 h in July. I applied pigment to each frog's dorsum by shaking powder from a small vial held a few centimeters above the frog. Two colors were used to reduce the possibility of confusing frogs.

Frogs were categorized as either calling males (frogs that called at any time during a night), females (animals > 40 mm snout-vent length), or non-calling adults (male-sized frogs that did not call). Non-calling adults were not killed to determine sex, but a sample of this category killed during an unrelated study in 1981 showed that 50 of 70 frogs (71%) were males (Woolbright, unpublished data).

I located marked frogs every 15 min throughout the night using a portable ultraviolet light source (Raytech Industries, Stafford

Springs, Connecticut) which caused the pigments to glow. At each check, I noted the perch site and whether each frog was calling. I recorded any movement since the last check as a straight line distance to the nearest 5 cm. Total distance moved during the night was calculated as the sum of individual moves. Rainfall, temperature and the condition of the foliage surfaces were noted throughout the night. Total rainfall was recorded by instruments at the field station. Frogs appeared undisturbed by the periodic checks. Male calling activity usually continued uninterrupted, and I seldom observed escape behavior. Any disturbance introduced by the sampling technique was at least equal for all groups. Only frogs followed for the entire night were included in the analyses ($\underline{n} = 30$ each season; see Table 1 below).

Observations ordinarily ceased just before dawn when frogs began to disappear from the foliage (0530 - 0600 h). However, I followed some frogs to their diurnal retreats on January 15 ($\underline{n} = 10$) and July 9 ($\underline{n} = 7$). I examined those sites the following afternoons to insure that they were still occupied. I measured the distance from each site to the occupant's most distant perch of the preceding night.

To determine the significance of movements, I watched 22 coquies (10 calling and 12 non-calling) for continuous periods of 15 min each. Observations were made during the wet season between 2100 and 2400 h. I used a headlamp covered with a red filter to minimize disturbance, and did not include in the analysis any frogs that showed evasive behavior. During observations, I recorded the distance and apparent purpose of

each movement. I also noted any insects that passed within 5 cm of the frog and whether or not each was pursued.

Long Term Male Calling Activity

In July 1982 and January 1983, I marked male coqui by clipping a unique combination of toes. I checked frogs at least twice each night for at least 2 wk to determine which frogs were calling and what calling sites were used. The extended leg position of calling frogs makes it possible to check toe clips without capturing the animal, so disturbance was minimal. Checks were made between 2000 and 2200 h when calling activity was at its height. In July, 312 additional checks between 2300 and 0200 h revealed only four calling frogs that had not been calling earlier. Therefore these later checks were discontinued.

In July, nine males were observed for a mean of 24 consecutive nights (range = 15-29). In January, nine males were observed for a mean of 17 consecutive nights (range = 14-19). If a frog was not found in one of his usual calling sites, a radius of 2-3 m around known calling sites was searched and all frogs were inspected for marks. Frogs were located in this manner on 39% of the nights that they were not calling in July and 60% in January. Frogs not located during checks were assumed not calling.

Calculation of the Female Availability Curve

Walker (1983) assumed that females become receptive at a constant rate throughout the 24 h diel cycle and that females maturing ova during the day postpone breeding until dusk. Following these assumptions, 4.2% (one twenty-fourth) of the

day's breeding females become receptive each hour, and 62.5% (accumulated over 14 daylight hours plus first night hour) are available during the first hour of darkness. An additional 4.2% become available each hour for the remainder of the night. The actual time that females mate (and thus are no longer available) depends on how long they spend in choosing and travelling to a male. D. S. Townsend (personal communication) observed 14 early evening courtships in the forest during 1979 and 1980. These courtships occurred an average of 77.5 min (SD = 59.6) after dusk. If we assume that these observations represent a normal distribution of choosing and travelling times for females available at the beginning of the evening, then 38.6% of receptive females actually contact mates within their first hour of receptivity, 37.5% make contact during the second hour, 19.6% during the third, and 4.3% during the fourth. (Areas under the normal curve were calculated from a table of distributions in Snedecor and Cochran, 1967.) Combining patterns of receptivity with choosing and travelling times gives rise to the predicted pattern of female availability (Fig. 3 below). This prediction was compared with the observed distribution of calling times for 14 males followed throughout the night during all-night movement and calling checks in July.

Statistical comparisons were performed using the Kruskal-Wallis one-way Analysis of Variance by Ranks (Siegel, 1956), the Mann-Whitney U-test (Siegel, 1956), the Chi Square test (Sokal and Rohlf, 1969), and the Pearson product-moment correlation (Sokal and Rohlf, 1969). A significance level of $\alpha =$

0.05 was used throughout.

RESULTS

Movement

There were no significant differences between calling males, females, and non-calling adults in distances moved or number of moves within either season (Table 1; Kruskal-Wallis one-way ANOVA; distance moved January: $\underline{H} = 1.39$, $\underline{P} > 0.30$; July: $\underline{H} = 1.58$, $\underline{P} > 0.30$; number of moves January: $\underline{H} = 1.10$, $\underline{P} > 0.50$; July: $\underline{H} = 2.99$, $\underline{P} > 0.20$). When group data within each season were pooled, no difference between the number of moves per animal in January and July was found (Mann-Whitney U test, $\underline{z} = 1.30$, one-tailed $\underline{P} = 0.097$). A number of frogs moved relatively longer distances in July than in January (Fig. 1), but the difference was not significant (Mann-Whitney U test, $\underline{z} = 1.48$, one-tailed $\underline{P} = 0.069$).

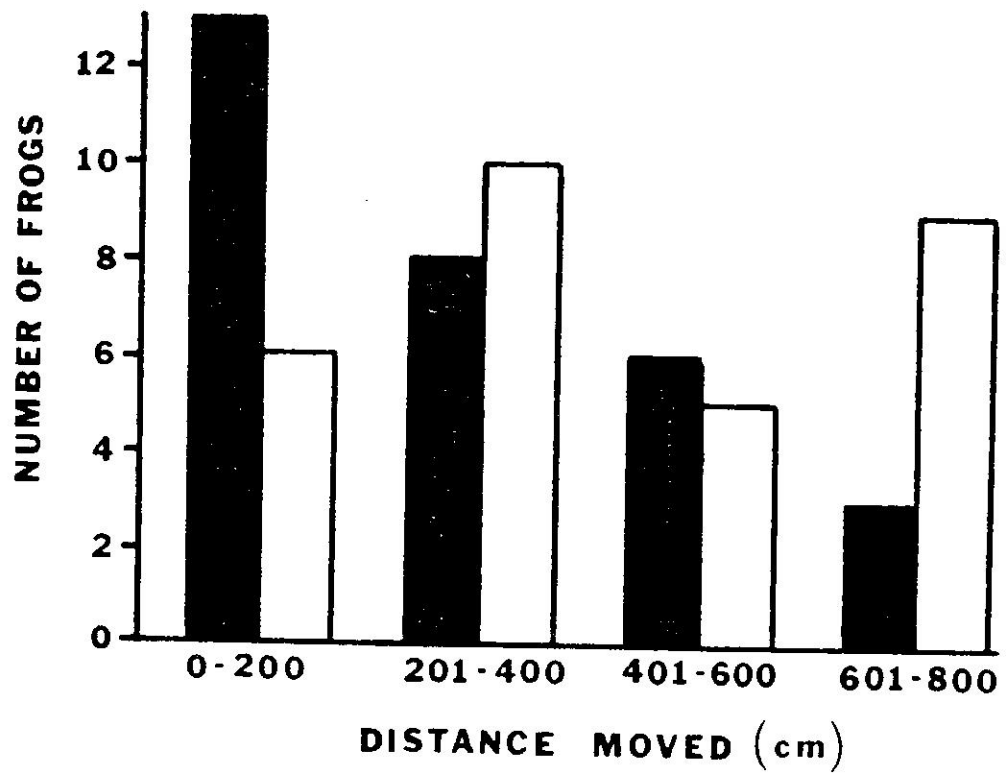
The proportion of frogs that moved during each hour was not correlated with either relative humidity (Pearson $\underline{r} = 0.2142$, $\underline{P} > 0.05$, $\underline{n} = 32$) or temperature (Pearson $\underline{r} = 0.08$, $\underline{P} > 0.05$, $\underline{n} = 32$). In July, frog movement was significantly associated with the condition of foliage surfaces: 57% of the frogs moved during hours when the foliage was wet compared to 35% when it was dry ($\underline{X}^2 = 11.967$, $\underline{P} < 0.005$, 1 df). In January, the distinction disappeared: 42% moved when the foliage was wet compared to 38% when it was dry ($\underline{X}^2 = 0.342$, $\underline{P} > 0.05$, 1 df).

Timing of movement was noticeably bimodal during both seasons (Fig. 2), with one period of increased activity in the early

Table 5.1. Mean distance moved (± 1 SE) and mean number of moves (± 1 SE) for individual E. coqui followed throughout the night in January and July, 1982.

Month	Sample	<u>n</u>	Distance (cm)	Number moves
January	Calling males	5	465 \pm 214	10.2 \pm 3.4
	Females	11	300 \pm 47	6.9 \pm 1.0
	Non-calling adults	14	244 \pm 59	5.6 \pm 1.0
	All frogs	30	301 \pm 50	6.9 \pm 0.9
July	Calling males	14	437 \pm 69	7.6 \pm 0.7
	Females	11	368 \pm 116	6.7 \pm 1.2
	Non-calling adults	5	668 \pm 307	11.4 \pm 2.4
	All frogs	30	451 \pm 76	7.9 \pm 0.8

Fig. 5.1. Total distance moved during the night by individual E. coqui. Solid bars are January, 1982 (dry season, $n = 30$); open bars are July, 1982 (wet season, $n = 30$).



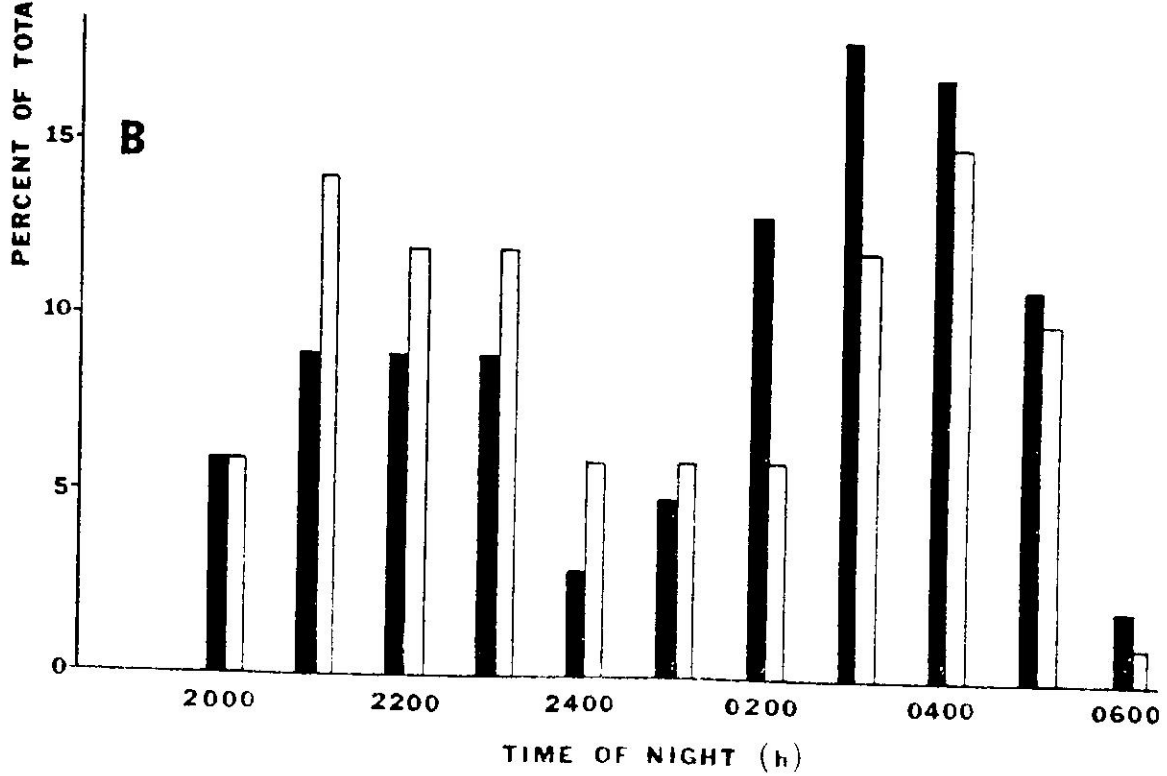
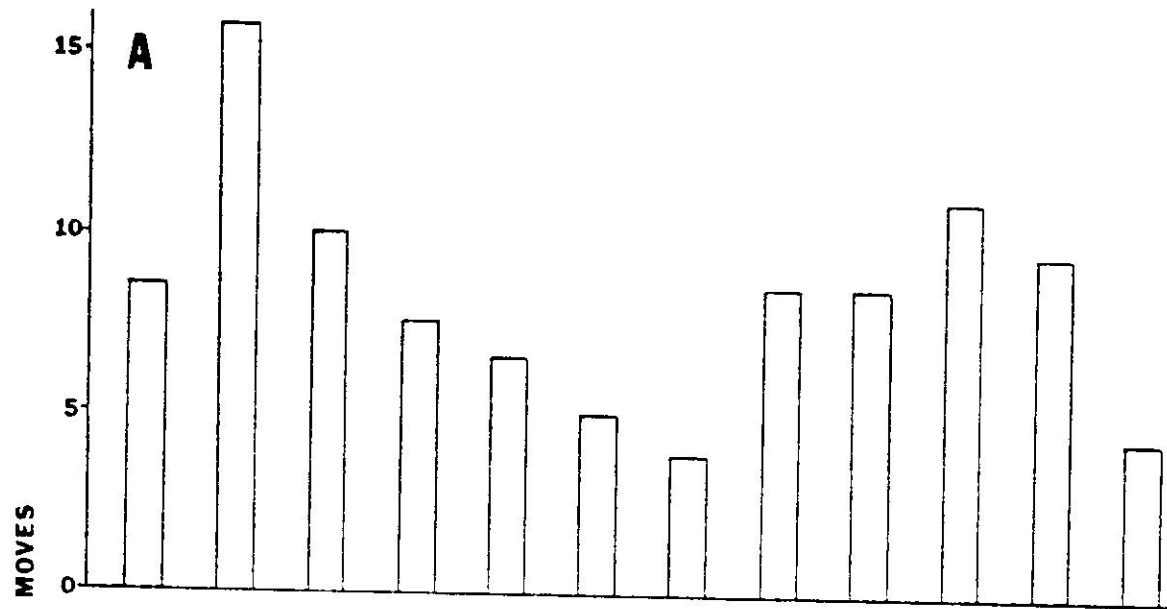
evening and another during early morning. In July, timing of movements differed between calling and non-calling frogs (Fig. 2B). Calling males made 40 of 115 moves (35%) before midnight while non-calling frogs made 72 of 141 moves (51%) during this time ($\chi^2 = 6.823$, $p < 0.01$, 1 df). No similar comparison was made for January data because of the small sample of calling males.

Seven frogs in July and 10 in January were followed into retreats on the morning following activity checks. All retreats were within 10 cm of the ground. In July, all frogs used cavities within curled leaves or between leaves and root surfaces. In January, six frogs used such retreats and four used crevices under or between rocks. The distance between a frog's retreat site and the most distant perch of the preceding night was significantly greater during the wet season ($\bar{x} = 172$ cm, SE = 27.1) than during the dry season ($\bar{x} = 113$ cm, SE = 8.9) (Mann-Whitney $U = 17$, one-tailed $p < 0.05$, $n = 17$).

During detailed behavioral observations, I observed a total of 18 movements. Six movements involved perch changes with no apparent purpose and covered distances of up to 20 cm ($\bar{x} = 7.5$). Twelve were associated with feeding attempts and covered distances of no more than 5 cm ($\bar{x} = 1.5$). Movements were performed almost exclusively by non-calling animals. Only two of the 18 movements were by calling males. I saw 26 insects pass within 5 cm of frogs during behavioral observations. Of the 12 insects associated with calling males, only one was eaten. Of the 14 insects associated with non-calling animals, 11 were

Fig. 5.2. Number of moves during each hour of the night as a proportion of the total number of moves recorded.

(A) January, 1982 ($\underline{n} = 30$ frogs). (B) July, 1982: solid bars are calling males ($\underline{n} = 14$); open bars are females and non-calling adults ($\underline{n} = 16$).



eaten. Calling males were significantly more likely to ignore these potential prey than were non-calling frogs ($\chi^2 = 12.83$, $p < 0.005$, 1df).

Male Calling Activity

In July, calling was most intense shortly after dusk and decreased throughout the night (Fig. 3B). Qualitatively the male calling pattern appears to match the prediction of female availability (Fig. 3A). However, males called less than expected during the early evening hours and more than expected during the early morning, and the two distributions are significantly different ($\chi^2 = 53.014$, $p < 0.005$, 9 df).

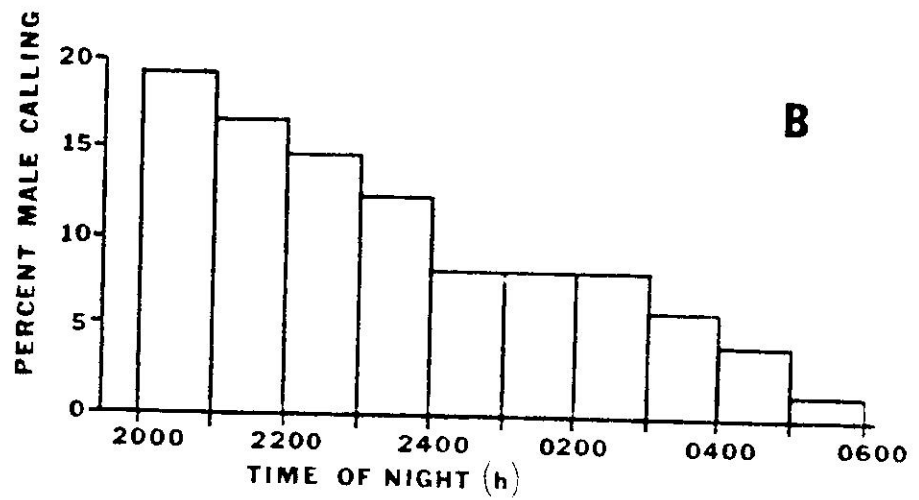
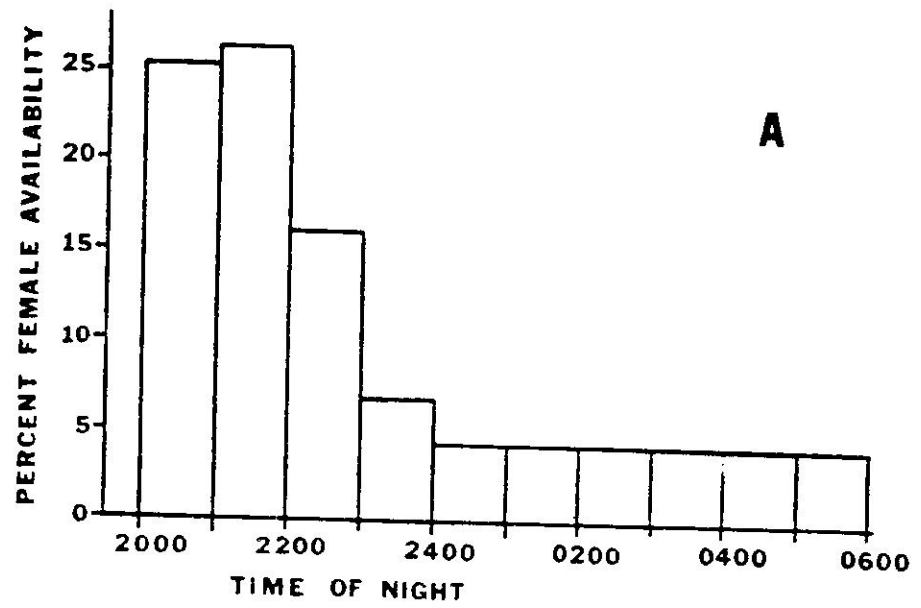
In July, 10 of 14 males began to call during the first hour after dusk. Males called for an average of 3.6 h (SE = 0.5) and moved little while calling ($\bar{x} = 1.4$ moves per frog, SE = 0.4). After calling, males averaged 4.5 h (SE = 0.6) of silent activity, during which they moved an average of 6.9 times (SE = 1.1). Movement was significantly associated with the non-calling period ($\chi^2 = 41.67$, $p < 0.01$, 1 df).

January patterns of calling activity were similar to those in July except that the calling period decreased to a mean of 2.7 h (SE = 0.54) and the non-calling period increased to a mean of 6.2 h (SE = 1.43). The difference in time allocation by males between seasons is significant ($\chi^2 = 13.21$, $p < 0.01$, 1 df).

Long-term Calling Patterns

In July, the number of nights that individual males called ranged from 37 - 79% of the nights checked. Overall calling frequency (frog-nights calling / frog-nights checked) was 56% of

Fig. 5.3. (A) Predicted availability of receptive females throughout the night. See methods for calculation.
(B) Percent of night's calling activity by hour.
Data are from 14 male E. coqui followed all night in July, 1982.



the nights. The proportion of males calling each night ranged from 20% to 83% and was significantly correlated with the daily minimum temperature (Pearson $r = 0.524$, $p < 0.01$, $n = 25$) but not with rainfall (Pearson $r = 0.381$, $p > 0.05$, $n = 25$).

In January, the number of nights that individual males called ranged from 6 - 50% of the nights checked, and overall calling frequency was 29% of the nights. Males called on significantly fewer nights in January than in July (Mann-Whitney $U = 8$, one-tailed $p < 0.01$). The proportion of males calling each night in January ranged from 0 - 67% and was not correlated with either temperature (Pearson $r = 0.159$, $p > 0.05$, $n = 19$) or rainfall (Pearson $r = 0.3176$, $p > 0.05$, $n = 19$).

Males used from 1 - 4 different calling sites during the months of observation. All calling sites for a given male were contained within a 2 m diameter.

DISCUSSION

Results indicate that the coqui is extremely sedentary. Individual coquies moved an average of 3 m per night in the dry season and 4.5 m per night in the wet season. Since these figures represent the total distance moved during the night regardless of orientation, they undoubtedly overestimate the straight line distance moved by an animal from his retreat of one day to that of the next. Such sedentary behavior is consistent with detailed observations of Rana pipiens (Dole, 1965), Pseudacris triseriata (Kramer, 1973), and Hyla cadaverina (Harris, 1975). In addition, however, the coqui does not migrate

to breeding sites, and mark-recapture studies show that individuals may be found in the same location season after season (Woolbright, unpublished data). M. M. Stewart (in press) found that a portion of the coqui population (largely subadults) climbs trees at dusk and remains in the canopy until dawn. Climbing frogs undoubtedly move much greater distances than those I measured, although I have no estimate of the magnitude of this difference.

Coqui movement appears to consist primarily of travelling from retreat to perch in the early evening and from perch to retreat in the morning. Average distance from retreat to most distant perch, doubled, accounts for 75% of the average total distance moved in January and 76% in July. Such movements probably explain the observed bimodal movement pattern (Fig. 2). The underlying low level of movement throughout the night probably represents foraging activity. Coquies eat an average of 3.3 prey per night (Woolbright, in preparation), and results from this study indicate that prey capture attempts usually involve movements of less than 5 cm. Thus foraging activity probably accounts for about half of the total number of moves made by a coqui during the night, but contributes very little in terms of total distance. These results are consistent with the characterization of the coqui as a sit-and-wait predator and may relate to its low aerobic capacity, low resting metabolism, and high anaerobic capacity (Taigen and Pough, 1983).

The trade-off between foraging activity and calling may explain the observed difference in timing of movements between

calling and non-calling coquies (Fig. 2B). Results show that males do not forage while calling, and that they move very little. Females appear to spend the early evening foraging and making associated movements while males spend that time in stationary calling activity and forage mainly during the early morning hours when female stomachs may be filling up. This scenario is supported by stomach content data that indicate that females have as much food in their stomachs at 2400 h as they do at 0600 h, while calling males have only about 18% of their night's food by that time (Woolbright, in preparation).

Anuran movement is generally related to temperature and moisture (e.g., Bellis, 1962, Clarke, 1974, Dole, 1965, Hadfield, 1966, Martof, 1953a, Pearson, 1955). The proximal cue for coqui movement appears to be water on the foliage. Although my data do not show any relationship between movement and either temperature or humidity, both were relatively constant on the nights of my observations. Temperature was correlated with calling activity, at least in July, and both temperature and rainfall are probably important determinants of seasonal differences.

Coqui movement patterns were only slightly seasonal. Although the distance between perch and retreat was greater in the wet season, the number of moves per night was similar for both seasons. The total distance moved per night in the wet season was greater than in the dry season, but not significantly so. It appears that the coqui copes with drier winter conditions primarily by use of the water-conserving posture (Heatwole et al., 1969, Pough et al., 1983) and therefore does not need to

drastically alter its movement patterns. Calling activity was more markedly seasonal. Males called for shorter periods of time and on fewer nights in the dry season. Reproduction is also depressed during the dry season (Stewart and Pough, 1983).

Undoubtedly, seasonal differences are at least partially explained by hydric constraints. Both movement and calling tend to increase evaporative water loss, which can be a critical factor in dry weather (Heatwole et al., 1969, Pough et al., 1983). However, my results suggest that moisture conditions cannot fully explain seasonal differences in activity. In January, fewer frogs moved even when the foliage was wet, and activity levels did not depend on foliage condition as they did in July. Lower January temperatures, as well as reduced rainfall, may be important in determining dry season activity levels.

As has been found for other anurans (Gatz, 1981; Greer and Wells, 1980; Kluge, 1981; Ryan, 1980; Woodward, 1982), male coqui do not call every night. Because non-calling males were sometimes found foraging near their calling sites during peak periods of calling activity, energetic constraints may limit the amount of time that males can call. It also seems likely that males track environmental cues (e.g., temperature, rainfall) that may indicate nights of greater or lesser likelihood of successful mating.

On several occasions, calling frogs were not found in their usual home ranges for periods of 4-10 nights, and their calling sites were periodically occupied by other calling frogs. Three

males were found at distances of up to 6.5 m from their usual locations during such absences. All three returned on subsequent nights and resumed calling. Similar behavior was reported for Rana pipiens (Dole, 1965) and Rana clamitans (Martof, 1953b). The ephemeral nature of male-defended oviposition sites provides an obvious advantage for such behavior to the coqui.

Qualitatively, data on male calling times appear to fit the predicted distribution of female availability fairly well. However, statistical analysis indicates that male calling times may not represent an ideal free distribution. Considerable evidence suggests that vocalizations are important in the spacing of male anurans (e.g., Fellers, 1979; MacNally, 1979; Rosen and Lemon, 1974; Whitney, 1980; Whitney and Krebs, 1975; Wilczynski et al., 1982). Acoustic competition between males could well result in the observed deviation by forcing some males into later, suboptimal, calling times. However, such conclusions are tentative because of the imprecision of the female availability curve. Potential sources of error in the calculation of that curve include: (1) The model inherently assumes constant and favorable weather conditions. (2) Courtship sampling effort may be biased towards early evening. (3) The assumption that females become receptive at a constant rate throughout the day may be false.

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Chapter VI

Reproductive energetics and body size of a prolonged
breeding tropical anuran

Abstract. Male Eleutherodactylus coqui expend more energy per gram body weight than females when exposed to the nocturnal chorus, and even more when calling. These metabolic expenditures, combined with the lower energy intake experienced by calling males, represent a pre-mating reproductive investment greater than the cost of egg production by female coquies. As a result, males appear to be on a positive daily energy budget only about 33% of the year compared to an estimated 75% for females. Analysis of energy expenditure suggests that females of this species should reach body sizes considerably greater than males.

Key words: Amphibia, Anura, Leptodactylidae, Eleutherodactylus coqui, reproduction, energy budgets, body size, sexual dimorphism.

INTRODUCTION

Knowledge of the energetics of reproduction is important to an understanding of life history strategies (e.g., Stearns 1976). The relative reproductive effort of the sexes may also be a key to predicting sexual selection pressure (Trivers 1972). Although males of some species may expend considerable effort in obtaining mates (e.g., Thornhill 1976), reproductive effort is generally considered to be biased towards females because of their large investment in gametes.

Male premating effort by anuran amphibians includes varying degrees of intermale competition for females or for resources, along with characteristic acoustic advertisement for mates (Wells 1977). Recent evidence suggests that such calling may be the most energetically expensive activity regularly undertaken by ectothermic vertebrates (Bucher et al. 1982, Taigen and Wells In Press). I previously suggested that these and other energetic expenditures may seriously reduce the energy available for male growth in anuran species with prolonged breeding periods, thus helping to explain why females of such species are typically larger than males (Woolbright 1983).

In this study I examine energy acquisition and use by males and females of the tropical frog, Eleutherodactylus coqui. The coqui has a prolonged, year round breeding season. In spite of apparent selection pressure for large male size, snout-to-urostyle length (SVL) of adult female coquies averages 29% greater than that of males (Chapter 3). This size dimorphism is not explained by differential predation on large males

(Chapter 3) as has been suggested for other species of anurans (Howard 1981, Ryan et al. 1983). I have previously reported that male coquies do not forage while calling (Woolbright 1985) and that calling males therefore experience a reduction of up to 35% of the nightly food intake of similar sized non-calling animals (Chapter 4). This study extends the analysis to consider energy budgets for both male and female coquies and gives independent estimates of energy intake, metabolic costs, and the energetic requirements of growth and egg production.

Because the Luquillo mountains have a seasonal pattern of rainfall (Odum et al. 1970) and because foraging success varies seasonally (Chapter 4), all of the above estimates are calculated for both wet (April - December) and dry (January - March) seasons. I compare male and female energy budgets to test the hypothesis that adult females are on positive daily energy budgets more frequently than adult males and to determine the relative reproductive effort of the sexes. I then extend energy budget calculations to larger body sizes to determine whether energetic constraints limit male growth before that of females.

METHODS

Study species and site

Eleutherodactylus coqui Thomas (Anura: Leptodactylidae) is an arboreal frog common throughout Puerto Rico (Rivero 1978). Coquies are nocturnally active throughout the year although less calling occurs during the dry season (Woolbright 1985).

Fertilization is internal (Townsend et al. 1981) and males brood the eggs in terrestrial oviposition sites during the 2 - 3 wk period of direct development (Townsend et al. 1984). Juveniles reach reproductive maturity in approximately one year (Woolbright unpublished data). Male coquies stop growing soon after reaching maturity but females continue growth and reach much larger body sizes (Chapter 3).

The study was performed in the Luquillo Experimental Division of the Caribbean National Forest in northeastern Puerto Rico. The study site, adjacent to the El Verde Field Station, has been described previously (Woolbright 1985).

Energy intake

Energy intake was estimated from fecal output of frogs collected in the field in both January (n = 110 males, 104 females) and July (n = 129 males, 108 females). I held frogs for 24 h in individual plastic boxes and collected all feces produced. Feces were dried to a constant mass at 60 C and each sample was weighed to the nearest 0.1 mg. The caloric value of dry feces was determined by bomb calorimetry with a Parr oxygen calorimeter.

The relationship between energy excreted and energy intake was estimated using digestive efficiencies. I determined digestive efficiencies of 5 male and 5 female coquies kept on damp paper towels in individual plastic boxes in each of two climate chambers. Chambers were kept on a 12 : 12 LD cycle. One chamber was kept at 24 ± 1 C to simulate wet season conditions in

the forest and the other was kept at 19 ± 1 C to simulate dry season conditions. Frogs were acclimated in the chambers for one week without food and then one cricket was placed in each box. Each day for the next month I replaced any cricket that had been eaten and collected any fecal pellets. For a final 7 days I collected fecal pellets but did not add food. Fecal pellets and crickets from each week's supply were stored in the freezer until the end of the experiment at which time all samples were dried to a constant mass at 60 C and weighed to the nearest 0.1 mg. Caloric equivalents of crickets and the feces of each frog were determined by bomb calorimetry. I calculated digestive efficiency for each frog as:

$$DE = (\text{energy in} - \text{energy out}) / \text{energy in}$$

where energy in is number of crickets eaten times mean dry mass of crickets times caloric equivalent of crickets, and energy out is dry mass of feces times caloric equivalent of feces.

Both fecal output in the field and digestive efficiencies were analyzed by 2 - way ANOVA (Sokal and Rohlf 1969) with sex and season as main effects.

Energy expenditure

Metabolic costs were estimated from oxygen consumption rates obtained using Thoday respirometers (Evans 1972) equipped with ascarite to absorb carbon dioxide. Tests were run in the laboratory for daytime and nighttime resting rates and on a table in the forest for nighttime stimulated rates (i.e., exposed to

chorus). I ran six chambers per test in January and 12 in July. Male and female coquies were placed in alternate chambers and one chamber per test was randomly assigned as a control (no frog). Chambers were assembled at least 1 h prior to testing to allow for thermal equilibrium and acclimation of frogs. Manometers were 2 ml pipets calibrated to 0.01 ml. Tests ordinarily lasted 1 h, although a slight decrease in ambient temperature necessitated stopping a few tests before that time. Oxygen consumption was calculated as the change in volume in each experimental chamber less any change in the control chamber. Volume of oxygen consumed by each frog was transformed to dry volume at STP. Immediately after tests I blotted each frog dry, voiding the bladder by palpation. I then weighed each frog to the nearest 0.01 g. Oxygen consumption in ml per g per h was compared between groups by Mann-Whitney U test (Siegel 1956).

To estimate the cost of egg production for females, I collected 265 freshly laid eggs in the field, dried them to a constant mass at 60 C, and determined their caloric equivalent by bomb calorimetry. The cost of producing one egg clutch was calculated as the energetic value of a single egg times the clutch size reported by Townsend (1984) for females of various body sizes.

To calculate the cost of growth, I collected 12 coquies from 9 - 42 mm SVL, dried them to a constant mass at 60 C, and fit a least squares regression to the relationship between mass and SVL. Dry carcasses were homogenized and caloric equivalents were determined by bomb calorimetry. I defined the cost of growth as

the change in dry mass times the caloric equivalent of 1 g of dry tissue.

Calculation of energy budgets

Energy intake was estimated by dividing energy excreted by (1 - digestive efficiency). Error in intake was propagated by the geometric method given by Swartz (1973). Metabolic expenditures were estimated by transforming oxygen consumption to energy expended assuming a respiratory quotient of 20.5 J per ml oxygen. To evaluate the potential for growth to occur, I calculated total expenditure as the sum of metabolic costs, fecal production, and egg production. I assumed energetic expenditures to be measured without error.

If expenditures fell within 1 SE of estimated intake, I considered the animal to be on a balanced energy budget for the day. A positive energy budget was defined to be when total expenditures were less than intake - 1 SE and a negative energy budget to be when total expenditures were greater than intake + 1 SE.

To calculate yearly averages, I assumed January data to be representative of the three month dry season and weighted them by 0.25. Likewise, I assumed July data to be representative of the nine month wet season and weighted them by 0.75.

All data were collected on mature adult frogs. To extrapolate data to body sizes other than the population means, I assumed that energy intake and oxygen consumption per gram body weight were constant across the limited range of body sizes

considered. The relationship between SVL and body mass was determined by measuring both parameters on a sample of 56 coquiés between 33 and 50 mm SVL and fitting a least squares regression to the data.

RESULTS

Energy intake

There was no difference between male and female digestive efficiency at ambient temperatures of either 19 C or 24 C (2 way ANOVA: $F = 0.1089$, $p > 0.50$). However, efficiencies at 19 C (mean = 77.7%, SE = 1.67) were lower than at 24 C (mean = 88.5%, SE = 1.27) (2 way ANOVA: $F = 21.3763$, $p < 0.001$).

Females produced about three times the amount of feces of males in both the wet and dry seasons (Table 1). The caloric equivalent of feces did not differ between the sexes (2 way ANOVA: $F = 1.1586$, $0.25 < p < 0.50$). However, caloric value was higher in the wet season (mean = 20.240 kJ/g) than in the dry season (mean = 18.879 kJ/g) (2 way ANOVA: $F = 26.0075$, $p < 0.001$).

Estimates of daily energy intake for males and females of average body sizes are shown in Table 1. Dry season intake is considerably less than wet season intake for both sexes. The apparent cause of this seasonality is that frogs spend more time in the water conserving posture (Heatwole et al. 1969, Pough et al. 1983) during the dry season and therefore consume fewer prey items (Chapter 4). Male intake is less than female intake

Table 6.1. Fecal output, digestive efficiency (D.E.), and estimated energy intake of male and female coquies in wet and dry seasons. Entries are mean \pm 1 SE (N).

	Feces (mg)	Caloric value (kJ/g dry)	kJ excreted	D.E. (%)	kJ intake
male	3.4 \pm 0.52 (129)		0.069 \pm 0.010		0.597 \pm 0.113
July		20.182 \pm 0.130 (6)		88.5 \pm 1.3 (10)	
female	9.1 \pm 2.20 (109)		0.184 \pm 0.044		1.597 \pm 0.425
male	3.1 \pm 0.72 (110)		0.059 \pm 0.014		0.263 \pm 0.064
January		18.879 \pm 0.182 (6)		77.7 \pm 1.7 (10)	
female	7.3 \pm 1.78 (104)		0.138 \pm 0.033		0.617 \pm 0.157

because calling males have lower food intake than non-calling animals and because intake increases with body size (Chapter 4).

Male energy intake can be further partitioned into intake on calling and non-calling nights, given what proportion of nights males call and what intake deficit they experience on those nights. Males call on an average of 56% of wet season nights and 29% of dry season nights (Woolbright 1985). Stomach content volumes of calling males average 65% of those of non-calling frogs in the wet season and 81% in the dry season (Chapter 4). Using this information, simple algebra predicts the energy intake estimates shown in Table 4 for calling and non-calling males in the wet and dry seasons. I assumed that variance in intake was a constant proportion of the mean regardless of whether or not the male was calling.

Metabolic expenditures

Oxygen consumption by male and female coquies is shown in Table 2. In July, daytime resting rates did not differ between males and females (Mann-Whitney $U = 63.5$, 2-tailed $p > 0.10$). Oxygen consumption was slightly, but not significantly, higher at night than in the daytime for both males ($U = 70.5$, 1-tailed $p > 0.05$) and females ($U = 67.5$, 1-tailed $p > 0.05$). However, when frogs were exposed to the nocturnal chorus, consumption increased over standard nighttime rates for both males ($U = 11$, 1-tailed $p < 0.01$) and females ($U = 12$, 1-tailed $p < 0.001$). This "stimulated" rate was higher for males than for females ($U = 11$, 2-tailed $p < 0.05$). Two males inflated their vocal sacs. Oxygen

Table 6.2. Oxygen consumption (ml/g/h) for male and female coquies in wet and dry seasons. Entries are mean \pm 1 SE (n).

	Day (rest)	Night (rest)	Stimulated	Inflated
Dry season:				
male	.071 + .008 (4)	—	.131 + .014 (5)	—
female	.079 + .004 (5)	—	.089 + .010 (9)	—
Wet season:				
male	.099 + .013 (13)	.141 + .022 (14)	.257 + .021 (6)	.681 + .019 (2)
female	.114 + .013 (12)	.132 + .018 (13)	.177 + .018 (10)	—

consumption for these animals was higher than for non-inflated stimulated males ($U = 0$, 1-tailed $p = 0.036$).

Oxygen consumption patterns in January were similar to those of July. Daytime resting rates were not different between the sexes ($U = 7$, 2-tailed $p = 0.278$). When exposed to the nocturnal chorus, consumption increased significantly for males ($U = 0$, 1-tailed $p = 0.008$) but only slightly for females ($U = 19$, 1-tailed $p > 0.10$). No males called during the January trials.

Oxygen consumption is related to energy expenditure by the respiratory quotient (RQ) and the time that an animal spends in the various states measured. On nights that they call, male coquies call for an average of 3.6 h in the wet season and 2.7 h in the dry season (Woolbright 1985). Assuming an RQ of 20.5 kJ/ml oxygen and a 12/12 LD cycle, I calculated the metabolic expenditures shown in Table 3. Estimates indicate that males require more energy per gram body mass than females in both seasons because of the elevation of oxygen consumption rates when exposed to a chorus. Males require even more energy on nights that they call. Total metabolic expenditures can be calculated by multiplying the costs shown in Table 3 by body mass. The relationship between SVL and mass is shown in Fig. 1. Because coquies move very little during the night (Woolbright 1985) I assumed that the energetic cost of movement was negligible.

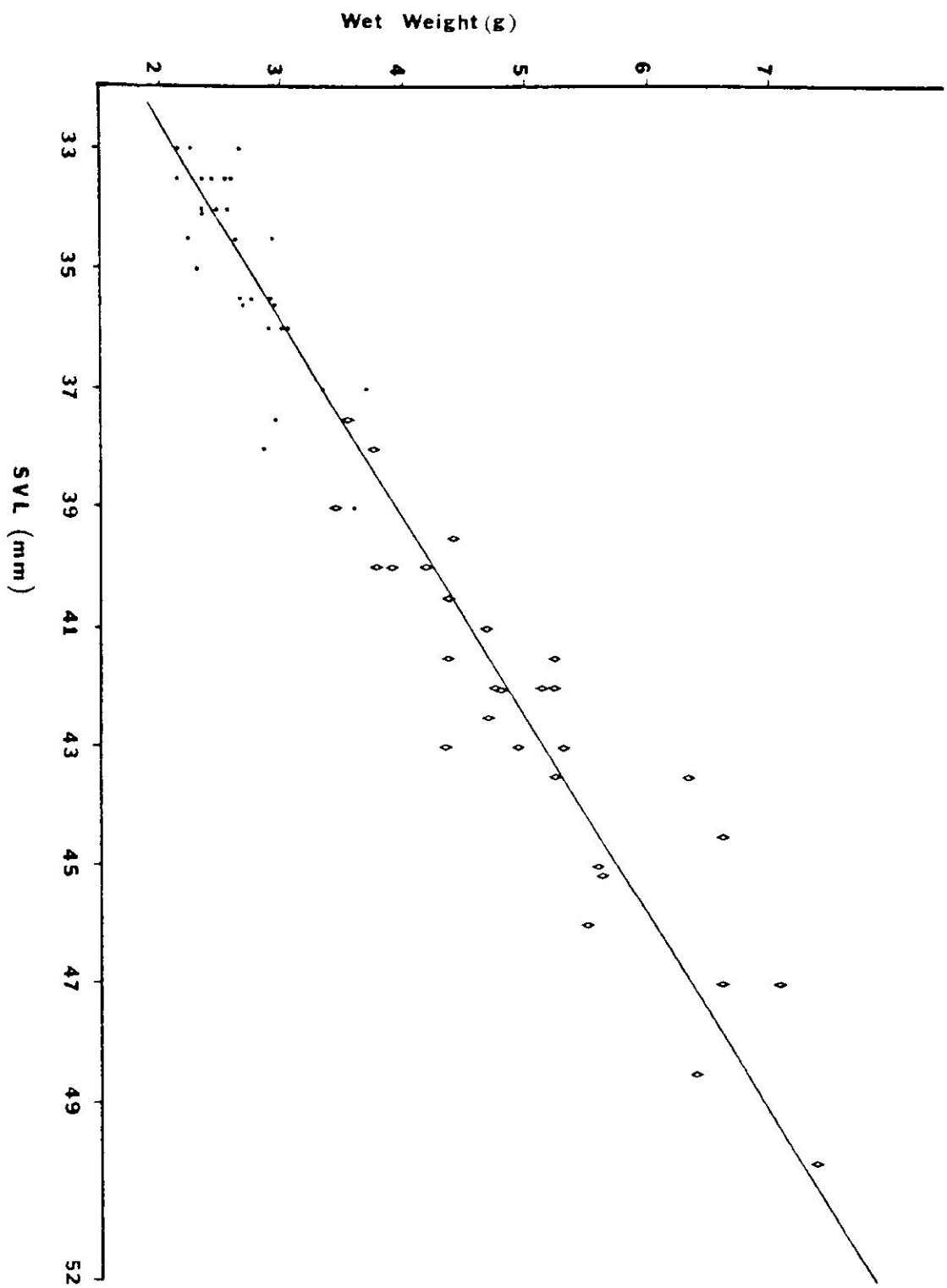
The cost of egg production

The mean dry weight of freshly laid coqui eggs was 8.7 mg. The caloric equivalent of eggs was 24.777 kJ/g dry mass. Thus

Table 6.3. Metabolic costs (kJ/g/day) for average size adult male and female coquies.

	Wet season	Dry season
calling	0.119	0.080
Male		
not calling	0.089	0.049
Female	0.072	0.041

Fig. 1. The relationship between body length and wet mass of E. coqui males (circles) and females (diamonds). Regression equation:
wet mass = $0.304 \text{ SVL} - 7.90$ ($F = 793.3063$, $p < 0.001$).



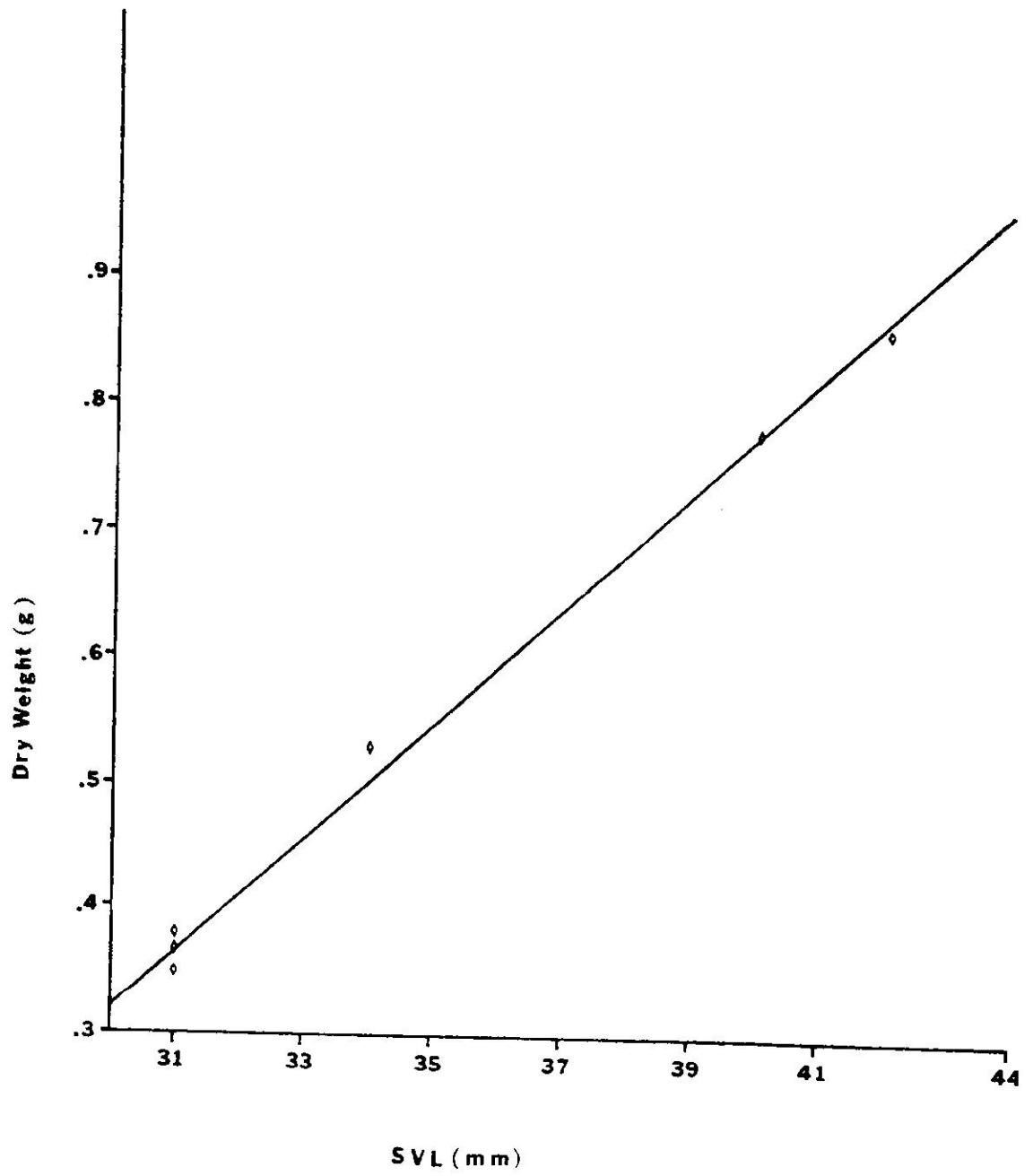
the cost of producing a single egg is 0.215 kJ. Townsend (1984) reported that clutch size increases with female body size by the relationship: clutch size = 0.81 SVL - 5.48. The cost of producing one clutch can be obtained by multiplying clutch size for a given female SVL by the energy content of a single egg. This method gives estimates of 5.265 kJ per clutch for a small (37 mm) female and 6.833 kJ per clutch for an average (46 mm) female. We do not know the frequency of clutch production by female coquies. A reasonable estimate, based on limited data from both laboratory and field, is one clutch each six weeks, at least for small females (D. S. Townsend, personal communication). However, if interclutch intervals remain constant at six weeks with increasing body size and therefore energy intake (Chapter 4), then the proportional allocation of energy to egg production decreases from 20% of daily intake for a 37 mm female to 12% for a 46 mm female.

The cost of growth

The relationship between SVL and dry mass is shown in Fig. 2. The caloric equivalent of homogenized coqui was 21.473 kJ/g dry mass. The energetic cost of adding 1 mm SVL can be calculated as the change in dry mass times the caloric equivalent. This can be further transformed into energy expended per day by multiplying by the size specific growth rate. Growth rates of adult female coquies are described by the relationship: mm/day = -0.004 (SVL) + 0.21, and those of males by: mm/day = -0.002 (SVL) + 0.08 (Chapter 3). Resultant estimates of energy

Fig. 2. The relationship between body length and dry mass of E.
coqui. Regression equation:

$$\text{dry mass} = 0.00001 (\text{SVL})^{3.05}$$



expended for growth by male and female coquies of various body sizes are shown in Fig. 3. Absolute expenditures per day decrease with body size for both sexes as a result of slower growth. Expenditure relative to intake decreases even more rapidly because of increasing energy intake (Chapter 4). Thus a 37 mm female expends 10% of her average daily intake on growth, while a 46 mm female expends only 3%.

Seasonal energy budgets

Exclusive of growth, gross energy intake is partitioned into three costs: production of feces, metabolic expenditures, and egg production by females. The total of these expenditures is shown in Table 4, along with energy intake estimates, for male and female coquies of average body sizes. These estimates indicate that males are on balanced energy budgets during the dry season on nights they do not call (low intake, low expenditure) and during the wet season on nights they do call (high intake, high expenditure). On wet season nights that they do not call, males take in more energy than expended; and on dry season nights that they do call, males expend more energy than they take in. Females do not experience either reduced intake or increased expenditure because of calling. Therefore females appear to be on balanced energy budgets in the dry season when intake is low and on positive energy budgets in the wet season when intake is high.

Sexual differences in energy allocation

To estimate overall trends in energy allocation, it is

Fig. 6.3. Average daily energy expended by male (circles) and female (diamonds) coquies for growth. Least squares regression equations fit to transformed estimates are:

$$J/\text{day} = -1.33 (\text{male SVL}) + 54.9$$

$$J/\text{day} = -3.50 (\text{female SVL}) + 198.2$$

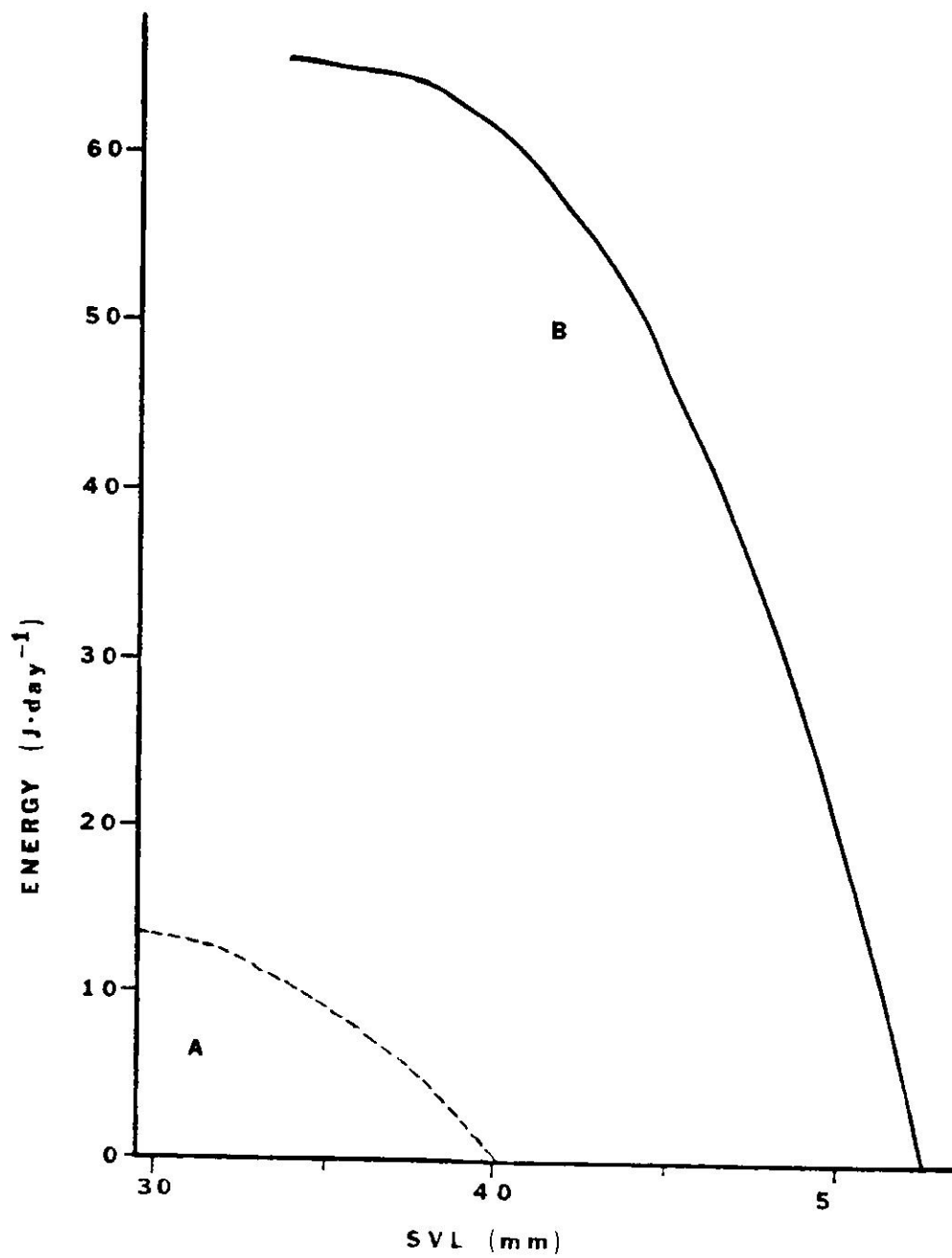


Table 6.4. Daily energy budgets (excluding growth) for 37 mm male and 46 mm female coquies. Entries are kJ/day.

	Energy intake	Energy expended	Balance
Male (wet season):			
calling	0.485 ± 0.097	0.454	balanced
not calling	0.746 ± 0.141	0.381	positive
Male (dry season):			
calling	0.226 ± 0.054	0.318	negative
not calling	0.297 ± 0.067	0.227	balanced
Female:			
wet season	1.597 ± 0.425	0.784	positive
dry season	0.617 ± 0.157	0.550	balanced

helpful to eliminate seasonal variability and look at average daily energy budgets on a yearly basis. Combining seasonal estimates of energy intake gives a weighted mean daily intake of 1.356 ± 0.453 kJ/day for females and 0.513 ± 0.129 kJ/day for males.

If males did not call throughout the year, their expected energy intake would be 0.629 kJ/day (weighted mean of non-calling estimates). Because actual intake including nights calling averages 0.513 kJ/day, males forfeit 0.116 kJ/day (18% of their potential intake) by advertising for mates. In addition males use a daily average of 0.049 kJ more than a similar sized female just by being exposed to the chorus, and an additional average of 0.051 kJ/day in the act of calling. The total of these metabolic costs, 0.100 kJ/day, represents an additional 16% of an average male's daily potential intake. Thus the average adult male "spends" 34% of his potential daily intake in premating reproductive effort. This figure represents a total yearly loss of 78.840 kJ for an average 37 mm male.

A similar sized female has an actual energy intake of 0.629 kJ/day, equal to the potential intake of a non-calling male. Of that, she spends 0.126 kJ (20%) in egg production. Thus her premating reproductive effort is approximately 60% that of a male, representing a total expenditure of 45.99 kJ per year for a 37 mm female.

This difference in reproductive expenditure is accounted for by differences in growth rates. Based on field measured growth rates (Chapter 3) and the relationship between SVL and dry mass

(Fig. 2), a 37 mm female spends an average of 0.065 kJ/day (10% of intake) on growth as compared to 0.007 kJ/day (1% of potential intake) for an equal sized male.

Body size

Assuming that neither intake nor metabolic costs per g body mass changes greatly across a limited range of body sizes, it is possible to predict the body size at which expenditures (excluding growth) equal input and therefore growth stops. I show this analysis for males graphically in Fig. 4, which predicts that male coqui's should be able to attain body sizes of about 41 mm SVL. An analogous analysis for females, assuming one clutch every two, four, or six weeks, predicts much larger female body sizes (Fig. 5).

DISCUSSION

Analysis by seasons indicates that male coqui's are on tighter energy budgets than females. Excluding growth, females appear to have positive energy balances during the wet season (75% of the year) and balanced energy budgets during the dry season. Males have positive energy budgets only on wet season nights that they do not call (about 33% of the year). Male energy budgets are balanced on wet season nights when they call as well as on dry season nights when they do not call. On dry season nights when males call, the combined effects of lower dry season food intake and the higher expenses associated with calling result in the expenditure of more energy than is taken

Fig. 6.4. Energy intake and expenditure estimates for adult male coquies. Cost of calling 1 represents potential intake not eaten because of calling activity. Cost of calling 2 represents additional energy expended because of calling or being exposed to a chorus. Energy intake and metabolic costs per gram body mass are assumed constant across the limited range of body sizes considered. Arrow shows predicted maximum body size.

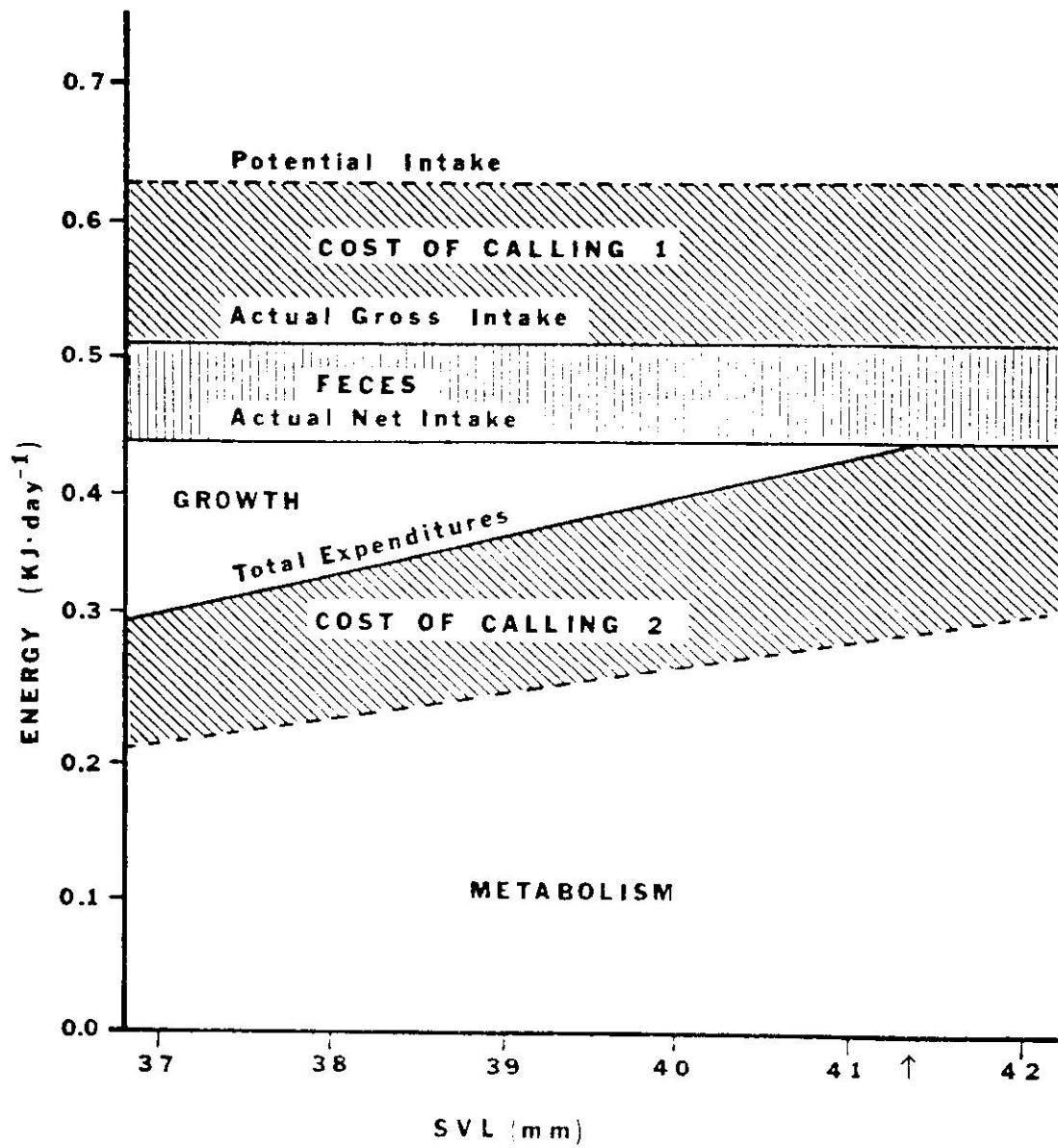
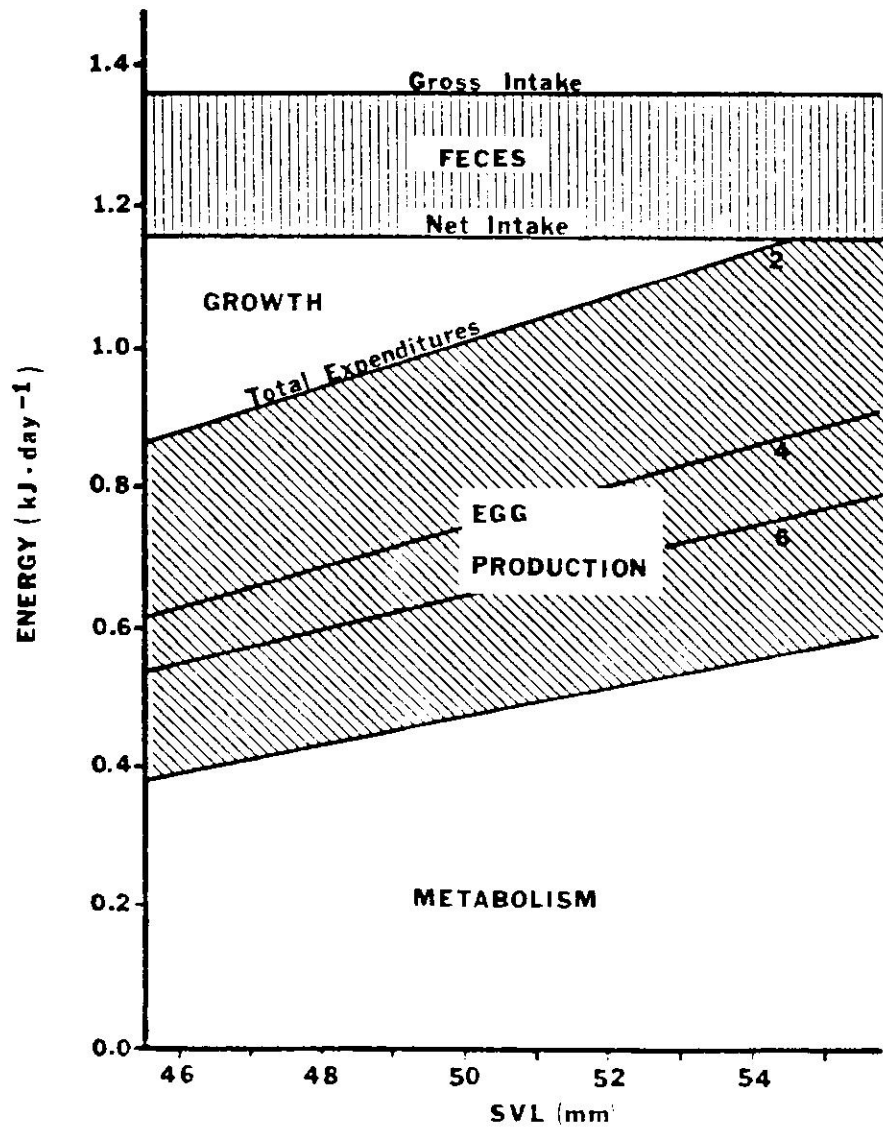


Fig. 6.5. Energy intake and expenditure estimates for adult female coquies. Energy intake and metabolic costs per gram body mass are assumed constant across the limited range of body sizes considered. The cost of egg production is estimated for interclutch intervals of 2, 4, and 6 weeks.



in.

These results suggest two testable hypotheses: that female growth should occur during the wet season and not during the dry season, and that males should accumulate fat deposits in the wet season and expend them in the dry season. Although I have suggested that growth may occur all year round (Chapter 3), I measured animals only in January and July. Therefore seasonal differences may not have been detectable in my data.

On a yearly mean basis, 37 mm males allocate 35% of their daily energy intake to growth and reproduction. Of this total, 18% is lost intake because of calling activity, 8% is additional expenditures because of elevated metabolic rates when exposed to a chorus, 8% is expended in the act of calling, and 1% goes to growth. A 37 mm female allocates 31% of her average daily intake to growth and production. This total is similar to that of males, but differs in its division; only 20% goes to egg production, while 11% is allocated to growth. Thus the cost of premating reproductive activity to male coquies appears to exceed the cost of egg production to females, and to pre-empt the energy that small females use for growth.

There are few data on other anuran species with which to compare these results. Female Physalaemus pustulosus expend 40.96 kJ per season on reproductive effort (Ryan et al. 1983) compared to my estimates of 45.99 kJ per season for 37 mm female coquies. However, P. pustulosus are considerably smaller than coquies (1.8 vs. 3.35 g for this comparison) and breed for only part of the year (259 days). Thus expenditures per gram body

mass per day of breeding season for Physalaemus females are 0.102 kJ while those of female coquies are only 0.038 kJ. Although the expenditure reported for Physalaemus included the metabolic cost of building foam nests, this cost was less than 1% of the total. Therefore female Physalaemus appear to allocate relatively more energy to egg production than female coquies. However, energy intake of Physalaemus was not reported.

Male P. pustulosus expend only 3.25 kJ per season (0.008 kJ/g/day) on reproduction. My estimates of 78.84 kJ per season (0.064 kJ/g/day) for male coquies are an order of magnitude greater. However, these figures include energy intake forfeited because of calling, a parameter not measured by Ryan et al. Eliminating this portion of the cost from my estimates still leaves expenditures of 36.35 kJ per season (0.030 kJ/g/day) for male coquies. The difference between the two species is explained by time spent at the breeding site and time spent calling. Physalaemus pustulosus are aquatic breeders and males spend only about 17% of their time at the pond (Ryan et al. 1983). Terrestrially breeding coqui males cannot leave the breeding site to reduce metabolic expenditures and they actively call on about 50% of nights year round. Adjusting reproductive expenses of male Physalaemus to a per day at the pond basis gives an estimate of 0.043 kJ/g, similar and slightly higher than my estimate for coqui males.

Estimates of reproductive expenditure are also available for Ranidella signifera and R. parainsignifera (MacNally 1981, recalculated by Ryan et al. 1983). Male R. signifera expend 2.22

kJ per season (0.047 kJ/g/day) on reproduction and male R. parainsignifera expend 2.30 kJ per season (0.024 kJ/g/day). Once again, these estimates do not include energy intake forfeited by calling males, and both species are aquatic breeders with males calling for far less of the year than coqui males (MacNally 1981).

Since my data for coquies indicate that potential energy forfeited by calling represents over 50% of the cost of male reproductive activity, it seems likely that both of the above studies underestimated male premating investment. In addition, neither study provided an independent estimate of energy intake, so it is impossible to assess expenditures as a proportion of the total energy budget.

When energy analyses are extended to larger body sizes, my estimates predicted that males should stop growing between 41 and 42 mm SVL. This predicted body size is about 3 mm larger than sizes actually attained by males in the field. The discrepancy seems reasonable in light of the potential energetic costs that I was unable to estimate. Male parental care seems likely to be the biggest of these costs. Townsend (1984) reported that parental males are more likely than calling males to have empty stomachs and that they may lose up to 20% of their body weight during the period of parental care. In addition, evidence suggests that large male coquies may call on more nights than small males, thus increasing costs above my estimates (Woolbright, unpublished data).

The difference between observed and predicted female body

sizes is greater. Based on a six week interclutch interval, I predicted that females should reach sizes of slightly over 70 mm SVL. Females in the field rarely reach 55 mm (Chapter 3). The most likely source of this discrepancy is my estimate of the period of time required for a female to mature a clutch of eggs. The six week estimated interval is based on only a few data points taken on relatively small females. Results of studies on male reproductive success indicated that 45% of male coqui obtain an egg clutch during a two week period of time (Chapter 3). Assuming an equal sex ratio, these data would argue that the average female must produce a clutch every four weeks. This is the same as the interval estimated for Physalaemus pustulosus (Ryan et al. 1983). A predicted maximum female body size of 55 mm would require an interclutch interval of only two weeks for the largest females. This level of clutch production would involve allocation to reproduction of 36% of a female's energy intake, similar in magnitude to the proportion expended by smaller females for eggs and growth combined.

It seems reasonable to expect the reproductive effort of females to increase with body size. In the case of the coqui, reproductive effort relative to energy intake actually decreases with body size if interclutch interval remains constant. Howard (1978) reported that large female Rana catesbeiana produce a second egg clutch during the breeding season while small females produce only one. If large females do lay three times the number of clutches of small females, my previous estimates of the selective advantage of large body size to females (Chapter 3)

would be quite conservative. Nevertheless, the selective advantage of large size to males would still be 33% greater than that to females.

The analyses presented here support the view that energetic constraints limit growth in male coquies before that of females. Males appear to expend (or forfeit) a larger portion of their energy intake on premating reproductive activity than do females, and to be on tighter energy budgets during much of the year. Predictions based on energy analysis alone suggest that males of this species should be much smaller than females.

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