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The Maptive Significance of Male Parental Care

in @ Neotropical Frog

by

Daniel S, Townsend

A Dissertation

Subaitted to the State University of New York at Albany

in Partial Fulfitisent of

the Requirenents for the Degree of

Doctor of Philosophy

Departuent of Biological Sciences

1984

CENTER FOR ENERGY AND ENVIRONMENT RESEARCH

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astm:

This study describes the reproductive ecology and parental care of the seatropical frog Eleutherodectyius cogei, seasures the benefits anc coste of parental cere to individual reproductive success, and integrates benefits and costs into a single view of the adaptive Bigaiticancs of parental care for this apscice

Eleutherodactyius cogui males cali from elevated perches at night

Eage are taid in non-ay

rie nest cites anc unfergo direct development,

hatehieg as tiny frogs in 17-26 days. Clutch size (mean = 26 efi

correlated with feuale body size. Parental care is parforaed exclusively by sles, who attend eggs and hatchlings. Males attend their clutcres 97.40 of the time by day and 75.8% of the ime at night Most of this Cine is spent brooding eggs. Males also defend eggs ageinet conibaliatic intruders. Care is provided chroughout develomuent; neither nest fidelity nor brooding frequency changes from

Parental cere significantly increases hatching success. In a field experiment, clutches froe which parental males vere removed failed 3.4 tines as often a control clutches (nales not removed), Experimental clutches suffered greater mortality fro desiccation and cannibaliss chan controls. Plotting average hatching success of experimental clutches agsingt the developmental stage at which males were removed yielded @ convex second order function, tiene, the benefits of parental care accelerate throughout development .

Parental males do less feeding than non-parental gales and suffer

small but significant losses in body ass during parental care.

---Page Break---

8 also call Le

than non-parental males and aacrifice

Spproximately one additional mating during « 20-day period of parental

A marginal value model of parental care is proposed which

integrates the tise-depondent benefits of attending esse

consequent coste of reduced reproductive activity.

?sing enpiricaity

determined values for E. cogui, the aoe

Indicates ehae by providing

care throughout pre-hatching development, maler maximize their lifetine

reproductive success. Tue model alec indicate:

that, starting with no

ears, either sex would have been favored to evolve care in E. cogui-

Mate coqutes

yy have evolved parental care because of their initial

association vith ease at defended retreat

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Dedicat ion

To sy children, Christopher and Carisea,

theirs will be 2 better world.

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constructive criticism of the wenbere of ay Doctoral Committee; Jerran

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this whole ordeal, Karyn deserves more than {will ever be able to

copay,

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Frequencies of cover categories for calling sites

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The nusbers and sizes (munber of egus) of clutches

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(including DAP) dering 1980.

horus sizes at Dicks House Plot on 31 complete

Survey aighis during MaccheJune 196) and Marchy June-

Juiy 1982) as a function of whether or not raiafall

2]Mfing the previous 24 nour period,

Frequencies of days when 0, 1, of 2+ clutches were

Geposized in Dicks House Plot from March to July 1980,

as 4 function of imsediate past precipitation

Srsoding ant nest attendance patterns of parental

aaies during cach developeental interval for

Tie fares of experinental and control clutches in

pale-reaoval cxperinente during 1980 and 198

Tu fates of experimental clutches divided according

fo initial developmental interval for 1980 and 1982
eonbinods

The frequencies of two levels of
a function of the level of nocturn

»

ching success a
attendance,
ted as the percent of nest checks when the
tal wale was in the nest.

?Te stomach contents of brooding sales and non-
parental cailing males sampled at down on two sornings
ane five mornings, respectively, during July 1982.

The frequencies of eapty stomachs and stomachs with
foot of parental wales at dawn as 2 function of the
dovelopacntal ineerval of their clutches at the tise

Of sampling.

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Sody weiguts vi poeeaeal

Galore Heage A) aed Le

Geveiopeensal porto oF

The yeoporiieny of mav-perest ?and pavental mates

chat! were callang ia Diexs aouer Plot on seven nigite

fron ees co June 195%.

Te nighely ocovaniticy af sacing for wales in Dick?

Mouse Plot cslestacet for 2h ones during April

earough fone 188) Gaz Tuas aad ey 902

A syeopsis of she asics dagiostés features used co

Mf eabejou2 feat ares woean + 1 58) Gor

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Application of the model to E. cogui using new

benefit functions vaich incorporate partial hatching

when there is ao parental care (c= 0).

a lucida dravings of E, cogui embryos.

Photomicrographs of E. cogui eabryos.

Average egg diameter (measured in the field) as

function of developmental stage.

Scattergram of developmental period against mean

daily tenperature for 27 clutches of E. coqu

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95

130

at

138

140

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NTRoDUCTION

Parental care has long been of interest to ethologi:

+ ecologists ?and evolutionary biologists. Te potential for wales or females to allocate post-fertilization tine and energy to offspring is a critical factor in sexutl selection (Trivers, 1972; Williams, 1975; Maynard Saith, 1978), the evolution of mating aystens (Orians, 1969; Eelen, 1973; Balen and Oring, 1977; Kleiman, 1977; Welters, 1982) and the evolution of social behavior in general (Alexander, 1974; Wiley, 1974; Brown, 1975; Wilson, 1975; Witeenberger, 1981),

Parental care is an integral part of the reproductive strategies of wannals and birds (Orians, 1969; Kleiman, 1977). In these two vertebrate groups, evolutionary questions revolve around how the allocation of parental time and energy should relate to mating syste

with the central

sue being whether one or both parents should be

favored to care for che young (Orians, 1969). Parental care by at least

fone parent is e

tial because of the large input of energy a

theruoregulatory buffering required to raise an endothernic off

ing.

These stringent physiological requirements are often not the case for lower vertebrates, both because of their ectothermic physiology and

because

ure and adult anis

5 often occupy markedly different

habitats. This is ehe case with ost tenperate and

any tropical

amphibians, in vhich the typical Life history involves an aquatic

larval stage chet is complet

Ly different in its physiology, behavior

and trophic niche from the adult. Not surprisingly, parental care is

unusual im ?roge, Known to occur in only about 10% of all species

(Mediarmid, 1978). Ie rarity raises questions, on one level, about

---Page Break---

hhow, when and why it arose and on # second level provides the ideal situation for investigating the evolution of reproductive atrategies in animals within retated taxa. Also, because che sex vaich provides care ay differ among congeners, enere existe che opportunity to investigate the relationship betveen environmental conditions, social aystens,

allocation of parental effort and sex:

pecific reproductive strategies

Pacental

re has been studied asinly in birds and eens:

recently, the evolution of parental care in lover vertebrates hai received attention, especially in fishes and anphibians (HeDiaraid, 1978; Perrone and Zaret, 1979; Bluser, 1979; Barlow, 1981; Baylis, 1981; Gross and Shine, 1981; Wells, 19815 Simon, 1982, 1983). In anurans, if should rarely be the case that a second parent can provide ?much additional effective care (effective in further increasing the survivel of the offspring), and since it seeas that cooperative behavior is rare in frogs, the dichotomy Setween whether one parent oF both parents should care (as in endothermic vertebrates) is « moot, question, The principal issues are whether uniparental care or no parental care should be favored and which sex should perform the care.

Trese two questions have been addressnd theoretically (Trivers, 197

Maynard Saith, 1977; Grafen and Sibty, 1978).

To understand the evolution or eaintenance of parental care in any animal, it is necessary to know how reproductive success varies as a function of parental care. More specifically, we need to measure how an increase in offspring survival due to care trades off vith the

conseqs

ces of reduced allocation of tise and energy to future offspring. Specification of benefits and costs for each sex is crucial to intecpretation of sex-specific parental strategies (Trivers, 1972).

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Interspecific differences in cost-benefit relationships, resulting frow different breeding systens (Maynard Saith, 1977) or differing degrees of paternal certainty (Werren et al., 1980),

yy alter predictions about the evolution of parental care.

Parental care has been documented in aost frog fanilies (McDiarmid, 1978). There is treaendous diversity in the ways that amphibians provide post-fertilization parental care to their offspring (atthe and Mecham, 1974; Lamotte and Lescure, 1977; MeDiamid, 1978). Wells (1981) recognized four wajor categories of anuran parental care ag attendance, tadpole attendance, egg transport and tadpole transport. In addition, viviparity occurs in a few species (Lamotte and Lescure, 1977; Wake, 1978, 1980), and recent evidence indicates that, in a fev species, parents say provide nutrition to larvae (Graeff and

Schulte, 1980; Heygolde, 1980; Zimsersenn and Zimaeraann, 1981). In anurans, parental care is practiced almost exclusively by species that lay eggs either in terrestrial or in specialized aquatic microhabicars. Many cases of anuran parental care have been suggested to be an ataptive response by parents to the probles of aaintaining a volnerable aaphibian egg in a terrestrial environsent (Myers, 1969; Meviaraid, 1978; Weil 1961), either co prevent desiccation of eggs or to protect chem from predators and pathogens. There are only # few studies which quantitatively assess the relative iaportance of anuran parental care in fulfilling these funceions (MeDiarmid, 1978; Simon, 1982, 1983; Taigen et al, 1984; Tomnsend et al., 1984).

In addition to the 4:

jersity of forms of parental care exhibited

by anurans, there is interspecific variation in which sox provider

parental care in several enuran groups (Wells, 1961). One of these is

---Page Break---

the genus Eleutherodactylus, in vhich there occur

sciee vith paternal

care, others vith saternal care and sone vith no parental care at all.

In this study, T have investigated the parental care aysten of the

Puerto Rican frog Eleutherodactylus coqui in vhich care is performed

exclusively by males. My goals in the study were:

(1) to describe che reproductive biology and ecology of the species;

(2) to describe, in detail, its parental care behavior;

(3) to document how provision of parental care affects offspring

survival,

i.e., to desonstrate the benefits of parental care;

(4) to est

?© how parental care provision affects future fecundity

of caring wales; i.e, to est:

sce the costs of parental care;

(5) to integrate b

wefits and costs into a single statement about

the relationship between py

ental care behavior and fitness in

E. coqui.

Each of these goals is treated as a chapter in the following thesis

---Page Break---

GENERAL METHODS

In this section, I describe some of the general methods used in thie study. Methods used only in particular parte of the study will be

described in the appropriate chapters.

?The Species

Eleutherodactylue cogui Tomas (Anura

Leptodactylidae) ie a

terrestrial breeding frog endemic to Puerto Rico. It is the most widespread and generally the most abundant species of sixteen native Eleutherodactylus (Drevry, 1970a, b; Rivero, 1978). The coquf was first described by Bello y Espinosa (1871), vho noted that the parent frogs were found with the terrestrial eggs and that development was direct, miniature frogs hatching from the eggs without any intervening free-living Larval stage. Until 1965, E. cogsi was nosinally subsused under E portoricensis, but Tomas (1956) recognized the existence of tvo species and nazed the second one E. cogui.

There has been an explosion of work on E. coqui since the mid 19608. Dery (19703, 6; Drewry and Rand, 1983) worked on the population biology, Life history, and voeal behavior of several Puerto Rican Eleutherodectylus. A great deal of descriptive and detailed experimental work on the vocalization, neurobiology, and calling behavior of E. coqui has been done by Narins and his associates (Narins

and Capran

+ 1976, 1977, 1978, 1980; Narins, 19828, b, 1963:

b

Warine and Hurley, 1982; Zelick and Narins, 1982, 1983). Aspects of the

Physiological ecology of £. cogui have been studied by Heatvole et al.

(1969), Pough et al. (1983) and Taigen et al. (1984).

---Page Break---

The coguf is aocturn

+ Achieves nigh densities in the Luquillo

Mountains of northeastern Puerto Rico (Stewact and Pough, 1983) and, a}

with its congeners, has divece developnent (Tomsend and Stewart, in

press).

The field work war conducted in the Iuguillo Experimental Forest

near the El Verde Field Station of the Center for Energy and

Eqvironnent Research in the Luguillo Mountains of sortheastern Puerto

Rico. The E, coqui population chat i stwiied inhabits second-growen

tabonuco (Dacryodes excelea) forest at about 250 m elevation, Motitto.

Sloanes perterians, ant ausubo, Mani le

2 bidentata, are also prominent

species. Three other trees are important tot!

population ecology of

Ex coaui: Cecropia peleaca, Didymopanax corotoconi, and Preatoea

tm. Dead 1

montana, the sierra

wes of Cocrops

and fallen fronds of

estoea are used extensively as divenal ¢

and nest sizes

by coqufes, and the axils of sierra palus arz often used as calling

sices by males (sce below). Cecrapia and Didvmopanax are both early

successional species which take advantage of teaporary openings in the

forest canopy, while Presto

is a sub-canopy pale which occurs

regularly throughout the fore

(Beet and Whitmore, 1973). The forest

has moderately seasonal cliaate. 4 cooler, dry season extends from Deceaber to March, when mean sonthly rainfall is about one third Lose than in the varaer wet season of April through October. Dry season ean monthly temperatures are about 21 to 22 C, while wet season monthly

teaperatures average about 23 to 24 C (Odum ct al., 1970).

Field work was done during June-august 979, Janvary-July 1980,

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land January, March, June-July, and October 1982. Most of the resulte

Giscuseed in this thesis were from the 1980 and 1982 field work.

Measuring, Sexing ard Marking Frogs.

?The snout-vent Lengths (SVL) of frogs vere measured in the field

by placing then inside a plastic bag, pressing them against a flat surface and measuring to the nearest 0.5 me the distance from the tip

of the snout to the distal tip of the pubis.

In areas where frogs vere maried,

1s could be sexed vhen

recaptured while calling o in amplexus. The following morphological

criteria were used to determine sex as well, Advi

tes in the EL

Verde popelation range frow 29.5 mm to 38.0 am SVL (see Chapter 2) and

have a vocal sac of thin flexible skin beneath the throat. Females

range fron 35.5 an to 52.0 ma SVL (see Chapter 2),

lack the flexible

skin of the vocal sac, and often have ovarian eggs visible through the

abdowinal vat

Frogs were marked in several

eas during the study, This vas done by clipping a unique conbination of toes; never more than one toe per foot or four toes per frog. Also, the first digit on the hind foot vas never clipped. Toes vere alvays clipped proximal to the firet joine. ?This prevented any substantial regroveh of clipped toes, and marked frogs were easily recognized for up to two years following initial

marking.

Seapling Methods

jatic diuenat

Frogs and nests were located in the forest vie syst:

surveys of the habitat. Surveys were of two types: complete and

---Page Break---

aetectivg

Complete surveys involved thorough seacching of the leat

Litter, turning logs and cocks, and inspection of all crevices or

cavities up to 250 cm off the ground (as igh as I could reach). The

leat litter was turned by hand and gost ©

ed leaves were opened and

inspected. Leaves sbove the ground were handled similarly. Crevices

and cavities, including palm axile, rock crevices, the interstices of

prop roots, tree trunk holes and cracks. branch axils, ete. were

inspected, if necessary with tne aid of a psalignt. Te objective of a

complete survey vss to inspect all accessible cavities, crevices and

oles in an area that could be potential retreat or nest sites

Selective surveys repre

1 templing of

y certain types of

cavities and crevices Iv au arwa. Often, clus involved sampling only

the sierra pale fronds, Cec

ropia leaves, Large cavities such as cree

holes and crevices in cocks, and pain axils, Data fron coaplete surveys

indicated that frogs overused th

62 cypes of cavities relative to their

generat abundance in

le habitat. Hence, selective surveys were used to

maximize the efficiency of locating frogs or neste rather than to

estimate population params

Bamboo frog houses were used in soverat parte of th:

stuay.

These consisted of 15.

25 cm lengths of haahoo with an opening near the

bottom and a removable plastic top. Banvoo hou were either hung on

trees (up to 200 ca above the grount), or placed horizontally on the

around. Frogs readily adopted thew as retreat and nest sites. Their use

hhas been of major inportance in various work on E. cogui (Townsend et

41,, 1981, 19865 Steware and Pough, 1963)

hen a nest ws

found, the attending parent was removed briefly

while the cumber, diameter and developmental stage of the eggs vere

---Page Break---

recorded, The number of eggs in the cluten and their arrangeaent

(number of layers, umber of eggs per layer) were recorded; sumber of hereafter referred to as the

size. Egg diameter vas

ured to the nearest 0.5 m= sith a snail clear plastic mm ruler.

Generally, the outside dianeter, including che egy capsule, of 5-10

eee in the clutch was seasured, Te developmental

ne of eggs was

determined according to a staging table vhich 1 constructed for E.

coqui. A complete description of the staging table is given in Appendix

1. For

ny purposes in what follows, T have divided the 15

prechatching stages of ay table into three doveloymental intervals,

T-IIL, each corresponding to about onecthiré of development

Developmental interval iV includes ati post-hatching stages. In

addition to clutch parazeters, I recorded the nature

Wf Location of

the nest site, ne

jane off the ground of the <tut

+ and several netric

characters of the nest, including its largest lines dimension, the

Longest dinension of the actual nest cavity and the perpendicular to

Length (ecg. the length and dianeter of pela fxond roll), and the

angle fro hor ize

1 of the substrate on which the clutch rested.

calting

12 surveys were condveted on 4 regular basie in several

during the study. Calling surveys vere designed to record the

eunber of miles calling, and eeveral characteristice of their call

sites, in prescribed aress of the habitat. A calting mal survey

consisted of passing slovly through an area vhile Listening for calls.

The identity of calbing males (whore frogs wore marked) var determined

by visual inspection of exposed toes. In the elevated calling posture,

it is possible to do so without capturing the frogs. The

character

ic8 and height above the ground of the calling site vere

---Page Break---

iso recorded. Ail surveys vere done between 2000 hours and 2300 hours,

and generally Yested for 1-2 nurs, For complete aueve

completely traversed st tess: twice to ensure that all calling ales had been found. Some partial surveys were performed ia hich an ar

was only partially covered, or traversed only once.

Woite sampling vas done in nary areas of the forest at El Verde,

fone large plot vas sampled coutinucusiy and intensively throughout the

study. Dicks House Plot vss 9 500 square mei

quadrangular area in

?hich 30 bamboo frog houses hal been hung. ALL major topographic

features, palms end creee were

oteed witha

cks House Plot. Twelve

reference stakes placed in cho plot allowed pinpointing the horizontal

Location ef any frog, nest of othe: {ceture in che plot. Beginning in
197%, all frogs of 24 mm SVL oF greater vere aarked upon initial

capture. Marking

ncinued throughout 1979 and 1980 field work, A

compete diurnal survey and a compete calling male survey vere done

during alterna

Weeks (each done biveekly) throughout 1979 and 1980.

Te 1982, a series of 5-7 easplote calling surveys were done on

consecutive nights prior co exch comp:

means are given + 1 Sf unless otherwise indicated.

Statistical tests used are che Stusent''s t-test, Pearson product-moment

correlation and One-Way ANOVA when variables are normal

y distributed

and hovoscedastic (Sokal and Rohlf, 196%). When those assuaptions are

violated or for small sample size, non-yarenetric statistics such as

the Mann-ihitney U-test, the ch

quare cest, and the Kruskal-Wallis

One-Way ANOVA are used (Siegel, 195). Alpha is set at 0.05 a5 the

---Page Break---

Level of rejection in all hypothesis testing. Date vere analyzed and

sone statistical procedures performed using the computer statistics

package SPSS (Nie et al

1975).

a

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a

cnaetea 2

TWE REPRODUCTIVE ECOLOGY oF E. CoQUI

Motes

Body size. Complete calling surveys of Dicks House Ploc vere conducted on 21 nights in 1950 (Table 1) ans 29 eights in 1982 (Table

2). Calling wa!

SVL vas recorded on 9 reyctar oasis only during 1980

(Table 1). Iadivitust sates ranged tron 29.5 am to 37.0 mm SVL and nightly means ranged frou 32.0 + 0.57 ar 8-9) £099.92 0.28 an (N= 20), vith an overal! eas of 33.4 3 9.50 0 (7 = 207), There vas significant variation among nonthty means of calling oale SVL

(keveea~

Tis Cneevay ANOVAS

49 AE 8a, p 5 0.02). Average

boay size a

ecreaged from dey co wat season, the difference steaming

primarily from the increased presence of smaller nales in the chorus

during April throsgh Jone (note extention of size range to lower values

ducing those wonths).

During 1980, 134 <lueches weve Jeposited in Dicks House Plot. The

SVLs of the parental meles vere

asoted of then (Table 4). The

overs

jan body tiae of parental moles was 33.4 £0.12 aa (W = 132).

Although there was a docren

bn mean SVL from January ?9 June (ae with

calling soles), there was not significant variation in body size anong

months (Krushal-Kallis One-Way AWOVA; H# 4.53, JE = 5, MS; July not

\cluded in analysis). The calling male and parental wale body size

Gistributions (Tables 1 and 3) in Dicks House Plot during 1980 vere not

significantly different (Mann-Whitney U vith s-tvansformation: © =

1114, p © 0.1335).

nest sices. Male coqufes use

---Page Break---

Table 1. The numbers and mean body sizes of calling males in Dicks

House Plot during 21 complete surveys in 1980. Note that

the April 30 sample is combined with May for monthly snaly:

dumber of Ssrout-Vent Length

Night calling males West SE Range

gan. 7 7 338 0.34 32.0-34.5,

18 ° - 7 =

20 6 334 0.29 32.5-34.0

2 4 338 0:20 33.0-34.0

Monthly Mean (SE) 4.3 (1.6) 33.4 on?

Fe. 2 2 - - -

19 2 0 : :

2 ° - : .

March 4 a6 a3.9 0.26 32.5-36.

u 20 3.9 0.27 32.0-36.5,

v Ma bus. 0.43 321003710,

25 ° ale on83 32.003510

Monthly Mean (SE) 14,6(2.3) 33.7 0.19

dors 2 8 33.2 0.36

5 22 Bae 0.30

ae 23 38 0.27

Monthly Mean (SE) 17.7(4.8) 32.6 0.20

april 10 a 32.2 ots 31.0-36.5,

may 7 4 33.3 01860 bi.o-3als

2 a 3218 0139 300-97.0

Monthly Mean (SE) 13.3(5.8) 32.9

une 4 a 22.0 0.57 29.5-34.8

7 20 32.7 ons. dols-34.5

2 » 32.8 ona? 291823700

25 2 332 0.27 dilo-ae.s

Monthly Mean (SE) sae 0.9

Grand Mean (SE) 1.7.9) 388 0.40 29.5-37.0

as

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Table 2. The numbers of calling males in Dicks House Plot during 29

complete surveys in 1982,

Number of

Night calling males

van, 7

10

2 4

ab

ua

Monthly Mean(se) 7,611.0)

March 6 a6

9 14

10 1

a a8

a a

a rey

Monthly Mean(Se) ?17,3(2.0)

Number of

Night calling males

Sune 10 16

n 15

rt 8

a a

Ma v

15 v7

Monthly Mean (SE) 14.0(1.5)

soy 8 2s

9 26

a0 20

n 2

a 20

Monthly Mean(se)

oct. 12

a

4

as

Monthy Mean (Se)

14,502.55

ua

---Page Break---

Table 3. Mean body sizes of parental males in Dicks House Plot from

Janvary £0 July 1980. Small July sample results from sampling

only during the first four days of the month.

Snout-Vent Length

Month " Tear sage

January 5 34.0 9.42 33,0-35.0

February M 33.8 0.37 32,0636.0

Maren 2 33.6 0.28 531,0-36.0

april 2 33.5. 0.27 31,0-36.0

May 30 334 0.27 31.0-36.5

Sune 30 33.0 0.28 40.0-37.0

sory 7 33.3 0.53 51.5-38.0

Summary ase a4 0.12 30,0457.0

---Page Break---

kedly different aicrohabitat

for calling and nesting. Tvo variables

vere measured for both types of sites: height

jove the ground and

relative cover. Height above the ground is the vertical distance in c=

e's calling position or to a clutch. Relative cover was ranked

1g 4 qualitative

le deviaed by Narins and Hurley (1982; p. 289)

to categorize the anount of cover around asle calling sites, follows: "1 = open with no surrounding cover; ¢.g., on an open surface, sudbank, rock, leaf, or bare tree trunk; 2 ~ generally open, but with

ree surrounding vegetation partially covering the frog; e.g., on a

tree trunk amid saell leaves or vines; 3 - closely covered by vegetation or substrate but vith at least one side and the anterior uncovered; ?.g-, between banboo shoots or in a pala axil; 4 - covered closely on all sides by vegetation and substrate but open anteriorly;

1g.) in a palm axil with Leave

near the dorsal surface of the frog: 5 = completely surrounded by vegetation; e.g., inside a tightly curled Leaf." Although Narine and Hurley (1982) used the categories only for ranking calling sites, the scale is entirely appropriate for ranking the relative cover of other sicrohabitats used by the frogs.

Twenty-one calling male surveys in Dicke House Plot during 1980 (3 partial and 18 complete surveys) yielded a total of 297 calling site observations. Figure 1 illustrates the distribution of perch neights

Most

los (92.62) called from sites that vere 25 cm or higher, while only 5 males (1.7%) used sites that vere less chan 10 em high. Only « few males (2.42) used perches higher than 3m. The average perch height wae 93.5 4 4.6 cm (8297).

Males employed a vide range of substrates for calling, but the

jority of them (252 of 297 = 84.9%) were relatively exposed

---Page Break---

a

Figure 1. The frequency distributions of height above the ground for

calling perches (top) and clutch locations (bottom) in

Dicke House Plot during January to June 1980. Means and

Medians were computed using raw data, N of calling perches =

297; N of clutches = 134, Hatched areas of lower figure

represent clutches in banboo houses: .

---Page Break---

median

me

Tmean

median

ee

sseag ae

?soyosed Buyjeo jo JequNN

e828

s949IM]9 Jo JeqUNN,

80 "100" 150" 200" 250" 300°

Height above ground (cm)

---Page Break---

1s

(categories 1-3, Table 4). The majority of these sore exposed sites

i= axils (96 of 252 = 37.3%), the surfaces and crevices of tree trunks and branches (65 of 252 = 25.8%) and the open surfaces of Leaves (33 of 252 = 13.12). Thirty-three wales (I1-12) uaed type 4 sites, consisting mainly of the doorways of banboo frog houses (8 of 33 = 24.22), the open ends of fallen sierra palm fronds (6 of 33 = 18.28) and hanging clusters of dead Leaves or palm leaflets (7 of 33 = 21.22). Only 12 sites (4.02) were of category 5, including calling from inside the curls of Cectopia leaves (6 of 12 = 50.02) oF from inside banboo frog houses (5 of 12» 41.73). Palm axils, ax a single category, vero the gost frequently used call sites, comprising 33.0% (98 of 297) of

all site

?The height distribution of 134 clutches deposited in Dicks House Plot during 1980 is shown in Figure 1. Note that the peak in clutch height frequency betveen 125 and 200 em is due entirely to basboo houses which vere concentrated in chat height range. The majority of

oviposition sites (92 of 134 68.7%) were less than 25 cm high (79.3%

of 116 natural m

8). The average nest aite height vas 47.8 cm + 6.0 em for alt nests; 30.5 ¢ 5.4 cm for natural neste (N= 116). The height distributions for calling sites and nest sites are significancly different (Mann-Whitney U vieh s-transformation: 2 * 8.293, p

0.0001).

The relative cover distribution of Dicks House Plot nest sites is siven in Table & and is significantly different from the calling site

Gistribution (Chi-square = 309.97, df * 4, p< 0.0001). Bighty-theee

percent of all clutches (111 of 134) vere located in category 5 nest

sites, in which che clutch and attendant ele vere entirely enclosed by

---Page Break---

a3

Table 4. Frequencies of cover categories for calling sites and nest

sites in Dicks House Plot during 1960. Categories after

Narins and Hurley (1962); see text for definitions.

cover Categories

calling sites

Nest sites ° ° > 2 an

---Page Break---

vegetation or substras

Males are using elevated, relatively open perches

call sites,

typified by pale

rile, tree trunks and branches, rock surfaces, and

open leaf surfaces. Oviposition sites, on the other hand, are in closed

cavities which are usually on or near the ground (less than 26 cm igh).

les

Body size and fecundity. From January to July 1980, 69 fenales

were captured in nest sites immediately following oviposition. Their average SVL was 41.4 + 0.4 em (Range = 35,5-52.0 ma) and average clutch size was 28.1 + 0.6 ongs (N= 58, Range © 16-41). ?There was @

significant correlation beeween fe

Le body size and eluten size (x =

0.56725 p< 0.01, Figure 2). In 65 cases, the SVL of the amplectant

ale we

algo recorded. The regression of f¢ SVL on fenale SVL for anplexed paire was not significant (Figure 3; F < 1.0). Wence, there does not appear to be positive assortative wating by body size, at least within the range of male body sizes that vere sampled (30.0-35.5 wm Sv),

A total of 357 clutches was found in all habitat surveys during 1980 (Table 4), including the 69 mentioned above. Average size of all elutehes vas 26.7 + 0.3 eggs (N=357, Range = 3-45 eggs per clutch).

Since many of these vere found at various stages post-ovipo

small clutches may have suffered partial predation prior to discovery,

yielding © lower estis

ee of clutch size overall

Two females vere recaptured depositing second clutches in 1980.

One female Laid 33 eggs on 20 April and 34 eggs on 14 June, with an

---Page Break---

---Page Break---

3

g

?

§

z

rarer

34 36 38 40 42 44 46 48 50 52

Female SVL (mm)

---Page Break---

---Page Break---

52

36 38 40 42 46

34

Female SVL (mm)

---Page Break---

interclutch interval of 55 days (8 weeks).

clutch on 5 May (the eget vere not counted) and « second clutch of 26 ?tans on 3 July, yielding an interctutch interval of 59 days (8.5 weeks). A third fensle vas captured Laying @ clutch (uncounted) on 11 March and had Laid a second clutch dy 21 May, yielding « maxiaus

interclutch interval of 71 days (10 weeks).

Seasonality of Reproduction

Calling activity vas recorded during every month of the study

(abies 1 and 2), Nightly densities in Dicks House Plot ranged from 0 to 29 calling sales and varied significantly anong aonthe in both years (Keuskal-Weltis One-Way ANOVA; 1980: H= 13.2, af = 5, p< 0.025; 1982 Ws 19.9, af = 4, p< 0,001). The principal source of the variation ves

2 difference between dry sea

n (Jan-March) and vet season (April-July) densities in the plot.

Clutches vere found during every oath of the atudy (Table 5).

?There was significant variation asong sosths in the number of clutches deposited in Dicks House Plot when coapated to an expected distribution

of equal monthly clutch frequency (Cri

quare = 22.99, ef = 5, ps

0.001), with the main source of variation being the lover frequency of clutch deposition during the dry season. Figure 4 illustrates the temporal distribution of deposition of 134 clutches in Dicks House Plot during 1980. No aore than four females ever deposited eggs in the plot fon @ single day. At least one fenate oviposited on 81 of 186 days (43,62) vith an average of 1,65 clutches per deposition day (134/81). Colling activity (Table 1) and egg deposition (Table 3; Figure G) were

low during January and aost of February. Following a pulse of

---Page Break---

Table $. Te numbers and sizes (number of eggs) of clutches found in

Dicks House Plot and in all habitat surveys (including DAP)

during 1900.

Dicks House Plot

January, 5 1.9 2.89 3

February 15 22300 2a a

Maren 26 2a Ls cy

april 3 20 la 2

May. a are ls, 2

Sune 30 30.7 ole 2

saly 6 we 129 5

ALL surveys

sanuary 2 aa ed °

February a ws 127 2

Maren °7 25.80.78 52

april 6 26:3 0.67 6s

may 86 2770.78 7%

sane 7 2811 0.68 2

saly 1s 216 0.89 Bb

summary as? 26.7 esa 08

---Page Break---

2

Figure 4, he tenporal distribution of clutch deposition in Dicks

House Plot from January 1 te July 4, 1980. Each bar wieeh

equals one day.

---Page Break---

tudy

youeW,

ue

? ty ?

---Page Break---

26

reproductive activity in late February (Figure 4), reproduction increased into March and continued at that level through July 4, the dace of the Last complete diurnal survey at Dicks House Flot. From March 1 to July 4, 1960, fesales deposived egge on 69 of 126 days (56.82).

Both calling activity and oviposition were associated with rainfall (Tables 6 and 7), Calling wale densities in Dicks House Flot

were significantly greater on nights following 24 hour periods in which

there

some rainfall chan on nights which followed 24 hours without

rain (Table 6). Feaules deposited clutches significantly more often

following 24 hour or 46 hour periods in which there was sone rainfall

than folloving similar periods with no rainfall (Table 7).

Courtship and Mating Behavior

lus cogui is a nocturnal frog. Frogs generally leave their diurnal retreat sites and become active in the forest within che first hour after dark. Calling activity begine before dark, the chorus is generally at full strength within @ half-hour of full darkness, and calling

heaviest before aidnight, declining in the early morning hours until dava (Drewry, 19703; Drewry and Rand, 1983; Wootbright and Townsend, Ms).

L have observed 18 partial or complete courtship

goqul. Courtship was alvays initiated by 4 female approaching a calling faale and asking contact. The initial contact by the female often resulted in a sudden pause in the aale's calling folloved by « suiten in the vocalization to @ lower amplitude, softer call. Within seconds

of the initial contact by the female, the male began to wove auay from

---Page Break---

Table 6. Chorus sizes at Dicks House Plot on 31 complete survey nights

Guring March-June 1980 and March, June-July 1982, as a function

of whether or not rainfall occucred during the previous 24

hour period. A. Complete table of chorus sizes. B. Reduced

table for statistical analysis.

»

Number of Calling Males

Tes eis rs ea

No rainfati a3 a a °

dats fal) oe 2 2 8

Munber of Calling Males

No fainfat) 8

Raitat 2 uv

ster Exact Tests $p < 0.008$.

---Page Break---

?Table 7. Frequencies of days when 0, 1, or 2° clutches were deposited

an Dicks House Plot from March to July 1980, as a function of

Anmediate past precipitation, A. When rainfall did or did not

oecur during the previous 24 hows. B. Daring the previous 42

hours.

a

Number of Clutches per Day:

TT Fo

No rainfali 2 a 10

Re infatl 24 2 a

x? = 6.59, of + 2, p ? 0.02.

umber of Clutches per Day

a i 3

Ne rainfal 2 ? 6

Ruinfall 29 Fr 2

$= 16.61$, df $= 2$, $p < 0,001$.

---Page Break---

the call site, alvays continuing to call. Typically, @ wale would sove

from 10 to 30 cm and stop, The fensle had to follow the male and

ther

get very close to him or actually

jke contact in order for the sale to

nove asain, Typical courtehip involved a long series of these

Leading-and-stopping oves by the aale with following moves by the fenale. Males alvays continued to call vhile leading, although the calls were usually much softer than the advertisesent calls that had been given prior to initial contact by the fenale. No male went more than 50-60 cm in one move before waiting for the fenale to catch up. On several occasions, when females took too long to follow the

hey he

turned around and vent back co che ar te

of his last stop. Fes

behavior during the leading phase vas variable. Some females did little nore than follow the male directly. In rwo other cases, females spent time investigating various curled leaves and cavities along the courtship route, One female did this to such an extent that che male backtracked three times to find the fesale and initiate leading again.

Without exception, however, the female eventually entered the nest

cavity that the male first entered and rem

ined. Once the female had

followed the male into the cavity, the f

normally initiored
anplenue by backing under the male vithin 15 minutes. The male's

calling bec:

progressively softer, vith an increase in the nuaber of soft, multiple-note calle (repeated co notes), and eventually stopped M1 courtships were observed before 2300 hours, and ost were initiated within the firet 1.5 hours of dark, Leading courtship lasted from 15 to 60 sinutes, the tine varying a9 a function of the distance between the call site and nest site and of the propensity of the fenale to follow

the male directly.

---Page Break---

once axplexut vas initiated, the pair remained in aaplexus for the reat of the night and into the following day, vhen eggs vere finally

Laid. Early in amplenus, the

le was atop the feasle in approximately

fan axillary position, but

were never geen to clasp the Female

Prior to oviposition, and often close to davn (after 5-8 hours of aaplexus), the pair a

june a secondary amplectic position, in which the

jes hind Legs come to rest on top of the male's hind legs. As a reault, the male's posterior end is firmly pinned against thar of the female and against the substrate. This position is maintained

through sur the reat of anplexus

ind oviposition.

[At some point between the initiation of saplexus and oviposition

the fensles ovulates ner full ovar:

n complement and the male

inseminates her, alenough not necessarily in that order. Two females that vere captured two hours after the initiation of anplexus vere found to have all mature ova still in cheir ovaries, so ovulation apparencly does not occur prior to anplexus. Also, females were observes to undergo very heavy abdominal pulsations for up to two hours prior t> oviposition; these may respond to ovulation. Fertilization in E. coqui is internal (Tomsend ot al, 1981) and while I do not know ?at vhat point during anplexus the wale insominates the female, t presume that it occurs after the onset of the secondary amplectic position.

oviposition begins 7-10 hours after the initiation of amplexus, and requires 3-5 hours co cosplete. Oviposition begins without any visible interruption of the abdominal pulsations that T have inter= preted as ovulation. As eggs are Inid, the female moves out from unter the malo, and eventually cones to sit directly in front of his when

---Page Break---

a

egg-laying is done, The gale is then directly over the new clutch in «
typical brooding posture (see Chapter 3). The male and female renain in

chese positions for the 1

of the daylight hours. As dusk cones, both
parents become more active and, virtually without exception, the ne!

male parent degine giving aggressive calls toward the fenale

nd may
even make several biting attacks in chasing her ovt of the nest (see
Chapter 3). Fenales usually return to their regular retreat sites
viehin one or two days of mating.

les that entered nest sites and initiated aaplexue did not

alvays romain and wate with che sale, In five courtships vitnessed

during 1980 and 1962, @ female left the nest site after the initiation

of amplexus without

sting with the male. I did not capture any of

these fensles mating at other sites, to 1 do not know their subsequent

ing history. In two of the five pairs, disturbance by the observer
vas a probable cause of the aborted wating. However, in the other chres
pairs, there vas negligible interference by the observer, and it seems

probable that females vere rejj

ing either ene

le or the nese site.

In none of the five instances had the peic entered the secondary

amplectic position; the Latest time that a (onale vas observed to teave

the nest was 0209 hours.

Developmental Biology

As with all other know Eleutherodactylus, £. coqui has direct

developeent. At oviposition, eggs are Large (3.6 4 0.1 an in dianeter,

N= 21) and unpigmented. Developuent occurs entirely vithin the egg and

at hatching # folly pigmented miniature frog energes bearing «

keratinized egg tooth, # tail remnant, and a yolk reserve (Townsend and

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Stevart, in press). A staging table describing tne development of E.

goqui is present,

in Appendix 1, KatchLings average 6.1

0.1 a svt.

?The egg tooth disappears within 36 nours of hatching, the tail is

jorbed within 3 days, and the yolk reserve is used up within 6 days,

by which time the hatchlings have dispersed from the nest site.

Developmental time (oviposition to hatching) ranges fro 26.3 days

in January and February to 16.8 days in June, and is strongly and

inversely correlated vith ambiont temperature (Appendix 1).

Discussion

Reproduction is continuous in E. coqui, with some calling activity and 2g depos:

we every month of the year (this

study; Stevart and Pough, 1983). Although continuous it is seasonal in intensity. Male calling activity (Tables | and 2) during the dry season (e.g. January-February) is about 25t of that in the wet season (e.8., June-July), alchough erratic rainfatl patterns withia season can give

tise to some variability. For example, January 1982 was unusually wet, and calling sale densities vere inflated relative to 1980, while a dry June in 1982 resulted in depressed calling aale densities (Tables 1 and

2). Rainfall has

ignificant effect on calling activity, with chorus

non ary ones (Tz

densities being greater on vet nights eh te 6).

Likewise, egg deposition varies significantly with season. There vas a significant increase in the number of clutches deposited in Dicks Novse Plot from January to June 1980. Within the wet season, the

Schedule of egz deposition varies significantly with habitat moisture; females ovipositing more frequently when the habitat is oist than when

it is doy (Table 7).

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2

Tere does not appear co be any non-ranion wating in the population with respect to male body size. The distributions of calling feale Sv and parental male SVL were aot different, and mean values vere identical for the two groups; 33.4 am (Tables 1 and 2), Large ales are not obtaining gates in higher proportion relative to their occurrence in the chorus than are ameller asles. This finding contrasts vith a number of studies of otner anurans in vnich 1e body size is etrong:y related to male mating success (see Arak, 1983 for a review). Furtheraore, there was no significant relationship between the male SVL land fevale SVL in mated pairs (Figure 3). There is no evidence of positive assorcative mating in the population.

Mote coquies are using aicrohabitate for calling that are markedly diftercot from nest sites. The vast wajority of nest sites (79,32) are vithin 25 em of the ground vhile males alaost invariably call from perches above 25 cm (92-68), In temas of cover, 3% of all nest sites vere entirely enclosed, with no opening. Calling sites, on the uther hand, cre virtually alvays open at Least in Eroat (96.02), and often (85%) «re wore exposed than that, The sajority of calling sites are comprised by the axils of sierra pale fronds, the open surfaces of aneub ond vine leaves, and the surfaces of tree trunks and branches:

Te relationship of feaale body size to clutch size follows the trend noted in gany other anurans, as vell as ectothermic vertebrates genera! iy. The significant positive correlation of era number with female SVL, has been describes for uredeles (Salthe, 1969) and for anurans (Salthe and DueLIman, 1973; Crump, 1974; Wake, 1978). However fone of che obstacles to interpreting Life history adaptations concerring fecundity has been che lack of data on how often fenales

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ponit ager within a breeding 96

jon. Lower clutch size to body size

regres

one in sone species may be offset by more frequent clutch

deposition, Only recently has it been found thac some temperate anivan

fenales can depcsit tus clutches 2 ore aeasor, (Wells, 1976, Howard, 1978; Pereill and Daniei, 1983). For any tropical species, feaales can

almost certwiniy produce two oF mers clusches per ys s¢ (Chibon, 19605

Wells, i980b; Kiuge, 1981; Welle and

personal communication)

Tre evidence presented in this study for ©

_ gogui suggests that females

can deposit # new eleteh about once every Evo months in the field. In

Laboratory populations on ad Libitus oot, feasle cogufes can produce

eggs every six weeks. These data suggest that E. coqui, females could

proauce

east tour clutches per year, sf egg production is Limited

primariiy to the wet ee

jon (March through October), and may be able eo

lay as wany as six or seven clutches 12 food is abundast and eg
production continues, even at a reduced level, during the dry seaton.
Fenale cogufes maintain 2 positive energy bucget throughout the year

and appear to have exce:

available

wergy for growth at all body sizes

(Lak, Hoots

ent, perso:

1 communication) so that energy Limitations to

ete production do not appear co be present in this population.

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CHAPTER 3

?THE MALE PARENTAL BEHAVIOR OF E.

In order to evaluate the net adaptive value of parental care, it

is inportant initially to know the basic care behavior repertoire and

to have some idea of the time budget of care provision for a species

Tis information hy

been gathered for 4 qunber of birds and mammals in shich parental care has been stodied (Kleiman, 1977; Martindale, 1962; Wolters, 1982), but there exist virtustiy no date of this kind for waphibiane (exceptions include Kluge, 1961; Simon, 1982, 1983). Knowing the tenporal patter of care provision is especially crucial for amphibians wnich exhibit egg attendance (which comprise the vast majority of species with parental care) because without having the egss

physically attached, the parent is free co pursue activities that are

alternative to care behavior. Alceraate activities may include aintenance functions (feeding, rehydrating) ant behaviors that

influence 2:

ing success (calling, territorial maintenance). The trade-off between caring for one brood and either survival or additional reproduction will be strongly influenced by the allocations cf time to alternative activities. Furtheraore, it is important to know the details of care behavior because sere presence at an oviposition site may not constitute functional parental care but only

coincidental presence in the sane microhabitat

epee (Woodratt, 1977), Testing predictions about the evolution of parental care vill require gathering auch data, perticularly when interspecific

comparisons are used to make inferences about evolutionary trends.

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%

im this chapter, I describe the major behavioral characteristice

and

yporal patterns of parental care in E. cogui.

Methods

pling method by which clutches were located was discussed

under General Methods. Moat clutches were left undisturbed and

subsequently checked at various times of day and night. During each

neat check, the position and bi

javior of the parent and the

developmental stage and condition of the eggs were recorded. Nest

checks did not appear to disturb the nest of parents greatly (but see

Methods of Chapter 4).

Agere

ive calle (see below) were recorded using a portable cassette recorder (Channel Master Model 6395) and analyzed on # Model 4500 Unigon Uniscan real-time spectrum analyzer and a Textronix Model 5103N Storage Oscilloscope. Sonagrans were sade on a Kay Mode! 60618 Sona-Graph with the band selector set on vide.

In all analyses, ?day', ?daytiae? and ?diurnal? represents the period 9601-1759 hours and ?night? and ?nocturnal? the period 1800-0600 hours.

Results

Sex of the Attending Parent

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

Frequency of Unattended Clutches and Multiple Clutches

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2 found only 11 clutches (out of 616) which never had an attending

parent. Males do not attend eggs in nore than one nest simulteneously.

Any pattern of complementary pre:

\cee and absences at Evo neighboring

nest sites would have been suspicious. 1 never found auch @ pattern.

?There vere canes of aultiple sisultaneous clutche

site (29 double clutches and evo triple clutches). However, multiple

clutches were usually contiguous inside the nest; only seven of the

double clutches had more than one body length separating then

Description of Perental Care

Parental care in E. cogui is characterized by ogg attendance beginning at oviposition and Layting throughout development, a period of 17-25 days. Mates often continue to attend hatchlings for 1-6 days after hatching. Males perform two eajor parental activities: brooding of eggs and defense of the nest and ess.

Brooding. A parent vas considered brooding at any tine that a part of its venter vas in contact with ite eggs (Figure 5A). Although males varied vith respect to how well they were centerd over their mgs, they typically covered most of the cluten. Males that brooded after hatching adopted an elevated posture near oF over the egs capsules. Because hatchlings typically grouped together on or near the capsules, they were often clustered beneath the male.

Nest defens

Parental males vere observed defending nests again conspecific intruders on 15 occasions during the study. Six contests vere obsorved in sufficient detail and length to allow quantitative analysis. These six ranged fro 10-75 sin (mean = 30 ¢ 10.2 win) in duration and took place before midnight.

---Page Break---

Figure 5. varetal behaviors in E. =A. yg brooding.

Parentas male Blockine a nest intruder.

C. Parental male delivering a sustainee bite to

---Page Break---

---Page Break---

ve behaviors by parental males observed during nest

defense included ager

ive calling, biting, sustained biting, blocking
and wrestling. Contests vaually consisted of long periods (minutes) of
inactivity punctuated by short burate (seconde) of activity. Parents
spent Si of total contest tine in active behaviors (calling, biting,
wrestling and chasing) and the ressinder in static positions, wether

separated froa intruders or in contact with them (blocking or sustained

biting). Prolong

contact (Lasting wore than 5 5) between parent and

intruder occurred in five of the six contests. An average of 51 of

contest cise ves spent in contact although the range in the six individual contests was Of to 982. Thera were tvo types of prolonged contact: blocking and sustained biting. In the typical blocking posture (Figure 5B), # parent was on top of the intruder, its front leg ?and forebody blocking the intruders head and forebody, and its hind lege partly extended in a bracing position, In sustained biting (Figure SC), # parent held some part of an intruder's body, usually the

head, is fee aout

Aearessive calling by parental =

4 was heard in 16 of 15

contests. Although the regular advertisement call of E. cogui has been extensively studied (Drewry, 19702, b; Narins ant Capranica, 1976, 1978, 1980), the aggressive call has never been quantitatively characterized, Therefore, I will describe it briefly. All variance estiaces in the following section on agaressive calla are 1 SD.

Agaressive calle vere composed of 4-37 (mean * 11 + 5 notes per call, N= 88) brief, rapidly repeated no: with dominant frequencies of 1.42.7 kilt (Figure 6), The calls always began with a note of 120 + 15 as duration (range * 100-160 as), followed by a sequence of notes,

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Figure 6. Tic aggressive call of E, cout. A. A sonogran of

Losnots call recorded during a nest-d-fense contest.

Mean dominant fequercios (bar equals 42 50; sample

size balow SD bars) of the first 10 notes of aggressive

calls by five different mules during nest-defunse

contests. sarpie sizes decriase be

138e some calls

had ceser than 10 notes.

---Page Break---

kHz

26

24

22

209)

3

pre Rem e nm on es

10 i 20

Time (see)

4 5 67 8 9 10

Note number

---Page Break---

?each of 60 + 5 mn (range * 40-70 ma) in duration. The period between

the first and second notes ws

250 + 20 we (range = 220-300 as) and
thar berween all subsequent pairs was 160 + 15 ms (range * 120-200 a8).
Individual aggressive calle ranged frow 0.6 8 (four-note call) to 5.7 8
C7enote call) in lengeh. The average dominant frequencies of notes
increased from 1.64 0.1 kz for the firet note to an asymptote at 2.5
£ 0.1 itz by the eenth note (Figure 6)

Ageressive calle were common in the six contests (gean = 14 4 9.1

calls poe contoat, range = 7-31), occurring in bouts of 2-5 calle, The

average overall rate of agaressive calls vas 0.8 catls/ain (range of
average call rate for individuel contests was 0.4-1.6 calls/ain).
Bizing by the defending parent was observed in all six contests
(wean = 4.5 43.3 bites per contest, ange = 2-10). Te frequency of
biting ranged {c08 0.2-0.4 dites/min in individual contests, with an

overall frequency of 0.4 bites/sin. Individual bites were rapid Tunges, usually at an intruder's head. On five occasions, in four different contests, the parent dit and held on to an intruder's head or body (sustained bite - Figure SC) for @ period of 0.25-22.0 min (nean = 6.5 28.8 mind.

Wrestling occurred during periods of biocking contact. Typically, the parental male grabbed or levered the inteuder's head or forebody and pushed the intruder avay from the eges. Wrestling bouts vere brief, tasting fro 5 to 20s. Nine wrestling bouts were obsecved during the three contests in which blocking contact occurred.

Intruders did not engage aggressive behavior (although, during one contest, an intruder gave several aggressive calls). Movenent by intruders seemed entirely

---Page Break---

directed at getting around the parent and co the pa

In four of the 15 occasions when neat defense was observed, the outcome was inconclusive because the froge were disturbed. In six of the other 11 cases, intruders ate aost or all of the clutch. Intruders were chased out of the nest and consuaed few or no eggs in five

Teaporal Pacterns of

rental care

doalysis of temporal aspects of parental care in E. cogui was based on 4879 nest checks sade on 510 clutches during 1980 and 1982. West checks vere divided between day (44.92) and aight (55.123, and ong the four developaental intervals (1: 22.43, 11: 27.2%, 111 39.5%, IV: 10.92). I arbitrarily established four categories of male position with respect to eggs: brooding, in the nest not brooding, at the nest enteas

Je, and absent from the nest. On about 67% of the

jons that males were absent from their nests, they could not be

te

percentage of nest checks in which males wore present in the nest or at

the nest entrance was 97.42 during che day and 75.8% at might for

pre-hai

fing clutches, and 90.3% by day and 44.

aight after hatching. The hourly pattern of nocturnal nest presence of males vith

pre-nat

fing clutches is show in Figure 7. The presence of parental

jes dropped to 92.2% between 1800 and 1900 hours, as frogs began to fenerge at dusk; it was lovest (68.82) betweon 1900 ané 2000 hours, the first full hour of darkness, and fairly constant at about 74% (range =

T2.4-16.42) for the rest of the night, incre:

jing after 0400 hours as

---Page Break---

Figure 7. Percentage of nest checks in which parental males were

found in their nests (brooding oggs, in nest not brooding,
and at nest entrance categories are combined) during the

day ona at uourly antervais throu

ene might. The darkened
lower area of wach bar indicates the percentage of checks
An wich gales were at the nest entrance. only pre-hatching

developmental stages were used.

---Page Break---

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all aales returned to their neste towards dam. There vas # concomitant

peak in wales observed in their nest entrances (12.42) during 1900-2000

hours (dark area of each

ae in Figura 7)

There vas individual vars of

fon an the population ia leve

nocturnal nest attendance, During the two years, there vere 96 nests for which I hag at least 4 nocturnal nest checks during prechatching development. The distribution of percent nest attendance is plotted for

jure 8, The distesbueion is quite skewed towards lower

levels of nocturnal nest sttensance and nas a Median of S4t presence.

Clearly the sajority of parental sales essibited high levels of

attendance; 67 of 96 (69.7%) aoies vere in their ests at least 702 of

comutes

nocturnal and normally spen

tne day in retreat sites

which ere similar to nest sites. Evidence

sales wore actually

providing care co eges, and aot merely occupying retreat sites that

happened to contain clutches comer from a

sideration of parental

male position in the aest. When in the nest, a male could sit either

fon the eggs or sonemnure else inside

1e nest. The circular area whose

Fadive is defincd by » clutch plus one male body length is the orca

where a male could sit and be considered brooding. That area was

usually much lose than 25% of the interior surface ares of a nest.

Hence, on @ random basis, ales should have boon found brooding esas

about 25% of the time that they vo!

present in their neste. In fact,

when found in their nests, parental males vere brooding eggs in 93.1%

of all daycine checks and 81.9% of all nocturnal checks

To test the hypothesis that the high Level of nest presence at

oa the non

night (~5.82) represents 2 departure

{\ ngeturnal accivicy

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4s

Figure &:

?The Crequency Kistosran cr nocturnal nest attendance

Levels Gor parental meee a)

mr nests during 1980 and

A9k2, Attendance Level is uaproseud as the percentage

Of net chwoke in whion e nale nes present in the

nest 2 at sts entrance, Gm)y nets with ut lease four jccturnal checks Sure incsuued, Arvow inéieates

the estan + oite

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44

Ere ee

sojew jo sequan

40 60 80

Percent Attendance

---Page Break---

?

terns of adult cogufes, two vets of observations were ade during

1982 (June 27-28 and July 7-8). During the afternoon of the first day,

the bamboo frog houtes in each of tyo plots were surveyed and the

numbers of parental males and non-parental adults were recorded.

During the following night all houses vere re-saapled at 2-h interv:

starting at least 1h after sunset and continuing until 1 h before dawn

(see Figure 9 for nocturnal survey time intervals). ALL houses vere

checked 2 final time during che afternoon of the second day.

(on june 27-28, 99 houses vere checked, Five parental males and 16

non-parental aduite were found curing the first afternoon survey. On

July 78, 187 houses were checked; the initial count was 17 parental ales and 54 non-parental adults. The results of the two nights were conbined and the initial counts of parental and non-parental frogs during the first afternoon survey vere designated as 100% (Figure 9)

During the first socturnal

vecky pare!

2 male presence dropped to

59%, while that of non-parental adults dropped to 142. During the

second check, parental presence rose to 86% ant subsequently renained at that Level. The presence of non-parental adults dropped to about 10%

and res

ined there until the last check, wien it rose co 22% as frogs

returned to their retreats prior to dav. The average presence for a11

nocturaal checks was 823 for parental mates and 12% for non-parental adults. The difference vas significant (Chi-square + 193.5, p= 0.001).

(on the following day one of the 22 parontal males (4.52) failed to return to his nest, whereas 23 of the 70 non-parental adults (32.82) failed so re-enter cheir retreat sites of the preceding day (Figure 9)

Nest attendance as @ function of developmental state of the

---Page Break---

a

Fagure 9.

?The percentage presence of parental males (clear bars} and rencparencal adulte (dark bars) in their nest sites and retreat sites, respective:y, during an initial afternoon survey (Day 1), five nocturnal surveys (81-5)

land the following afternoon survey (Day 2) of two

house plots on June 27-26 and July 7-6, 1982. The

punber of fzegs in each category on Day 1 (parental

mules: M+ 22) nou-parental adults: N= 70) was set

as 1008.

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quasaig SB014 10 %

Nt N2. NG 4 NS Day2

2015-

Day?

0430-

0530

0030- 0239-

2330 0130 0330

2230-

2130

Time

Interval [hows!

---Page Break---

elute!

?To investigate whether parental cre Sehavior varied vith the

of agg, ail nocturnal neat checks vere partitioned among the four development a! intervals. For this analysia, the male position categories ?in nest ro brooding? and ?at nest entrance? were combined into one ?aot brooding? category. There vas a significant difference in parental aztendance across developmental intervals (Table 8) only when post-hatching nest checks were inctuded. There vas no significant difference in parental dehavior of attendant wales across

the pro-haeching developmental intervals

Poacussion

Male parental care in E

cogei is characterized by attendance of

eggs at a terrestrial oviposition site. Males exhibit very high levele

of nest Fidelity. They

found in their meses 97.42 of che tine during the day and 75.8% of the Eine at night during pre-hatching development. Night-tine attendance, and hence presence in the nest site, is significantly higher chan aight-tine presence of aon-parental

adults in their re!

at sites (Figure 9). lence, pavoneal care

represents # vignificant shift ia

activity budget of parental aales. Furtheraore, the distribution of attendance ievets is very skeved towards lover levels, with the majority of parental ates (69.7) sponding at least 70% of theiz tin at might in the nest (Figure 8).

Wiehin the context of egg attenda:

| parental alee exhibic evo types of care-giving behavior: eug brooding and nest defense. Erg brooding is the aajor activity of parents. Males maintained contact

with the eggs 89.13 of the tine that tney are in the nest at night and

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Table 8. Erooding and nest attendan:

during eack dev

checks (Percentage

Patterns of parental mal

interval for nocturnal nest

fan total in parenthe:

Mate position

brooding are en cy

los) (6.8) (27.6)

In nest, nut brooding a 1s »

aan 37.3)

Aoewnt from nest nas 2 28t ae

Wnote tables «° = 112.9, af = 6, F< 0.01.

Tabie without avi x? = 0.78, df = 4, p> 0.95.

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so

93.13 of the tine during the day. Overall, then, parental sales spent 67.5% (89.1% of 75.82) of the night and 90.0% (93.1% of 97.43) of the day brooding their clutches.

Comparable data for temporal patterns of parental behavior and details of care behavior are virtually unavailable for anurans. Simon (1983) found that Cophixalus parkeri parents remeined close to their clutehes throughout an 85-100 day developaental period, and vere invariably found brooding the eggt. However, he did not differentiate yytime and nighttine attendance nor did he provide easple sizes for evaluating attendance data. Stomach contents of brooding parents indicate markedly lower foraging rates, suggesting that attendance levels are high enough to preclude normal foraging

activities at aight. Kluge (1981) found thac aele Myla rosenbergi

exhibited high nest attendance during pre-hatching development but that

once eggs hatched, attendance

13 (alehough in a second year

prechatching attendance levels were auch lower). In this species, ense

are aquatic ar

pre-hatching development lasts only 1.5-3 days, a9 the
tenporal and behaviors! constraints on parental care provision are
quite different from those operating in terrestrial species vith tong
Pee-hatching periods.

Brooding.

probably the ost common type of parental behavior in anphibians (Salthe and Mechan, 1974; MeDiarmid, 1978; Wella, 1981). This {a not cerribly surprising. Brooding is generally a siaple behavior which vould require relatively Little innovation in wotor patterns or neural pathways in order to evolve. Also, since eggs are often deposited in the regular retreat site of the parent, there say be

no need for a microhabitat shift in order to provide care. There

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snould be no added energetic cost of brooding, at le

¢ initianly.

Finally, brooding may have « relatively large effect in increasing

offepring surviv

The Denefite and costs of brooding behavior in E.. cogui will be addressed in the next two chapters.

?The evolution of nest defense behavior probably represente the redirection of territorial behavior to s parental care function. In B. cogui, both males and females vill defend retreat sites from conspecifics (personal observation; MoM. Stevart, personal communication). Nest defense by parental males aay be more intense and prolonged than retreat site defense, dur now serves @ function more divectly related to fitness, That nest defense is more intense than defense and constitutes somewhat separate category as a parental care behavior is supported by several observations, First, intruder males were never observed to engage in aggressive behavior, bot rather appeared intent on approaching and ingesting the exes.

Second, parentat

es never pursued intruders beyond the entrance of

che nest

Third, nest defense contests lasted longer and generally

involved higher levels of wrestling, biting and sustained biting than

Aid retreat rite defense.

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cuaPrER &

THE BENEFITS OF MALE PARENTAL CARE

Rethods

During April-June 1980 ané June-July 1982 attendant meles vere

removed from their clutches in some nests and the fate of these

experimental clutches vas compared to that of control clutches which

had atcendant

les throughout devolopaent, Parental males were Fenoved over the vhole range of pre-hatching developmental stages, from inpediately post-oviposition to Stage 13. Experizental and conteo!

clutches were gonit

sd daily until they hatched or failed. There vere two major causes of clutch failure: desiccation and predation. I observed two types of egg predators: invertebrates and coqufes. tn eases where the predator vas not evident, 1 used criteria based on field and laboratory observations of predation to identify the predator, All invertebrate predators left 3 residue from their feeding activity, vhether eapty egg capsules or partially chewed eggs. Coqufes alvays ate eggs whole. Hence when eggs had deen chewed or others Partly consued, invertebrate predstion was inferred; when entire eggs Aisappeared, cannibalism vas presumed to have taken place. I have no evidence that any other vertebrates consuae the exgs of £. cogui. In the course of almost 4900 individual nest checks (see below) 1 never had an instance of actual or suspected predation on cogul eggs by vertebrates other than coqufes.

Thave observed both filial cenaibalian, the parent eats its on eggs, and heterocannidalisn, a conspecific eats the eggs (Rohver, 1978), in E. cogui. Filial cannibalism vas associated vith aajor

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Aisturbance of the nest, parent or eggs. Tere vere two sources of auch disturbance, One was the investigator: vhen a nest was firet discovered, the parent var captured and various paraaeters of ness and

weed. Following auch initial disturbance, a parent was

observed to eat ite eggs on several occ:

ons, but only when eggs were in early developaental stages (i.e., during developsental interval 1). The second type of disturbance occurred when a conspecific entered nest and ate ost of the eggs in the clutch, The parent sonetiaes consuaed the renaining ages but, again, only vhen they vere in early

stages of developaent. The:

vere instances when heterocannibals ate

part of a clutch but the pat

mnt continued to care for the rest of the

ens. On the banie of this evidence, I vaed ene folloving criteria to

assign cannibs!

ized clutches: (1)

| at the first nest check following

initial disturbance, @ clutel

had disappeared, 1 considered it filial
cannibalien; (2) if che parent vas found attending the eggs during
checks subsequent Co the initial disturbance and the clutch later
disappeared, I considered it heterscannibalisn. Using these
conservative criteria I may overestinate the incidence of

heterocannibalise on contrai clutches. Mowever, aay bias

1 act

against the hypothesis that resoval of parents causes inereasod clutch

failure from heterocannibalisn

Results,

Male Renoval Experiaents

Parentai males vere renoved {rox 31 clutches in 1980 and 73

clutches in 1982. The fate of these experinenta

clotehes was compared

with that of 98 control clutches in 1960 and 108 controls in 1982.

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se

Average initial cleten eizoe for experisental end control clutches were

26.6 40.9 and 28.2 4.0.5 eggs/clutch reepectively ia 1980, ant 26.5 +

0.5 and 24.6 40.5 egge/clutch in 1982 (che control and experimental

clutch sizes were aot significantly different in either year)

Most clutches either succeaded or

Led completely. of 206

os and 104 experimental ctutches, 280 (90.38) had either

hing, vhese = hatoning = (amber of eggs Ch

00% hs

hacched/initisl egg cone) X 100, Hence clutches were wzor eoses (502 or greater hatching) of £3

wes (less then 50%

hatched). Teere were very few tarderiine cases: 10 clutches (3.2%) nad

between 49-60% hats!

ing. 1h a few clutches, more than one agent of exe

mortality vac involved in ceasing failors. Tn thoae cases, the agent

responsible for most of the of egg mortality was cited the cause of cluteh failure,

Fungal infection and daveloyuontal abeorsalities, aajor causes of 2g oortatity in other anuran species (Sulthe and Mechan, 1974; Siaon, 1982, 1983), vere of minor impact on the Res of Ex cogui. Fungi infected only dead eggs, usually (note Hist tad failed to develop. A low incidence (1-3 egge/elutch) of aimoras: on son-Boveloping ogee ?as found in many clutcher. There vere eo diffecsnces in the incidence of fungal infection or abnorsal developacat detveen experimental and contro! clutches.

Te the 2 years, 27 experimental clurches (11 ia 1980 and 26 in

1982) failed from predation. On che basis of direct evidence 1 sould

esige one i

se to invertebrate predation (IP) ant 21 to

heterocannibalien (HC). Using the criteria outtined in the Mechods for

the

ining clutches, T assigned 3 to 1P and 12 to WC. Sixty-nine of

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the control cluccnes failed from predation during the 2 years (40 in

1980 and 29 in 1982). 1 could assign 26 on the basis of direct evidence: 8 to IP, 2 to HC and 16 to filial cannibalien (FC). On the basis of the Mochods criteria, I assigned the rest as follows: 5 to IP, 23 to HC and 15 to FC. Because experinental clutches were not subject to failure from filiel cannibatisa, the 31 control clutches that failed for this reason are excluded from further analysis.

The sucess race of experiaental clutches was significantly different from that of control clutches in both years (Table 9). Combining the resutts from both years, 76.92 (80 of 104) of all experineni

1 clutches failed, a® against 22.52 (40 of 175) of atl

ntcol clutcher. ?the ini

sed frequency of failure in experimental clutches vas caused by significantly more frequent desiccation

(oni:

quare + 77.94, df = 1, p <0.001; both years) and cannibatian

(Chi-square * 12.06, 4f = 1, p < 0.001; both years). Predation by invertebrates was not significantly different between experimental and

control clutches (Chi-square * 1.46, ¢f =

P + 0.05; both yeare).

Wren clutches were assigned to the three developmental intervals according to the stage of the egge at discovery or male removal, there was 4 significant decrease in clutch failure from developmental interval 1 t0 TL for both experimental and control clutch groups

(Table 10). However, vhen the fate of clutches at each developoental inverval were compared between treataents, there were significant 4ifferences in hatching success for each developmental interval. Thus, although there vas a significant increase in hatching success of

experimental clutches from

srly to late developaent, hatching success

still significantly lover than for control clutches at

ry

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developmental interval .

Evidence fros

Mon-Experiaencal Neat

Corroborative evidence chet parental care resulte in significantly ed hatching success cones from combining the observations of nocturnal nest attendance (Figure 8, Chapter 3) vith records of hatching success for those nests. Of 96 nests for which T have at least four nocturnal nest check records (Figure 8), I leo know the hatching success in 66 of thea. ALL 64 were clutches in natural nest sites (did not include any bamboo houses); 45 vere on the ground (less than 25 ca Off the ground) and 19 vere elevated. Hatching success was extrenely bimodal, as with experimental clutches, and vas scored similarly; clutches with S02 or greater hatching vere consi dered successful, those with less than 50% as failures. Also, because of the snall oumber of es that exhibited low levels of nest attendance, I combined percent attendance into two categories, 0-75% and 76-1002. The relationship between nocturnal attendance level and hatching success (Table 11) vas significant (Chi-square = 5.14, $p < 0.025$), with significantly aore clutches hatching (761) when nocturnal attendance ws nigh than when it vas low (482).

Discussion

1m the first part of the discussion, I vill exasine the prosiaste functional benefits of male parental care in E. cogui in the context of What we know about the functional significance of parental care in amphibians. In the second part, I will consider how the enhancenent of hatching success that results fros parental care affects reproductive and hence fitness of caring males.

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Table 11, The frequencies of two levels of hatching success as a

function of the level of nocturnal attendance, computed

a5 the percent of nest checks when the parental mae was

in the nest.

Percent __Bereent hatching

attendance 0-49 50-100

= 5.14, p < 0.028,

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ar le

© four functional roles resulting in incre

Je offspring

survival have been ascribed to anphibian parental care (MeDiaraid,

1978; Kelts, 1981): (1) provision of an appropriate hydric regime, (2)

reduction of predation, (3) reduction of fungal infection and (4)

reduction of developaental abnormalities.

Provision of

appropriate hydric regime. A

parental care in E. cogui is to prevent desiccation of eggs. When wale

jor function of

parents were removed from their eggs, IT of all clutenes (542 of those
clutches that failed) died from desiccation (both years combined).
Provision of parental care (control clutches) reduced desiccation to
negligible levels (1.1% of all clutches; 5.0% of clutches that failed),
?The physiological basis of egg nydroregulation by coquf wales has been
documented by Taigen et al. (1984), vho proposed a aechaniea for the

transfer of water from parent to egg across the aale's ventea

integuaent and suggested thar brooding also functions to reduce

evaporative water Lo:

Further, they shoved that incre

4 egg vater content had a significant positive effect on hatchling mass. Thus, extensive brooding by sale cogufes aay serve both to insure hatching ?and to axisize hatchling size. Both consequences are potentially important components of fitness. Although the provision of an appropriate hydric regime may be an iportant function of parental care in other anurans (Jameson, 1950; Myers, 1969; Wells, 19804; Weygoldt, 1980), our study is the first to demonstrate its inportance in the field. In some anurans parental care apparently does not serve this function (Kluge, 1981; Blomers-Schlosser, 197: 5 Scheel, 19703

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McDiarmid, 1978; Simon, 1982, 1983).

Reduction of predation. Conspecifice are the principal ese

predators in E. coqui. Neat defeni

by parental males is a significant

counter to this threat. In male-removal experiments, 31.7% of the experinental clutches were consumed by conspecifics, as against 14.3%

of the control clutches, @ two-fold difference in the incidence of

heterocannibalise, Parental defense of eggs ageinst conspecifics appears to be important in at least tvo other anurans, Hyla rosenbergi

(Kluge, 1981) and Cophixatus parkeri (Simon, 1982, 1983), Filial cannibalism occurred in E. cogui only vhen disturbance of the eggs by

the investigator or an intruding conspecific occurred during

rly

developaent. Filial cannibalism probably is not an adaptive response in

this speci

s either as a source of utrients for an energy-stressed

parent (Rohwer, 1978), oF to remove eggs infected vith fungi, as hi

been found in sone salamanders (Highton and Savage, 1961; Tilley, 19725 Forester, 19793). Once a male coqu{ began to ingest his om eggs, he ate gost or all of thea. There was no evidence of discrisinstory ingestion of only dead eg

inst invertebrate predators may be an important
fonction of parental care in other amphibians (MeDiaraid, 1978; Simon,
1982, 1983). tn Ex coqui, egg predation by invertebrates vas
infrequent and the presence of parental wales did not change ite

relative incidence. The results of the aale removal experiments

suggested that asles are either indifferent to invertebrate egg

Predators or unable to defend clutches against thea. Observations of

88 predators in the field and leboratory corroborate this conclusion.

?The ain invertebrate ogg predators were an ant (Paratrichina sp.) and

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e

the larvae of a suall phorid fly (Megaselia scalarie)(Villa and

Townsend, 1983). The ants occasionally invaded coquf neste by the

thousands and deci

ted any clutch therein, Megaselia scalaris is a

very saall fly that could oviposit on coqut efi

vithout being noticed

by male frogs or while males vere temporarily out of the nest. The larvae develop very quickly and completely destroy a clutch of coquf ces, reducing it to a sliney mass, vithin 48 hours. Te incidence of predation by either of these predators was leas than 22. There vere several other invertebrate egg predators of more minor effect (taking only 1-3 eggs at 2 tine), including @ cricket (Amphiacuste portoricensis), two land snails, and a spider.

Reduction of fungal infect ior

ten

been suggested for sone

frogs (Blome!

Schlosser, 1975; Simon, 1982, 1983) and some eal

wanders (Highton and Savage, 1961; Tilley, 1972; Forester, 19798)

that an attending parent may reduce fungal infection of

s either by

secreting an antibiotic substance or by esting infected

sto prevent infection of other eggs. However, neither Forester (19798) nor Simon (1983) were able to isolate a substance or to demonstrate that skin swabs had a fungicidal effect, In E. cogui, fungi grev only on exes ?hat were already dead and never appeared to spread to noraal living eggs. Fungi vere observed to infect dead eggs in clutches with and

without attending sales.

Reduction of developmental abnormalities. Attending parents aay reduce the incidence of developmental abnoraslities by jostling or turning eggs during early developaent (Salthe and Mecham, 1974;

Forester, 1979a; Simon, 1982, 1983). In E.

soqui, eggs are adhesive

and are often depo:

?ted on vertical surfaces. Hence, there

Little

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e

chance for the male to

snipulate the egge. There ws

no indication in

the gale-renovel experinencs that eggs deviated fro noraal

developaent.

Frou this brief review, it is clear that there is aarked

Lity among speci

in the incidence and relative importance of

the four functions proposed for amphibian parental care. Fran these

Limited a

no clear relationship emerges betyeen form and function

of parental care in anurai

For example, Cophixalus parkeri (Simon,
1982, 1983), Centrolenelts valerioi (MeDiaraid, 1978) and

Heutherodactylus cogui (this study) seem to differ substantially in
the functional basis of parental care, yet all three exhibit prolonged

attendance of eggs.

Fine

Benefits of Male

Male parental care in E. coqui involves high levels of nest attendance, extensive brooding and elaborate nest defense against conspecific cannibals (Ghapter 3). Te reavite of the male-renoval experinents (Tables 9 and 10) desonstrate that this parental care signiticantly increases egg survival and hatching success, Only 23.1% of the clutches fron vhich attendant aales were renoved hatched as coapared to 77.5% of the clutches receiving care.

Another vay of examining the results is to see how the expectation of hatching changes a2 a function of the length of the care period, ive. how hatching success changes as 4 function of removing a progressively Later stages of development. I did this by plotting the tuean percent hatching of clutches against the stage of developaent during which the attendant ale was resoved. The an percent hatching

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6

(4 1SE) vas computed for each stage for which N*5; when sample size vas

aller, the results for adjacent stages vere combined, and the value

plotted a

?inst the average value of the evo stages. The results are

shown in Figure 10. No eggs hatched vnen males were removed imnediately

aiter oviposition or during Stage 1. After Stage 1, hatching success increased slovly through aid-developaent and then accelerated sore quickly tovarde Stage 15 and hatching. In order to approximate the data land obtain a benefit function, I used a multiple linear regression

model (Nie et al., 1975), in which P(C), percent hatching as a function

of wale-renoval at Stage C, was the dependent variable and ¢ and c?

vere entered as the independent variables. A quadratic polynomial gave

4 significantly better fit than « linear aodel, yielding the function.

P(c) = 0.50 - 0.26 + o,42c*

The benefit function, P(C), dravn in Figure 10 describes the

expected hatching success of a clutch after Stage x (vhen the male v.

repoved). However, the probability of a clutch surviving to Stage x ix

not incorporated in P(C). Incorporation of

is pre-renoval survivorship aay be inportant in examining the net fitness of parental care strategies in E. cogui, especially since clutches do not have 100% hatching success even with complete parental care (Table 10). The

devaluation of expected hatching succ:

5 by stage-specific survival IIL obviously change the benefit function of Figure 10 t0 4 new fonction, Since a consideration of how benefits and costs interact to detersine net fitness vill require specification of the benefit function, T vill suggest here the circumstances under vhich one or the

other type of benefit function vould be more appropriate, and derive

---Page Break---

Figure to.

hing success of clutenes as a function

ov the Gevelopwcntal etage at which the parental male

was veneved. Each point represents the mean hatching

UF at least five chutehes which had the

Fareutal sale rencved at that stage of develorment.

The Linc cervesents the best ft curve from a multiple

ysis in which F(C), the percent hatehang,

Fed as the dependent

sable and ¢ and c?,

4 squared form: of the stage of

eativah, wore entered

iedgentont variables,

---Page Break---

ONIHDLVH %

quauidojerog yo oFeys

O2|

Ov

o9|

08

ool

---Page Break---

the function which incorpora

survivorship up to the stage when the

aale vas resoved.

Af we posit that parental

Les are capable of assessing the developaental stage of their clutches, and that selection can operate

(via differential hatching success) on short-tere decision

king by

ental males, then males might decide how long to care on a

day-by-day basis. If that is so, males would be favored to ?decide! whether to atay and care or to abandon solely on the basis of future expectation of hetching, without regard to the clutch'e past

survivorship. Simply put, a male can only decide to stay if he still

has a clutch, and if he has one then past survivorship is 1.00. Hence, post survivorship is aot important in

?ing a decision. In this case,

the first benefit curve (Figure 10), in which hatching success is plotted only as 2 function of what happens after male renoval, is the appropriate one.

Suppose, instead, that a nal

5 care strategy is more or less set prior to breeding. This could be a consequence of either genetic or

ontogenetic factor

Imagine that a

e's strategy is to ?care for X

days, then at

sndon', In that casc, selection should act on the strategy as a whole, adjusting X to saxinize reproductive success. The expectation of hatching aust take into account the entire history of the cluteh, including its survivorship to X (with parental care) aad its survivorship from X onwards (without parental care), 1 will

designate this second function as S(C). To calculate 8(C), t fir

describe the 1(X) curve for clutches vaich received parental care throughout developeent. The 1(X) curve represents the probability of a

clutch surviving from oviposition to Stage X, given normal parental

---Page Break---

o

care to Stage X. Only clutches that were found within one day of oviposition and followed to hatching or failure were used. There were 60 such clutches during April-June 1980 and June-July 1982. 1 designate the total number of eggs at oviposition as N(O) and the number still viable at Stage X as N(X). The ratio, N(X)/N(O), then constitutes the

stage

ecific survivorship of clutches receiving parental care and is plotted against stage of development to generate I(x) (Figure 11). To obtain $(C), the total expectation of hatching of @ clutch as a

function of care to X and no care after X, I compute the product, 14x)

times P(X), for each X. S(C) is plotted

the lower curve in Figure
M1. Note that the incorporation of 1(x) does not change the shape of

the benefit curve; it only lowers the

yaptore.

---Page Break---

Figure 2

A plot of the stage-specific survivorship, 100, of 60

clutches followed from oviposition to hatching or failure.

S(C) is the conjugate curve derived from plotting the

proguct of PIC) and 100 for each developmental stage

at which parental males were removed. See text for detaiis

of curve computation and plotting.

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CHAPTER 5

?THE COSTS OF MALE PARENTAL CARE

Incroduetion

Male coqufes inv

4 great deal of tige in caring for developing

eggs (chapter 3). While this cine investment results in highly

significant bene!

ts in hatching success (Chapter 4), any a

Lysis of

how natural selection acts to a

tain parental behavior in the

Population aust consider the costs of providing care in teres of wale

reproductive succe

Costs of parental

sre are postulated to be of two types:

increased risk of gortality and (2) decre.

ved future fecundity, 4

variety of causes way give rise to these costs. Performing parental care might involve a temporal or spatial shift in activity or

icrohabitat of the car:

?iver into a state in which exposure to

Predation was greater (Forester, 1979). Alternatively, behavioral or

Physiological processes specific to caregiving aay use energy that

Fesults in a decrenent in the care-givers physiological condition and

hence incr:

Woe the risk of mortality. While an energetic cost aay

result from greater

tabolic expenditure in giving care, auch a cost y also originate from reduced energy intake if foraging activity is

constrained by the teaporal demands of care-giving (Fitzpatrick, 1976;

Rohwer, 1978; Krzysik, 1980; Forester, 1981; Simon, 1983; for en

exception, see Kaplan and Crump, 1978). While the consequences of a

tive energy budget caused by providing care may not be severe

fenough to incr:

1e mortality risk, they say decrease the energy that

can be devoted to future reproductive effort (Walters, 1982). In

---Page Break---

fevales, this

'Y correspond to reduced production of mature of

For

Le frogs, which have indeterainate growth and in vhich fecundity is

highly correlated with body size (see Chapter 2), energetic demands of

care could result in slower groveh rates with consequences for

fecundity throughout the rest of a female's lifetine. In les, an

energy cost probably translates into # reduction in reproductive activity following the period of care while they make up the energy deficit; nence it increases the time until males can begin to advertise for gates and translates into a lover rate of success in fertilizing

For aales, the time spent caring

yy itself consticute a cost since it may preclude reproductive activity, leading to the sane Jn this section, I (1) consider what the costs of parental care

are, (2) present esti

es of the proximate magnitude of those costs, and (3) suggest how they might affect male reproductive success, A discussion of how benefits and costs interact to determine net fitness

(reproductive success)

postponed until the next chapter.

T exanined two types of costs of parental care for E. coqui ales

Feoulting from the prolonged period of nocturnal egg attendance:

reduced feeding opportunities and reduced calling activity.

Methods

Estimating energetic <%

Attendance of eggs in an enclosed nest site may reduce the

opportunities for m

parents to feed. The a)

lability of food itene

in nest sites such as Cecropia leaves, rolled sierra palm frond:

---Page Break---

n

banboo houses and other enclosed cavities is assused to be lower than

levels of food available in the open habitat, where aost non~parental ndults are found at night. Hence, renaining inside a nest site vith « clutch may reduce nocturnal food intake of parental asles relative to that of non-parental adults that are active in the habitat.

To seasure the feeding levels of parental

les, 1 sampled the

stonachs of brooding males just after dawn on tvo mornings in July 1982. A syringe stomach puap (Legler and Sullivan, 1979) was used eo flush the stomach contents of parental males taken from their nests on the mornings of 4 July (0515-0830 hours) and 14 July (0630-1030 hours). Tis technique is highly effective for recovering total stomach contents and, since gut passage tine for coqui vas estimated to be 16-18 hours at teaperatures sisilar to those in « study, stomach contents are assuaed to represent those items eaten during the previous Bight (L.L. Woolbright, personal communication). To be sure that all contents were regurgitated, each frog was punped three tines. Stomach

wediately preserved in 702 ethyl alcohol and Later

examined under a dis:

jeting microscope (12K). Each item was identified

to order and measured for average width and Length to the nearest 0.01

me. By treating items

cylinders, voluse was calculated using widen

the diameter.

No male vas

pled on more than one day (four males that vere

wapled on July 14 vere not included in the analyses), and males that

vere attending hatchlings were not used. Comparisons of the atonach
contents of these brooding males are wade vith those of non-brooding

adults which vere sampled at about 0600 hours on five mornings in 1982

Ddetween July 4-19 by L.L. Woolbright (personal communication). The

---Page Break---

non-brooding adult

taken by capturing and preserving frogs,

Later dissecting out their stomachs and analyzing the contents in the

?Another vay of estimating an energetic cost of

ental care is to
sonitor weight changes of parental frogs aver the course of the care
period, During May-June 1980, I did this by weighing brooding frogs

early and late in development. Males were resoved from their nes!

Haced in a plastic bag and seasured for SVL to the nearest 0.5 nm vith
P

aap ruler. The

1e was then removed from the bag, gentle pressure
applied to the groin to eapty the bladder (bladder contents vere
weually voluntarily expelled while the frog vas in the first bag),

patted dry with a paper towel and placed into a second bag. The dag and frog were weighed to the nearest 0.05 g using @ 10 g Pesola balance. The frog vas then removed, the bag reveighed, and the frog's veight determined by subtraction. Both weighing procedures vere performed until three consecutive veights vere obtained thet varied by Less than

0.1 g and the average of those three vas used.

In eight

se the sane male was veighed early and late in

developwent. Additional independent samples of 22 males

rly in
development and 12 males late in development were also taken. All weights and measures vere wade between 1100 hours and 1700 hours

(average times of measurement are given in results).

Calling activity was monitored from January through July 1980 in

Dicks House Plot at biveekly intervals. At each survey, the entire

Plot was searched for calling males. For each male, its position in the

---Page Break---

Plot, the characteristics of the call site (type, height off the

around, orientation), and the male's identity (frogs vere aarked by

toe-clips) were recorded. Because Dicks House Plot ws

surveyed

biweekly (complete surveys) for frogs and nests, 1 also knew the

location of every nest and the identity of each parental on any

siven might, Tous, I knew which of the calling males on any night vere

parental males and wh}

were not. I then estimated the percentages of

parental nales that vere cal

ie and of non-parental wales that vere

calling

the ratios of calling males to total males in each category.

The total number of non-parental males in a plot on any night was estimated from the mark-recapture records. Because surveying and warking in Dicks House Plot vere begun in January, well before the

dates used here for est

ting these two ratios, I used the number of

?marked sales present at any time as the total eature mate complement. A

sale vas counted as present in Dicks House Plot on any date between ite initial capture (or after it attained an SVL = 29.0 am) and its final

capture. Malee that vere captured only of

vere not counted unless the capture date coincided vith a particular survey date (and then only for

hat dace).

To estimate how successful parental males were at obtaining new clutches versus non-parental sales, I cospared the proportion of non-parental sales that obtained clutches during 1980 in Dicks House Plot with the proportion of parental wales that obtained second

slutches during that time.

Results

Energetic ¢

---Page Break---

Five (33.38) of the 15 brooding &

4 bad food in their atoaacha

on & July, while 15 (502) of 30 wales puaped on 14 July had food. The Feaaining aales on both dates had eapty stomachs. Only two of the 21 on-parental, calling wales (9.5%) sanpled during July had empty stoaache, Te difference in frequency of enpty stomachs between Parental and non-parental calling sales was highly significant (Table

412A). Of the 20 parental males thet nad food in their ouachs, the wean number of iteas per stomach was 6.0 + 1.8 (RangesI-31, N+19; one male had a large item that could not be extracted and is not included in volume statistics).

Non~pacental colling mates had 2.1 + 0.4 itess Per stomach (Rangen1-8, 4619). Average volune of food (Table 128) was not significantly different between the tvo groups when only males with food in their stomachs were compared. Hovever, vhen groupe vere compared using all males (empty and vith food), they were significantly different (Table 128). The Large variance within groups in food volume is a problen in asking very strong inference from the volume results.

In order to assess whether parental asles change their foraging habite (and hence their food intake) as development of their clutcnes Proceeda, I compared che frequency of empty stomacns among the three developsental intervals (Table 13). Although there vas a tread cowards 2 decreasing frequency of eapty stomachs from early to Late developaent, it w

not significant.

T next con

ider the results from weighing parental wales. Every

fone of che eight

les that vere veighed twice lost weight between the

first and second measurements (Table 14). Mean weight loss was 0.36 +

0.07 g over 10 co 13 day intervals. shen weight Lo:

vas corrected for

the number of days betveen measurenents, the mean weight loss per day

---Page Break---

Table 12, The stonach contents of brooding males and nor-perental

cailing males sampled at dawn on £40 mornings end fine

mornings, respectively, curing July 1982. A. ?The freqvene

cies OF stomachs that were either empty or contained fea.

4. Mean 4 SE (8) volune of stomach contents

a

Empty Stomache

stomachs with food

Brooding males 2 20

calling maies 2 a9

x? © 12.95, » < voor,

p.

Volume of stomach contents

Broodin: canting

pales nates woop

AIT stomachs 125.8 456.9 225.3 475.0 174 sae

(r= as) (w= 19)

fonty stonach 654295 tess 462 283 <.c02

with food ww oa) mean

?Mann-Whitney vetest.

An the two groupe,

---Page Break---

76

Table 13. the frequencies of empty stomachs and stomachs vith food

of parental males at dan as a function of the develoseentad

intexval of their clutches at the time of sampling. The

Proportion of row totals are in parenthest

Developeental Empey Stomachs

interval ?stomachs with food

x 6 (67) 339

u 9 (56) 7 (aay

ur 20 (.50) 20 (.50),

---Page Break---

Table 14. Body weights of parental males measured early (before Stage

4) and late (after Stage 12) in the developmental periods

of their clutches. Means + SE.

rary late

aevelopent evelopment student's ©

Sane males measured

early and late (8)

Mean tine of aston. 2580 he

sve 33.1 4 0.57 -

Mass (3) 2.864012 249 40.11 s.a6ee

ALL males (inelua~

ng eight above)

Mean tine of 1420 he iano n.

easurenent

sve 33.140.26 23.39 4 0.36 ns

Mass (5) 2.81 40.07 2.584 0.08 2.104

8 30 20

p< 208.

P< .00L.

MS ~ not significantly different.

---Page Break---

7

vee 0.031 + 0.005 & per day

Tf 1 anaune that per diem weight loss

constant throughout the parental care period, # total weight loss of

0.527 (SD + .255) is obtained over # 17 day period (the average

developmental period in May-June). This aeans that the average wale

would lose 18.2% (0.53/2.86) of his initial body weight by caring from

oviposition to hatching. Average initial veights for these eight aales were 0.086 + 0.008 g/mm (2.86 + 0.34 @ per frog) vith final average

weights of 0.076 + 0.006 g/am (2.49 + 0.30 per frog).

Reproductive costs.

?A potential cost to parental sales in wis

mating opportunities

vould exist if, (1) by providing care, males reduced che time spent

calling oF the effectiveness of calling (if neste are inferior call

sites) aod (2) gravid females are available. Nest sites and calling

sites for

coqui are almost mutually exclusive microhabitats (chapter

2). Nest sites, as closed cavities that are near the ground, sake very

poor calling sites and are never used

such by parental males. Hence, by spending a lot of time in their nests, parental wales wight reduce the Eine they spent calling and pay a cost in reduced probability of attracting gravid fenales in the area.

?To estimate and compare the frequencies of parental males that called versus those of non-parental males, I used seven of the complete calling surveys of Dicks House Plot made between March 1 and July 4, 1980 (Tabte 15). Te average number of marked males present in Dicks House Plot on those datos w

81 (67 non-parental wales and 16 parental

sales). Te proportion of son:

yrental males that were calling (Table

15) ranged from 23.42 to 31.9% on individual nights, while 0-102 of

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Table 15. the proyortions of non-parentai and parental males that were calling in Dicks House Plot on seven nights from March to June 1980. A. Records for individual nights. B. The frequencies of caling versus non-calling states for non-parental aca

- Parental males; cell totals represent summed frequencies for all seven nights.

a

Non-parental males Parental males

Number Percent Number Percent

Calling calling W calling calling

enn

March 4 ous 23.4 wn 67

March 1 6420 cree rr) o.0

march 17 a ou 23.3 wo 0

apis 9 2 31.0 wo a.

april is 2a 318 awa 6.7

. May 21 mas ae moa

gure 7 ee 28.4 wok 10.0

Colum: Means 67.3 19,4 28,8 190.64

7 cabling Son-ealling

Non-parental males 136 338

Parental males 4 93

x? = 26.53, p © 0.001.

---Page Break---

jarental males called on any of those nights. Combining the results for

ala

fen nights, parental wales called significantly less frequently than did non-parental males (Chi-square = 26.53, df = 1, p< 0.001). During the 126 day period froa 1 March co 4 July 1980, 114

clutches were deposit,

in Dicks House Plot on 69 daye (1.65 clutches Per deposition day)(chapter 2). At Least one clutch wes Laid in Dicks Mouse Plot on 54.8% of the daye during that period. There is no question therefore that gravid females vere available on « regular

bai

* during March-July 1980 and that parental males that did not call vere missing potential opportunities to mate.

1n order to obtain an estimate of 4 mating cost from parental care, I calculated « nightly probability of wating for calling males in Dicks House Plot on each might during April-June 1980 and June-July 1982 when a complete calling survey had been perfored (Table 16). The nightly probability of mating was computed as the number of clutches that were deposited in Dicks House Plot on a particular day divided by the nusber of males that vere calling on the previous night. Clutch deposition for 1980 is derived from Figure 4, t have siailar information for the clutch deposition chronology in 1982. Calling wale densities are obtained from Tables 1 and 2. The resultant nightly ?uating probabilities are presented in Table 16

Nightly meting probabilities ranged from 0.0 to 0.235 feaales per calling male-night, with a median value of 0.050 (W = 71). I have included nights when no fenales sated (probability of 0.0) because by calling on those nights, some males vill have expended energy that

y

Preclude their calling on some other night when gravic

fanaies are

available.

---Page Break---

Table 16.

?The nightly probability of mating for rales in Dicks House Plot calculated for 21 nights during April through June 1980 and June and July 1962. The Nightly Probability Of Mating (KPM) was computed as the ratio of the nunber of females depositing clutcnes on a particular day (the second @ate given below) to the munber ef calling males on the Previous night (the first gate of the palrt below), number of Number of

Dates calling males rating females Nw

3980

apr 2-3 5 ° 9.000

April $10 22 2 9.091

april 16-17 2 2 orga

pei 3e-may 3 a a 2.009

may 7-8 4 ° 0.000

say 71-22 3 2 0.083,

ae u 1 cocoa

78 2% 3 9:00

2-22 1 2 2.105

Dae 24 ° 21009

1962

June 10-11 1s 1 0.063

Sune 11-12 6 i 01067

dune 12-13 8 2 0.325,

Sune 3-18 u a o:091

Sane 18-15 n 4 0.238

Dune 15-16. yn ° 0-000

daly 8-9 2s ° 2-000

July 9-10 2s 1 2.036

Duty 19-11 20 1 21050

Suny 11-12 23 2 0.035,

Suny 12-13 20 a 0.050

Median 0.050

a

---Page Break---

During the period 1 Janvary to 4 J

ty 1980, 129 clutches vere

deposited in Dicks House Plot. Of those, only 2 (1.62) were laid in the

nest sites of aales that were attending « clutch at the tise. The other

127 (98.6) clutches were Laid with non-parental

Discussion

The resulte suge

fe thar there are costs incurred ae a result of

parental care by male coqufes. Energetic costs eppear to sten from a

reduction in the number of nights that parental males spend foraging

compared to calling non~parental males, since parental ales had eapty stomachs significantly more often than non-parental calling males, but there was no difference between the two groups in the stomach volume of

those males with stomachs containing food. It seens that when parental

Nes do forage, they are obtaining sbout as auch food as non-parental

calling sales.
Toe reduced energy intake as a function of nest attendance in £.

equi may not resuit overall in a depressed energy budget for parental

ales relative to non-}

rental calling wales. Because nest attendance

is generally passive, con

sting largely of brooding (chapter 3), netabolic rate is probably Little different from resting rates, and certainly lover than for a frog that is active or calling. Taigen et a1, (1982) estimated that oxygen consumption rates for active frogs wore about seven tines higher than for resting frogs. Woolbright (versonat comaunication) measured oxygen consuaption rates of inactive

males and inflated

les in the field at night (when they were exposed

to the chorus) and found they vers significantly different, vith

inflated

having rates about 3.5 tines higher than inactive males,

---Page Break---

Hither of these est:

es would suggent that the pas

ve nature of exe

brooding requires much lower enezgy expenditure than that of activities

such as calling.

?The weigh

Lows data suggest that deosding males are at an

energetic 4

vantage during the period of parental attendance. The

SlEhE parental males that were weighed twice lost an average of 18.22

(Range = 7.3% ~ 31.73) of their initial body voight over @ 17-day

Aevelopeencat period.

Evidunce of energetic costs from parental care in amphibians has

been found in several s

cine. TE

y (1972) and Rreysike (1980) found

that brooding females of Desncenathus oo

us had significanety

Tedwced foot intake relative to noa-brvading fenaies in the population.

Fitzpatrick (19/3) reported that the brooding period in the sane

sAlanander reavited in a depletion of fs¢ body and carcass 1i

content in females, In contrast, Kaptan and Crump (1978) found that

Fensles of Axby

ona opacun brooding clutches in early developmental

stages did aot differ in dry weight, tor

calories, or ueight-specitic caloric content from females brooding clutches in tate developmental stages and concluded that chore vas no energetic cost to parental brooding in this saisnancer. Te only attenpt to eeasure energetic

costs of parental care in anurans is Simon's (1982, 1983) work vith

Sophyxaiua parkeri, a New Guinea wicrohylid frog in which both sexes my care for separate clutches. Sinon (1963) found that attending Parents, of both sexes, had significantly Less food and aore plant

Raterial in their guts than non-brooding adul:

Further, fat body weights of brooding males was negatively correlated vith developecntal stase, Because the developaental period of C. parkeri is 85-100 days,

---Page Break---

4-5 times that of E. coqui, energetic costs are Likely to be aore

important for the foi

BE appears that the reduces cailing aad consequent Love of

additional eating opportunities aay be a more substantial cost of

parencal care in E. aqui. Parantal aelos «

2 significantly tess

frequently than non-parental males, ani obsaic significansty fewer

clutches. Te incidence of doubie clutches in Dicks Mouse Plot is very anall suggesting that parentat aster are

ificing opportunities to

mate. Wow many opportunities to =eaate does a male aise during «

period of parental cere?

One way of calculating su-h an esciaate of mating opportunities

Bissed would be to cransforn e ightly provabidity of gating into a

probability of mating for an ent

peviod of pareut

care. In the

above Results, I derived an esticate of 4 wightly mating probability by Gividing the nuaber of receptive gravid females im an area (Dicks House

Plot) by the munber of mater

ng in the area for each night (Table 16). Tis is essentiatly a randon-mating estinate, since T am assuming that any calling wale has an equel chance of getting a sate if fenales are available. The median nightly probability of mating in Dicks House Plot for 21 nights during 1980 and 1982 was 9.050.

Another estinate is generated by taking the most successful

fn Dicks House Plor during March-July 1960 and calculating an a posteriori estimate of their mating probability. Two sales in Dicks Wouse Plot each obtained 5 clutches during March-July 1980. Assuming that such a male called on 552 of the nights during that perio (the

average long-term calling rate from woolbrignt and Townsend, Ms.) and that his calling schedule vas indapeadent of female availability

---Page Break---

(fenales mated on 55% of

fe nights during chat period, Figure 4), such

fomale would have called on 36.33 (55 x .55) of the nights when

females aated in Dicks House Plot, Thiv is cyuivalent £0 38 nights

(0.303 X 126 nigats). To odessa t

ches by calling on 36 nights

the nightly probability of nating for such a wale vas 5/38 = 0.13.

This is a reasonable estiaate of che ow

us nightly wating probability

for an individual wale in Dicks Houec Hoe

T now have two estimates of asic nating probability; @ randoa

ating estimate and a maximum mating estimate. if X is the nightly

Probability that a naie can get « feusie, tren 1/E witi Se

of the nunber of cays requiced for # sale tu get one fexate, Hence, on

4 random mating basis, a sate should be able te sate once every 20

Rights (1/050) while # male with the macisus probability of aating

could get a foxate every 7.7 nig

(1/13). These require that the pale call every night of the period. Anather way of envisioning 4 cost Of parental care would be to calculate how any fezales a male would

pass up by aot

Hing durisg a period of parental care. Using a 20-day sare period (the average developments! peri? for March-July), the aale in s ranton aating popelation would miss one female (.05)(20), while «

?axisun male vould siss 2.6 fenstes (13/20). Thus, a gale vith a

mating probability somewhere betucen that of ri

paximun male vould sacrifice 1.0-2.6 potentiat additional clutches if he did not call white caring for a clutch, This is a substantial cost.

The next chapter addresses the question of shat sort of benefit level is necessary to offsar such a cost and accous

for the high fidelity,

complex care behavior observed in male cogufes.

---Page Break---

He

CHAPTER 6

WAY SHOULD MALE coQU/#S CARE? - MODEL AND SUMMARY

care by male coquées yialde significant

benefits in offspring aurvivat but eh

there are costs from providing

that care in tenes

reduced future

production. In this chapter, 1

Present a model which integeates the denofits ant costs of parental

care into a single statement about the

ationship of parental

behavior to fitness. 1 then usc the aodel to anatyse the net adaptive

value of male parental care in asd to an situations in

Which the mode! would wake 4iffer

tions abour the evolution of

perental care in anurans

A Ceaphical Model of Anuran Parental Care Evolution

The aoiel is an adaptation of tke marginal value model of Charaov (1976). The basic fora of tha model as it applies to parental investaent and the evolution of aating systems was anticipated by

?Trivers (1972), and has been applied co assessment of wale

ting

strategies in dung flies (Parker and Stasrt, 1976; Parker, 1978). Maynard Snith (1977) and Graton and Sibiy (1978) have applied it to exaninations of parental investment. As with the foraging applications for which it was first developed, 1 am inte

ced in examining how an

aninal can maxinize its rate of return vhen it can choose between tyo

of wt

alternate types of behavior ea

ch can contribute to the return

Choices could be either of a proxinate of evolutionary type. In the

foraging model, it is the probles of how Long to stay and forage in a

patch, and che rate of return

wrod ia snorgy per unit time. In ay

---Page Break---

application (after Maynard Smith, 1977) the dichotomy is between continuing to provide care to a current clutch veraus attempting to wate again, In males, an atteapt £5 mare would involve engaging in the appropriate reproductive behavior £0 ateract a feasle, auch as calling. For females, the atteapt to resate would involve foraging at an

appropriate level to mature a nev complement of eggs. The currency in

thie case ie ©

rate of offspring production. The marginal value theoren indicates that when the rate of return from curing declines to

?4 level that ie cousl to the wean rate of return from both activité then the animal sho

ornate activity, Tae svitening

value is the margins rate of return, below which an aninal loses

fitness as ie delays switching.

The model ie presented in Figure 12. It assuses a continuous

breeding season, such that

les and Fenalos brood more than once per

season and, in particular, that feasies are relatively asynchronous in

their oviposition schedules (Ealen and Oring, 1977; Maynard Soith,

1977). The ordias

represents the probability of hatching for a

clutch P(C), 98 # function of tse anount of tine that 4 parent

c. Tere

provides ca some asount of time, &, that as animal ust

spend before iz can gate again. For a sale, this might be the number of

nights he ust call to get another fozale. for a female, it ie the time

required to produce another clutch, The reaating time, R, is

incorporated into the model by extending the abscissa beyond the origin

to the left. If we know the fora of PC), *

we care benefit function,

and specify R then we can calculate the rate of offspring production

for any given period of care, C*, by computing the ratio P(CT)/(oT+R).

That rate of offepring production is equivalent to the slope of a line

---Page Break---

Fasare 12.

4 matuinal value modei of parestal care evolution,

© is ttre spent cart

for 9 clutehy Pic) aa the

probability of aster

aS 4 fiction of the ancune

of care, cr R is the tine befove o% animal con renate.

?Tue maxinad +6

te OF offupring production, when R= Ry,

As predicted by the clcpe of the tangent Line Grawn

ku the (igare. see text for detaite.

---Page Break---

Stope of tangent: ?P(C)_

a

P(

CHR,

---Page Break---

aravn from R through the point [C*,P(C*)]. According to the marginal

value theorem, the maximal rate of offspring production will be given by the tangent to P(C), dram fro R, that has the highest slope. tn Figure 12, that tangent has been dram and yields a value of C, Ct, which is associated vith che saximum rate of offepring production, and corresponds to the Stage at which the parent should abandon the current cluteh and attenpt to remste.

Application of the Model to Parental Care in E. coqui

In order to evaluate the net adaptive valve of parental care in cogui ve need to simultaneously analyze those consequences that contribute to fitness and those that decrease fitness. Put another vay, we need to express and analyze, using s common currency, the benefits and costs of parental care. The sode! presented above gives us the means 2 do so, Reproductive success is expressed as a rate that incorporates both benefits [the probability of hatching per clutch per unit of parental care time, P(C)) and costs (the number of clutches per unit of calling tise) to yield an estis

¢ of net reproductive success

ber unit of otal time (care cine plus calling time),

For £. coqui, P(C) is the benefit function chat vas derived in

Chapter 4 (Figure 10) using the resuite from the male-renoval

experisents, A romating time for males (R) vas estim:

fed using the

nightly probabilities of mating estimates in Chapter 5 (Table 16). The

median value of nightly ating probability in Dicks House Plot was 0.0%

fenales per calling male-night. By taking the inverse of this value, 1

obtained 20 as the amber of nights chat a male would have to call to

obtain one female. I also calculated # renating time for the most

---Page Break---

successful wale in the plot as 8 days.

We now have the evo necessary parts of the model to integrate

coats and benefits and ex:

ine the net adaptive value of wale parental

care in E. coqui. In Figure 134 1 have plotted P(C) and dram the

nt Lines for the two res

ying times, R= 8 and R= 20. For either

value of R, the tangent to P(C) with the highest slope yields a value

of parental attendance, C*, of Stage 15. Thus, the model indicates ha

in order to maximize reproductive success, a male parent should provide care right up co hatching, then leave the clutch (or hatchlings) an¢ begin calling to attract another female. This result is robust over @ wide range of renating tines because of the y-interce and shape of the benefit curve. First, P(C) gooa through the origin,

wi

means that without provision of some parental care no eggs will hatch. Mates will never be favored to abandon eggs coup!

Jetety, since abandoning the clutch yields zero reproductive success, regardless of hhow fast they can get another clutch, Second, the benefit of providing care accelerates throughout pre-hatching developaent i.e., the second Aerivative of P(C) ie positive. Tue benefit from parental care

accelerates most rapidly toward the ond of development, and then

becoues asynptotic after Stage 15. Once parental

ire starts, parental ?males get progressively greater increments of hatching success for each ?additional unit of time spent providing care. As long a8 the costs of care are fairly constant over the period of parental care, males vill realize the highest reproductive success by staying with their eggs through Stage 15. Because of the sharp asyaptote, large changes in renating time cause negligible shifts in predictions of how Long males

snould care. In Chapter 4, I shoved that there was @ distinction

---Page Break---

Figure 13. Application of the model co male parental care in

Sogui. Tangent dines aro drove for two valuey of

renating tine, R* & days and R= 20 dave. Ay Using

the benefit function vic), after Figure 10, By Using

the benefit function £/¢), after Pigure 12.

---Page Break---

---Page Break---

between P(C), a function describing hatching auccess from the

male-renoval onvarde (Figure 10), and S(C), which describes expectation

of hatching over the entire

velopental period (Figure 11). In

Figure 198, S(C) is used as the benefit function, and generates the

© predictions sbout length of the parental care period, for the sane

reasons discussed for P(C).

Tre results of the model are in close agreement with the observed

pa

ital behavior exhibited by E

oqui males (Chapter 3). Parental

susles showed high fidelity to their elutches throughout developacnt, spending 97.43 of the time during the day and 75.8% of the tive at night in their nests (Table 8, Figures 7-9). Nest fidelity did not change from early to late developmental intervals (Table 8). Mates vere in their nests at night as often during Late developaent (76.02) a8 during early development (76.62), However, after hatching nest fidelity dropped significantly (Table 6), such that gales changed from being in the nest 76.03 of the time at aight during developuental interval 111 to 44.9% of the tine at night during interval 1v (post-hatshing).

The application of the wodel to parental care in E, coqui is soneubat trivial, Knoving that hatching success is sero ia the absence

of parental care, it is obvious chat males should never be sete:

abandon eggs altogether. On the other hand, only by knowing the shape of the benefit curve is it evident vhy asles should continue to care Whroughout pre-hatching development. Ia the next section of the chapter, I consider sone less trivial cases in which the sodel aay

yield predictions that are sore useful in hypothesising about the

evolution or gaintenance of parental care in anurans.

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More General Applications of the Model to Anuran Parental Care

In the rewainder of the chapter, I will consider first a more realistic evaluation of temporal patterns of parental care in E. coqui,

a5 a means of examining how short-tera variations in parental

attendance

be incorporated into the model and now they affect the consequent predictions. Also, 1 witl expand the view from parental in a single species to amore general consideration of the evolution (or maintenance) of parental care in anuran amphibians.

In the initial exploration of the model's application to parental care im B. coqui, I used one benefit curve, P(C), that ves based on hatching success after male cenoval and a second curve, s(C), that combined post=renovai hatching auccess with pre-renoval survivorship. For both curves 1 am plotting che results of male removals and, in effect, simulating the consequences of a male completely abandoning its clutch at sone developmental stage. In fact, it seees unreasonable to expect that mates would shift from a nigh level of parental care to

plete abandonment of their eggs. It sceas more reasonable to expect that wales might decrease their level of care by some interaediate amount. Because nest sites are often the sane as their normal retreat sives (both prior to and after parental duties), it is more realistic to presuae that parental males would, at a sinimum, spend the daylight hours in the nest site with their eggs. In that case, egg brooding during the day could contribute co maintenance of an appropriate hydric state end contribute to reproductive success, albeit at a potentially lover tevel. The experimental removal of males probably aisreprescnts

the real situation of how males wight abanton their eggs. Since 1 did

---Page Break---

not do any field experiments in wich I resoved males and then provided the equivalent of sove parental care (rather chan none) after removal,

Twill adopt the following

?ario. Suppose that # male care

continuously for hie eggs (both day and night) up &

Stage x, chen

adopts a behavioral pattern of attendance during the day and absence at

night. Using the 4

2 from the male removal experiments 1 will assuse

that, if @ parental male vere to adopt this strategy, the rate of

clutch failure £

8 desiccation would be one-half of that observed in

the actual experimental recovals, for any developmental stage. The
o

incidence of cannibalism and predation would not be altered, since they
occur, virtually without exception, at nignt. The results of this
analysis are presented in Figure 14, with Figure 14A shoving the new

benefit function P'(c), and Figure 148 illustrating the new 8°/¢)

function, Note thar che pri

ry effect of incorporating these new
results is to raise the yintercept of the curves by a considerable

asount. In the case of P'(C), the change in the intercept is not sufficient to change the prediction for either level of renating tive.

Alternatively, in the case of :'(c) the tangent vith the highest slope

for a uate with a remating tine of $ days intersects at the ordinates

Such a male would have a higher lifetime reproductive success if he

adopted a strategy of daytine egg brooding only, abandoning the eggs

?and calling at night. A male with R +20 should still be favored eo

give complete care through pre-na

hing development. In fact, one can

calculate the point of trade-oft between the two endpoint strategies

(here

fetime reproductive success is equivalent) for either F(C) or

SC). To reiterate, the two strategies are (1) give care continuously

both day and night from oviposition to hatching, and (2) stay with the

---Page Break---

vs

4. Auplication of the pede? to &. Gaye using new

when there is

the sow benefit faction PC). Be

benefit tunctaon Stic).

it functions which incorporate partial hatchiog

no Parental care (C - 0). Ae Usiag

for sere detatte.

---Page Break---

a)

A

20

B

20

---Page Break---

ge during the day but leave at night (i.e,

?intain @ noreal diel

activity pattern but brood the eggs vhen in the nest site). Tre trade-off point ia repr

jented by the x-intercept of the straight Line

that passes through the y-intercept and is maxis

Ly tangent to the function. For P'(C) this occurs at R= 4.5 days, for '(C), at R= 9 days.

In the above analysis, it appears that «

Le with the maxiaun nightly probability of mating (yielding an R= 8 days) should not Provide care at night if, by adopting auch a strategy, his cluten suffers only half the Level of desiccation of a clutch that received complete parental care. There are two reasons vhy such @ parental strategy is unlikely in this popvlation of coqui. First, a renating time of 8 days probably represents an unattainably low rewating tise for any male in the population. Second, even with a stretegy of care onty during the day, the rate of desiccation of eggs would be sufficiently great during early development that few clutches would survive if parental males did not care continuously for at least the first few days of develoyment. Hence, my assuaption that only half of the clutches that perished from desiccation in the male removal experiments would have done so under @ daytime only brooding schedute is probably unrealistically lov for che first few days of development. Consequently, the y-intercept for either P'(C) or $*(C) wuld be lower than depicted in Figure 14, Taigen et al. (1984) shoved that coqul ees lost vater rapidly, regardless of their developmental stage. Hovever,

eeu that had had a longer period of parental brooding gain in vater
content as a result, and would be expected to better withstand

desiccation from a change in parental behavior than would younger exes

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(faigen et al., 1984).
The crucial point of the above exposition is that if survival of

eggs without parental care

high enough there is the possibility of
variability un reweing tine resulting in markedly different predictions

about optinal care strat:

It is important to reiterate the point
that the only reason for the existence of 4 sharp trade-off point

between no parental care and complete parental care is the shape of the
benefit function. As long as the function is convex (boved toward the

abscis:

), only the two endpoint strategies can yield waxiaal

reproductive success.

What are the implications of incorporating this nev benefit curve,

in oh

there is some level of hatching success without any parental

care, into the model? The principal result is that x

cing time

becomes a critical factor in eaking predictions about parental strategies. 1f there is individual variation in the renating ¢i

the population, there could arise the case in which wales that

relatively great success in attracting fer

Nes (e.g-, wore larger, had

better territories, etc.) might be expected not to care for eggs, since

ing times vould be short enough to yield @ maximum tangent

to the benefir curve with an intersection at the ordinate (sucha the

le vith R= 6 days in Figure 148), Males that were less successful (ies, had longer remsting tim

) would have a maxiaum tangent to the

benefit curve that intersected it near the asyaptote (such as the gale vith B= 20 in Figure 143), Such males would be predicted to exhibit complete care. If individual variation in remating tines wae sufficiently great so that some aales fell on either side of the

Erade-off point, we aight predict @ behavioral polymorphise in the

---Page Break---

Population wich respect to parental care. Some individuals would

exhibit complete parental care while others would provide no ea

There ie no intermediate strategy vnich would be optimal in teres of

Lifetine reproductive success.

A similar argument can be made for the evolution of facultative Parental care (Wells, 1981), If adverse environaental conditions which csused cotal clutch failure in the absence of parental care during one part of the year (such as Figure 138) were less harsh during another season, survivorship of abandoned clutch:

aight be increased (as in

Figure 148). Under euch seasonal variation, it would be advantageous for ales to care for clutches during one part of the year (e-g., R= 8 days in Figure 198) but co abandon clutches during tines of more favorable conditions (e.g., 8+ 8 days in Figure 143).

Up to this point, I have considered only the question, "If the fale is the care-giver, how should he provide care in order to eaxinize his Lifetiae reproductive success?". A fundanentally more interesting

question is, "When parental care evolves, which sex should provide

in the next section, I will consider how the model described herein aay be useful in waking predictions about the evolution of sex-specific

parental strategies in anurans.

In the above discussion, 1

de the point chat a benefit curves,

such as P'(C) or $'(C), which intersected the ordinate sufficiently

above the origin could generate circumstances vherein individual

variation in the remating tis

of males could lead to warkedly

4ifferent predictions about the presence or absence of parental care.

Consider the following situation. Imagine a species Like

coqui, but

without parental care. Given a mutation vhich causes its bearer to

---Page Break---

spin attending eggs, vhich sex (if either) should evolve parental care? twill suppose, ae is likely for anurans, that one parent ia better than none in improving hatching success, but two parents are Vicele better than one (Maynard Seith, 1977). Hence, if one sex evolves parental care, the other sex vill not, since it can contribute little ore to hatching succes

1 also

june that there is no difference in

?the quality of parental care that either sex could provide. This is

Feasonable for egg attendance in anurane. There exists a benefit curve

of the form P'(C) in Figure 144, and we can ests

we the relative

Femating tines of males and fe

les. Resating tine for fensles vould

correspond to the tie it took to produce a new clutch,

There are two possible alternative situations. In the first (similar to Figure 148), the two sexes have different reaating tines,

If the yointercept of P°(C) i

sufficiently high (relative to its

asymptote) and the reuating tine of one sex is sufficiently short, ve

would predict that the sex with the longer res

ting time should evolve

care, the other sex should not. In E. coqui, the male has the shorter

Fenating tine, A sale in a randoaly mated population had ar

ating

Hime of about 20 days. Fesales, on the other hand, require 8 to 10

weeks to produce a new clutch in the field, a reaating time that is

about three times longer than gales. If the intercept of P'(C) or

S'(C) was higher (or developmental tise vas longer such that the slope of the tangent Line through the intercept vas lover), the trade-off

point might fa1l betveen R for fenales and R for

es, in which case

we would predict that females should care, but males should not.

?Again, the issue here is not to focus specifically on

investigate a general prediction of the model. If the benefit function

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from providing parental care intersects the ordinate at # sufficiently

high value (as in Figure 148) relative to the height of the asyaptote,

and te

ting times differ between the aexes, there exists the possibility that selection would act against the evolution of parental

care by the sex having the shorter re

ting tine and favor its evolution in che sex having the Longer reaating tine.

In the alternative situation (similar to Figure 144), it is irrelevant vhether or not the sexes differ in their renating tines Since both have remating tises thet are greater than the trade-off point on the abscissa, The maximum tangent lines dram from R of either sex vill intersect the benefit function at the asyaptote. In this case, either sex would have higher fitness by evolving parental care. Wnich sex does #0 would depend on initial conditions in the population, a

point that Maynard Saith (1977) aade in ex

ining che applications of game theory to parental care evolution. When one parent is much better that none, and two are little better than one, there are two possible

ESS's, one in which the female deserts, one in vaich the gale deserts.

"Given that two ESS's often exist, it is hard to predict which will actually evolve, since this depends on initial conditions" (p.4)-

The situation in E. cogui is akin to that of Figure 14a rather than Figure 148, as can be seen by isagining the tangen* line for females vith R= 60-70 days on Figure 14A or 148 and comparing it to the tangent Line of the random males (R= 20 days). Clearly, if these wating times for male and female coqufes are representative, then from an initial condition of no parental care, either sex would be favored to evolve it. Why males, rather than females, becane the care-giving sex is a question that we can address only by a consideration of vhat

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factors, other than fitness benefite and coste, may have predisposed one sex to care over the other. We need to examine the possible initial conditions (Maynard Saitn, 1977) which could bias the possibility of one sex versus the other providing parental care. Wells (1981) provided a thorough review of the initial conditions which may influence the evolution of sex-specific parental strates, in anurans. Te folloving analysis sues auch to his paper. Tt has tong been realized that there is a strong qualitative association between fwode of fertilization and sex-specific parental care patterns. Species vith internat fertilization a0% often have at least feaale parental care. Many internal fertilizers, such as birds, have biparental care dur few have exclusively male parental care, Species vith external fertilization nore often have male parental care, although there appear to be a fair nunber of species vith external fertilization (presuaed in the case of many frogs) and female parental care (Cross and Shine, 1981).

Several hypotheses for iis association have been suggested. The first and perhaps aost compelling is that in species with internal fertilization, mates should be Less certain of their genetic edness to their brood (females should never be uncertain about

genetic relatedness) and hence Less apt to invest heavily in

post-fertilisation care if they are raising somsone else's offspring.

By this argument, male parental care should be rare in species with

internal fertilization. Since, with «

nal fertilization, both

Parents on average should have © high certainty of relatedness to

offspring, this argument does not predict which sex should be favored

to provide care under the latter mode of fertilization. However, in a

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Fecent review of parental care patterns in fish

ind amphibians (the

to groups in which both external and internal fertilization ars found) Gross and Shine (1961) tested predictions from a paternal certainty model against the parentel patterns of the two groups and found no correspondence. Also, it has been pointed out by Maynard Smith (1978), and demonstrated by Worren et al. (1980) that vhen paternity is uncertain in a population (i.e., cuckoldry occurs), then all males vil!

suffer potential for cuckoldry, and relative reproductive success vill

depend onty on hatching su

ese of the clutch. Only under special

conditions will level of paternity play an ispo:

role in whether

aales evotve care. Put another vay

low paternity aay be a cost of

?ating ins population vith internal fertilization, but it vill not
Fepresent any special cost in the provision of parental care by ales.

A second hypothesis that has been advanc

od to explain the

ciation between external fertilisation and mele parental care is

that

Hes aust be present shen eggs arc laid, and thereby have the

opportunity to evolve care, if it is advantageous to do ao. In internal fertilizers, of course, fenates either lay eggs after the male has lef

OF Restate the young and consequently males have a tov probability of

Deing present to provide care during development or after hatching. As
Wells (1981) pointed out, this hypothesis aay be sufficient to explain
how male perental care is maintained once it arises, but aot to predict
which path evolution would take from a starting point of no parental
Another hypothesis to explain the evolution of male parental care

postulates the occurrence of a epecial preadaptive association between

@ sale and his brood, In particular, if wales defend territories which

---Page Break---

include oviposition sites, then by having clutches Laid within their
territories, aster may have the opportunity to associate vith eggs, and
increase hatching success, vhile continuing to attract new females

(Wiitiaas, 19755 Ridley, 1978; Perrone and Zarct, 1979; Wells, 1981;

Gross and Shine, 1981). This is an attractive and parsigonious argunent

for the evolution of male parental care, and seens to agree vith the

few data which are available for anurans (Wells, 1981).

Eleutherogactylve coqui iss good species with which to ex.

some of these hypotheses. In the first place it has internal

fertilization, On the basis of the paternity hypothesis, we should not

expect male paren?

care. Buen ¢

rhe

ial conditions under which

Parental care evolved in thir species were auch thet the level of

paternity was an important factor in whether sales or femsles wore

selected to care (erren et al., 1950), and tov certainty of paternity

selected against sale parental care, thece does not appear to be 4

potential for cuckoldry. There are three lines of evidence against

cuckoldry in £. cogui. First, ay observations of courtship, amplexus,

and oviposition suggect that gale insesinat ion and fesale ovelation

oceur very clo:

together in ime, auch that there ie onty a salt

difference in the tise at shich males and fensles commit themselves to

@ gating. Presunubly, if males comitted themselves very early in

aaplexus, there wight be tine for a female to leave the nest and find

another male with which to mate, thereby holding the second mate.

Second, the secondary anplectic position is assumed very close to damm, and is prosusably followed by inseaiaation, such that @ fonale Leaving at that point would have to wait at Least another day to ace. Third,

females seem to have no control over wether or mot to lay eggs once

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they have ovulated, In situations where 1 separated amplexed pairs, handled fensles and placed thea in plastic bags in the laboratory (conditions under which females eight be expected to reverse the

decision to ovipos

y and retain their ovulated eggs if they could), all females Laid their eggs within the time frame of @ normal wating. This suggests that, once ovulated, the process is irreversible and non interruptabie. It may be that en irreversible commitment to lay eggs is ?sade even earlier, before ovulation occurs, via a physiological

sequence that is triggered by some other

etic event, such as che
secondary anplectic position. In suamary, even if low paternal

certainty could be a factor in E. coqui, there does not seem to be a

potential for cuckoldry in the spacies and hence low paternal certainty
hhas not deen an obstacle to the evolution of wale parental care in the
species.

The hypothesis that

Les are tess likely to be present when the

858 are Iaid with internal fertilization does not hold for E. coqui,
Since sales are present throughout oviposition, and both the gale and

fenale renain in the nest following ovipos jon for the remainder of the daylight hours.

The territoriality hypothesis appears to be a strong candidate for the evolution of wale parental care in E. coqui, as vas suggested by

Deewry (19706) ani Wetis (1981). Nest sites

re usually within 2m of the usual calling site of parental males, and are certainly contained vithin the mate's usual acoustically defended area. Females travel to

males to

ke and are lead by the sale to a nest site that is veually close to his call site, often, ¢ nest site has been a former retreat

site of the aale, not of a female. Fensles have been found to travel up

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to 20m from their norms! disinal setieat sites to mati

= Both males and

feo

s will defend diurnai retreat sites, so aale defense of

oviposition site itself is likely to have been the case, The required

position of wales to ewive cares

ertainiy present. once

saale be}

wed a clutch ia his usaai iurnal retreat site, a

tendency

imtain contact with it wight increase its probability of hatching.

Strictly diurnal attendance wos probusly increase 4 aale?s

Teproductive success, and involve relat little cost in reduced

future matings, a5 suggested by

gare in, aowever, given the Felationship detween sonefits and costs Lio gore prolonged care, again

8 in Figure 13, ve should expe

ny inicial association to evolve to

the situation of protongad, nigh £4 hat we find in £. cogui

today. one interesting bit of benaviora! evidence for the tertitoria!

association of a ale with # cl

bis that, whem dusk comes on the day of oviposition, tne parental mate bogins to give aggressive calls, of the same type as thoso in nest and cetreat defense encounters. These fare undoubtedly directed at

ix still in the nose site,

and result in her imninent depos

¢ from the seat. In three cases, T

have even seen the mato deliver several capid

posterior as she left

In this thesis, 1 have addressed the issue of parental care ina

neotropical frog from an evolutionary point of view, considering how

costs and benefits to liferine reproduc

ive success contribute to an

animal's fitness under different pacteras of parental ace. An equally

ation is that of che physiological conteol

Of parental behavior. Soue of the observations made in this study

suggest several intriguing questions about how pareatal behavior may be

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turned on or off and vhat mediates the transition from high levels of

calling and call site defense to

h levels of nest site attendance

and nest site defense at aight. Perhaps the proxi

ee control of

ental dehavior is by changes in the levels of reproductive hormones.

The developaent and aaintenance of thi

brooding pouch in some marsupial

hylid frogs is aediated by progesterone (dei Pino, 1983), There are

very few data on the hormonal controi of reproductive behavior in phibians (but see Moore, 1983). A partial expi

ion for the

Aichotony of sex-specific parental strategies in anurans that has perplexed Maynard swith (1977) and others could Lie in sex-specific hormonal attributes that have served af preadaptations for parental

care. ve

Weed detailed studies of parental care Cand ite absence) in

Ry wore anurans before ve can understand whether the evolution of

ental care has a cingle explanation or resulte froa some coubinat ion of demographic, behavioral ant physiological factors.

A narginal value model of parental ©

?cis presented that

incorporates the time dependent bonofits of attending esge and the

consequent costs of reduced calling activity, and relates the tvo

paraneters via a cosnon currency of rate of offspring production. Te

model indicates that aale coquies maximize their Lifetiae reproductive

by providing nigh fidelicy care from oviposition to hatching.

ditional analysis of the godel indicates that three critical

paraneters in analyzing the evolution of parental care strategies in anurans are the shape of the bane fit func

ion (hatching auccess as a

function of the care provided), the level of hatching success realized

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aor

when no parental care is provided, and the relative lengths of tine

before individuals of either sex can gate again. Under sone

circumstances (with certain values of these three parazctera), the

model makes specitic predictions of which sex should evolve care. Under

other circuss

wnces, either sex would be favored to evolve care from an initial condition of ao parenta! care, and initial conditions such as

node of ferti

ation and territoriality must be examined to account
for the evolution of sex-specific parental strategies. tn E. cogui, the
model indicates that either sex would nave deen favored to evolve

parental care initially, ince either sex would have realized a

Significant increase in reproductive success over no parental care by
doing so. IE appears Likely that ates evolved care im E. cogui
because of their initial association with eggs stemming from
territorial defense of ovipmtis sites, Regardless of vhether the aodel
an predict which sex will evelve care, it predicts the extent to which
Parental care shovid be provided. It also aay serve to detect

situations in which we should expect to see facultative parental care.

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APPENDIX 1

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

MATERIAL AND METHODS

Deseriptions of morphological features are based on Laboratory observation of Living and preserved materiel. During July and August 1979, eggs were collected in the field at various stages of development and observed in rhe Laboratory through hatching. Eggs were examined twice daily by eye ans under a stores aicrsscope at 7-30X. Laboratory teuperatures range! fro 21 to 24.5 ¢. Adds oaal observations were je on materia « served in 19% buffered formalia during April-Joly 1980 and June-July 1982. Preserved eabryos vere ?measured sing an ocular sicrometer on a Bausch and Lomb stereo sicroscope at 10K (to the nearest 0.05 ma) oF 25x (to the nearest 0.01

fan). Drawings wore mad using =

Ld stores microscope vith a camera

lweide ate.

1-4. Baz weabranes vere

fed for geanurements and

drawings, except for early stages of sevelopacnt (through neurutarion).

During 1980 and 1932, the staging table pre!

ed here was used in

the field co record developmont in over 500 clutches of E. cogui. In

any clutches che disneter of 3-10 exes was periodically measured to

the nearest 0.5 mm with @ plastic mm culer as developacnt proceeded.

Also, records of daily nin

an and saximun temperatures were available

at the El Verde Station

nesuuTs

Staging Tabie for Eleutherodactylus coqui,

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Prechatching development was arbitrarily divided into fifteen

stages, bared on readily di

cernibie changes

pajor aupects of

externel morvnology (e.g., eyes, limbs, gills, etc.). Each stage
fepresenta at least one day of developaent during the ware wet season
of Aprii-July. The sajor features of each stage are summarized in

Table 17, witn mors dezait provided in the following section.

Eyes.+ The large oyes of E. sogui eabryos are distinctive throughout
devetopaent. Twit position is evident as Large anterior bulges in the

cephasic region Ly Stage 4 (Figures 13 4-8). The iris first shows

pigment in

4 (Figures 15 Co) and darkens progressively until

black io Scage 10 (Figures 16

?F), The pupil reasins clear throughout

Eis pe of, Jutimg Stage 10 the pupil begins to darken and the iris

to Lighter

By Stage 13, the pupil is dark and the iris attains the

Loe Gosvacteristics with the upper nalf golden and the lover

nate

The embryos of E. cogui bear a single pair of suatl gills for less than one third of the developmental period. The gills first appear as buds from the will arches during Stage § (Figures 15 C-p), elaborate into short stalks bearing 2-4 terminal

jolutions by Se.

6 7 (Figures 15 1-3, 168), ant then regress rapidly, disappearing from external view by Stage 9 (Figures 15 M, 16 D). Fale yellow to anber blood can be seen circulating during stage 5.

At full devetopaent in Stages 6-7, the blood is orange, As the gills

develop, progressively higher densities of red blood cells are observed

Moving Cheaush them, accounting for the change in hue.

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Figure 15. Camera lucida drawings of E. cogui embryos. A) Stage 4, dorsal view. B) Stage 4, caudal view. c) early Stage 5, dorsal view, D) early Stage 5, lateral view. £) late Stage 5, dorsal view, F) late Stage 5, lateral view. 6) Stage 6, dorsal view. H) Stage 6, lateral view

3) Stage 7, dorsal view. 3) Stage 7, lateral view.

K) Stage 8, dorsal view. L) Stage & lateral view.

1M) Stage 9, lateral view. N) Stage 11, lateral view.

©) Stage 12, dorsal view, P) stage 12, ventrolateral

view. eed = endolymphatic calcium deposit, £1b = front

Limb bud, g = gill, gb = gill bod, hb = hind Limb bud

Scale = 1.0 nea

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Figure 16, Photomicrographs of E. coqui embryos. A) early Stage 5.

dorsal view, 8) Stage 7, dorsolateral view (arrow indicstes

ADL boa). ©) Stave 7,

ers view. D) Stage 9, dorso-

iavera view. E) Stage 10, ventyai view. F) stage 10,

lateral view. G) Stage 10, dorsal view. #) stage 12,

ventral view. 2) Stage 12, lateral view. 3) stage 14,

Yertoolaterai view. K) £99 tooth of a Stage 14 embryo.

Seale = 1.0 mm: scale in &

plies to BD, scale in E

applies to Bev.

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Endolynphatic Calciua Deposita.- During Scage 6, there first appears « Pais of symmetric points of pure white material ianediately posterior to the mesencephalon and anterolateral to the rhombencephalon (Figures 15.G-H). Tese initial points enlarge into small quadrangular patches by Stage 8 (Figures 15 T-L, 16 8-C), then develop forward extensions fron their anterior lateral corners toward the rear aedial region of the eye. From external view, these extensions reach the eye by the end of Stage 9 (Figues 15 M, 16D). During Stages 10-12, the forward extensions widen dorsoventraily (as seen in lateral view), and the original posterior areas viden cephato-caudally and aedially. By Late Stage 12, the white areas on the evo sides are joined at the midline (Figures 15 0, 16 1) and, viewed dorsally, the ECD resembles a shallow

horseshoe with # thickened bi

fe and slightly apread ares, After Stage 12, it begins to fade and is no longer visible by stage 15. Tais is

due to evo processes. There i

regression of the calciue deposit, such that by hatching, it is about one-third of ite size at full development (ate Stage 12). Concurrent increasing pigmentation wasks vhat renains of the structures from Stage 14 on.

Preliminary analysis of these structures dissect

from a Stage 11 embryo (Figure 15 X) indicates that they are 28% calciua by weight.

Treir position at Stage 6 (Figures 15 6-H)

volves quite clearly the endolymphatic sac (Lymn, 1942) vieh subsequent elaboration and forward ?extonsion during Stages 7 through 12 (Figures 15 1-0, 16 8-0, F-G, 1). Tere is Little doubt that they are homologous with the calciua

carbonate deposits which have deen described in tho endolymphatic

Of many aquatic anuran Larvae (Dempster, 1930; Carlstrom, 1963;

GCuardabassi, 1960; Pilkington and Sipkiss, 1966; Etkin, 1964). I will

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an

refer to thes as endolympha:

© caleive depo:

ee (ECD).

Dissection of the ECD at full developoent, frow Stage 12 eadryos,

reveals a structure vith @ posterior portion that is more or less

doraoventrally depr

fed. The forvard extensions from the anterior

lateral corners begin

narrow terete stalks becoming progressively
wider and laterally compressed tovards the eye. Deterioration of the
ECD, beginning in late Stage 12, involves progressive reduction of all

parts. By Stage 14 (Figure 16 J) tae narrow terete base of the forward

extensions completely disappears, leaving separate anterior and
posterior sections. By hatching, the entire structure is reduced to
about one-third of its fullest extent at Stage 12, Their size continues

to decrease iter hatching.

Exp tooth

during the latter part of Stage 12 (Figure 15 P), and develops into a

An eng tooth first appears at the prenaxillary symphysis

Prominent, black, bicuspid structure by Stage 14 (Figures 16 J-K). The

tooth proje:

® peryendicularly froa tip of the upper jaw, and is 0.12 +
0.01 wa (mean + SD) vide and 0.07 + 0.01 mm (mean + SD) tong at full

size. It sloughs off within 1.5 days af hatching.

Body vall.- The pigmented body val! appears in Stage 7 as a saall disc flanking the trunk between the front and hind Linbs (Figures 15 1-J, 16 3), This disc and its leading edge, which covers the base of the foreliabs, are well-defined by melanophores vhich are not evident elsovnere. No pignentation appears on the yolk surface beyond the borders of the body wall, The disc expands from Stage 8 through Stage

12 (Figures 15 1-8, Py 16 D4

+ WD, progressively surrounding the large yolk reserve, The body wall completely encloses the yolk by the end of

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Stage 12 (Figures 15 P, 164).

Liabs.- Lieb bots first appear in Stage 4 a8 rounded evellings lateral

to, and slightly separated from, the neural tube (Figure 15 A-B). The

buds increase in size and join the erunk in Stage 5 (Figures 15 C-0, 16

A). The hind Limb buds are slightly larger than the fore Ligbs

Ehroughout development. Both front and hind tiab

8 are roundish in

appearance early in Stage 5, becoming sore oblong as the stage

otopresses (Figures 15 E-F). Elbow and knee joints appear as

constrictions during Stage § (Figure 156) ant are quite evident in

Stage 7 (Figures 15 1-5, 16 8-C), Foot padéies are also evident in

Stage 7. Suds of at Least three digits on front and hind feet are

(Figure 15K), Limbs and tors elongate fron Stage 9

Phrough 13 (Figures 15 M-8, P, 16 E-J), at which point they reach full

Length, rela their Lengeh at hatching. Toopade appear in Stage

13 (Figure 16 4).

Tail.- A tail bud covers the cloaca in Stage 4 eubryos (Figure 15 8). The tail stem curves to one side in Stage 5 (Figures 15 ¢, 164) and has @ onal sembranous fin in Stage 6 (Figure 15 6). Elongation of he

tail to full Length vith a large mesbrsnous fin accomplished by

Stage 10 (Table 18, Figures 16 £-C) and reasins so through Stage 12

(Figures 15 0-P, 16 H-1), At full Length, ic bends at the vitelline

Benbrane and extends laterally about two-thirds of the way to the

snout. It beging to regress after Stage 12 and at hatching is about

one-half of its former length (Table 18). It is resorbed completely

vithin 2 days of hatching. The tail is translucent, heavily

vascularized and unpignented throughout developoent .

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Behavior.~ There is a progression of behavioral events which are

Feadily visible in Living enbryos. Rapid rotation of endryos begins in

Stage 3. Rotation ceases in Late Stage 5 or early Stage 6, vhen the Firat evidence of wid-body flexion is observed. The tail soves for the first tise during Stage 6, but tail thrashing strong enough to sove the eabryo does not occur until Stage 7. Tail thrashing is the aain source of locomotion through Stage 12, Twitchiag and flexing of the Limbs is

first apparent during Stage 10, and by Staze 13 the embry moves inside

the egg solely with its limbs. Hatchlings are fully aobile.

Size during dey

Presented in Tabie 18. Through the end of Stage 3, the developing

opment. ~ Measurements of eabryonic dimensions are embryo is siorcer then the diameter of the exg. In Stage 4, the exdryo

first

eds the egg disneter and bexins to curl around the Large yolk
Feserve (Figure 15 AB). Frow that point on, enbryo Length is the
longest intraoval dimension. Total length is the longest dimension of
the eabryo in dorsal view, and is measured co the most posterior edge
of the curled tail stem. Snout-vent length (SVL) is acasured to the
angle which the hind limbs make with the base of the tail. Because

tof

embryos are curled around a Large yolk reserve during @:

developuent, SV is not ste:

tly resresentative of their true Length.
Froa Stage 14 on, the yolk is reduced sufficiently in size to allow

flattening the eabryos or hatchlings and seasuring a true SVL. Hence there is # large change in SVL from Stage 13 co hatching. Tail lengtn is a measurement of the central tail stem. Yolk vidth was measured as

whe great.

wt transverse vidth of the eabryo in dorsal view, It is

relatively constant through Stage 8, as the embryo lengthens. In Stages

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9-12, the elongating enbryo progressively pinches the yolk antero-posteriorly while the expanding disc envelopes it laterally.

This apparently causes che yolk to bulge laterally (Table 18). Fron

Stage 13 on, yolk width decreases,

Measureuents of egg dianerer in the field, although subject to

Breater error due to variation in the hydric state of eggs, closely

parallel Laboratory seasureaeats of total length (Zable 18, Figure 17).

Fee 4

0.78, p< 0.01).

eter wis significantly correlated with developaental stage (r =

Coupacicons with Other Puerto Rican Eleutherodactylus

T used tnie staging table to record tevelopeent in two other

Eleutherodactylus: £, portoricensis and E. antilte

Microscopic

examination of developmental series of these species reveals orphological detail and developmental chronology vhich are virtually identical to £. s9qul. Eabryos are almost indistinguishable from those of E. coqui through stage 11. At that stage, the sharper angie of the canthus rostralis and narrower snout, diagnostic of adults (Rivero, 1978), are evideot in che eubryos of both species and pigmentation differences begin to appear. Laterally and ventrally, the eabryos of E. antillonsis develop an alaost black ground color which is flecked vith white, » pattern that is quite distince at hatching. ta B.

portoricensis color differences are not so sarked although hatchlings
are @ light orange-bromn rather than dark brow as in E. cogui.
Development of the ECD, gills, Liabs and tail, and expansion of the

Piguented body wall are equivalent, in external view, to that of £.

enqui. Hatchlings of both E. portoricensis and E. antillensis nave

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Figure 17, Averoge egg eisneter (reagured in she 261d) as a functacs

Of developmental stage. For cach stage, wean $2 8D and

Sample ize (Melow brackets) axe given. Tutal sample «
163 clutches. Ov = Oviposition. Reysession Line
Y= O12 + 4.1) comrezation cosfticients r= 9.76,

P< 0.01

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Stage of Development

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Pignentes egy recth at hatching

Teaperature and Revelopeent

Ik wos vot possible to raise eggs under constant temperature

conditions at £1 Verde. Weare, I exsained the relationship of

teuperatore and tevelopment by regressing the developmental period

(number of days fron oviposition co hatching) of clutches in the field

against acbient temperature aa measured by daily winies and maxis

recorded at the BI Verde Fieid Station. For ead

i clutch, T calculated

the average of oh

sinimm and matiaua for cach day of devetopaent ,

then t20k the mess of the daily averages (Figure 18). Developaental

period ani sega datiy temperature were etgniticantly and negatively

correlated (y=

95, p< 0.01). This relationship also holds for

regressions of developmental period on mean daily winiaa (x = 0.94, p

? 0.01) and mean daily maxima (¢ = -0.94, p < 0.01). The slope of tho

sion Line (Fig

18) illuetrates che strong effect of Keaperature on developaent. A drop of 1 C in mean daily temperature Feaults in 2.5 day prolongation of develouneat

The strong negative correistion of teapersture and

velopmental

coqui vas reflected in a strong seasonal effect on

developmental rate. In Table 19 I present the mean daily teaperature for each month (computed as above) amt che average developsental period for clutches which had the major portion of development during a sonth (for any month, this included clutches Laid between the 21st of the Previous sonts and the 20th of the curzent oath). From Jan-Feb to June average developucntal rate dropped by 9.5 days, corresponding to aa

increase in average daily teaperature of 4.0 ¢ (Table 19).

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Figure 18, scattergran of develop

ntal period against rean daily

Renpersture for 27 clutches of £. coqul. Regression Line:

ve

7X 4 78.2) corretatien coefficient: © = -0.96,

P< 001.

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Mean Daily Temperature (?c)

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DISCUSSION

T have described a continuum of external sorphological changes in living eges of E. cogui which form the basis of 4 developmental staging table for thie species, The table has been used repeatedly in the field fo stage the eggs of two other Eleutherodactylus as well, tn order to

examine its potential as a general scheme for

Bing the eggs of

Eleutherod

tylus, T present (Table 20) equivalent stages and figures

from other developmental studies of Eleucherodactylue and discuss

similarities and differences.

The reduced nature of external gills has been noted in other

Eleutherodactylus endryos. Gitlin (1944) noted che brief tenure of

reduced gills in £, antilten

+ He found gill buds in eabryos of
about 3.5 days (his Figures 2, 3, 16, 17), correspooding to early stage
Sof my achene. Gills were reduced ar seven days (presumably reaching
Peak developaent prior to that time), almost gone at 8.75 days, and

completely gone by 9.75 days, Because reduced gills at seven days were

contained within © dermal pocket, they would not have been visibie

externally after chat tine in Gitlin's specieens. Since Gittia?s seven

day eabryos correspond to ay Stage 9, disappe

ince of the gills at
that stage in wy achene may represent @ sisilar phenomenon. } have

observed the small gills in esbryos of E. antillensis as vell. chihon

(1960) also reported the presence of reduced gills in E.

which vere w

le at three days (his Figure 5), corresponding to ay

Stages 7-8, but nad

ppeared by 4.5 days (his Figure 6),

corresponding to Stage 8 or early Stage 9 of ay scheme. Alanson ot al.

(1960) ee

fbed transitory external gills arising in Stage 111 (ay

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Stage 5) ant disappearing in Stage IV (ay Stage 8) in E. johnetonei, land Hughes (1959) found blunt vascular papillee on the surface of the

third pharyngeal arches (thir fill arch?) in E. planirosteis, Noble

(1925, 1927) described tvo pairs of gille in E. inoptatue of

ola, the anterior pair larger than the posterior pair.

A complete absence of gills has been reported for other

erodactylus, Jameson (1950) and vallett and Jameson (1951)

reported that gills vore absent in Hylactopheyne (Eleutherodactylus)

augusti. Wovever, they examined exbryos which, according to other

features in ay scheme, vere already past the point at vbich external

Bills disappear. Earlier developmental stages of this species vould

have to be exawined to determine whether or not external gills occur

Reported absence of gills in several other species is more credible

since Larger ranges of developmental stages were exagined. External

sills apparently are absent in the embryos of E. nubicola (Lysn, 1942),

fone or two other species of Jamaican

tylus (Sampson, 1904),

sniola (Noble, 1925), and

Brazilian £. guentheri (Lynn and Lute, 1946).

The reduction or absence of gills in Eloutherodactylus ts

coincident with possession of a very large, sembranocus, vascularized

1, The hypothesis that respiratory function is carried out primarily

by the tai

has been proposed repeatedly since Peters? (1876) early

observations and is probably true. My observations suggest that the

tail is also a motile organ during part of developuent. Tail beating

is an important source of aovenent for at least one-third of

developaent in

coqui.

Te carly appearance of Liab buds in Eleutherod

ctylus embryos vas

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one of the first aspects noted in early report

of direce develo,

in thin genus. Peters (1876) stated that Gundlach found all four

extresities present a short stusps at an early stage in

coqui.

Sampson (1904) found that the liabs appeared early and simultaneously

in the Jamaican ep.

jes he exexined. Gitlin (1944) noted that the hind

Hiabs actually appeared about six hours before the front lisbs in E.

(portoricensis).

40 0g tooth has been seen in enbryos of every Eleutherotactyius

patil

reported thus far (Lynn, 194:

Lynn and Lutz, 1946; Lute, 1944; Bayley,

1950; Adanson et a1., 1960; Bogert, 19695 Woke, 1978; this study),

although in sone species it

y Be quite small (Noble, 1926),

Typ

ally, it {s doscrived as « bicuspid structure (eingle-spined in a few; Noble, 1926; Goin, 1947), partly or completely black, and situated

the prosaxill

Ty symphysis approxinacely perpendicular to the upper

jaw, In E. cogui and £. antillensis, the egg tooth is black over its

4istal half, Several authors have also observed the hatching of

sctylus and have described the scraping action of exbryos

Priot C0 hatching. Stage 15 eabryos in this study have been observed on

many occasions to poke at the eng capsule vith their enoute just prior

t0 hatching, apparently rupturing the aeabranes with the egg tooth.

?The pignented disc that appears during Stage 7 in ay table and

expands to for the body wall is analogous to the "dermal fold" of

Sampson (1904), She described the der

1 fold as a sandvich layer of

esoderm surrounded by ectoderm whose free a

rior edge covered the

base of the forelinbs early in development, but later disappeared. In

eabryos of E. nasutus (Lynn and Lutz, 1947, p. 4), the "dermal fold

oes not only envolop the base of the forelinbs but continues backward

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to the inl

reron of the and Lisbe." In #, coqui and £, antittens:

the dinc for! on Stage 7 covers the base of the forelimbs and extends

back £0 tne vase of the hid Limbs. The anterior edge of the dise,

whieh covers tne

Limb base, disappeace a2 the Linbs grow and the

Gigs exparte, the fermat tid hae been described in Es nubico

(uynn,

1982), E. guentheri Ciymn and t

(Goin,

1947).

Endotyeihaci> caiciue Sesposits (ECD) have been reported in the

eabryos oF cylue. and tate (1946), in

obsorvar sone of tiviny Ee foucd snall eyametrical centers

of ossification os the occ jens that roughly correspond

te tea ay table, durleg Wich £cb are prominent. Lynn

and tote (1647. 2, L described "a paix of arches of incipient osit

tien on se cueiput? in living exbryes of E nasutue that vere

at a sage squisclorr to ay stage 7, Loter in the paper (p. 5) they

state chat these "ossificetion arches...(are) more contiguous and are

» widdorssl region? in eabryoe equivalent

fo my stoee 11. Cnitor (19652 soted the appearance of ?otocyste? at

ig and stated that they are

welledew ?ones at 4.5 days (hia sigue

6). From Nis deseripeion and

illustrations, these structs

S are clearly equivalent to the ECD in E.
g0qsi. Chidon's 1960) Figures > and G correspond to Stages 7-8 and

Stage 9, respectively, in ay sches

Io E, johnstone? from Jamaica,

ughes (1962) odsorvad that otoiitns first appeared at 5 days and vere

Large by day 7. in hig Text-Figure

6 1/2 day enbryo is illustrated

which bears a sn

ed area posterior and dorsal to the eye which

correaponte ora

y to the position and shape of the ECD in a Stage 10

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eabryo of E, coqui. I have also observed ECD in the esbryos of Puerto

ices and £. portaricens

absence of ECD in the embryos of other

eabeyor

yy be coincidental artifact of the heavy

concentrations of calcium in the ECD ond fixation of a

erial in acidic

media [i.e., picric acid, Sampson, 1905; Bouins ftuid and Zen

fluid, Lynn, 1962; Lavdowsky's mixture (formalin, alcohol and acesic

4), Goin, 1947; Bouin's fluid, Hughes,

59; Heidenbain's Susa

Feagont, Adaasoa ct al., 1960]. Indeed, io ay study, ECD vere always oovious in Live embryos but when I fixed soo initial series of eggs in Bouin*s Solution ant in 10% unbuffered formalin all traces of the EoD were lost. Atl Later series vero fixed in 10% buffered formalin, vhich Preserved the ECD completely, If the ECD are to serve as a diagnostic

feature for staging Eleuthes

embryos, it is inperative to fix

aceytus,

material in buffered or alkaline wedia.

The endolymphatic sac, an insignificant dorsal out pocketing of the endolymphatic duct in ost vertebrates, is excessively enlarged in aephidians (Despster, 1930). tn anurans,

and left sacs are fused

?and the structure extends over the hindbrain ond vertebeal coluon vith

anterior extensions around the midbrain and protrusions between the

vertebrae of adults, Deposits of calcium carbonate are found ia most

parts of the endolymphatic sace of larval and adult anurans, vith

crystals often filliog the entire structure during the latter part of

wmetauorphosis. The presence of ECD in £2.

|sutherodactylus therefore

appears to be the hoaslogous

uation in these terrestrial frogs. tn

aquatic anuran Larvae, the deposits can only be seen in situ in cleared

?specimens because of the heavy pigacatation early in development. In

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Eleutherodactylus however, the auch later appearance of pigment renders

the progressive foraat

ion of ECD quite visible, providing an isportant

Giagnostic feature for staging eabryos, The early appesrance of ECD in

E: coqui is similar to early concentration of calcium carbonate in
post-hatching aquatic larvae. Whiteside (1922) noted chat calcareous
deposirs exist alnost from tho earliest stages of formation of the

entolymphetic sac in Ra

ig larvae.

The functional significance of ECD in anuran Larvae was long the

subject of speculation. Early suggestions (e.g., Caupp, 1897 as cited

in Denpster, 1930) tha calciue

tored in the endolymphatic sacs of

pre-netamorphic larvae aight be mobil

zed for bone formation during

set asorphis climax aveited definitive proof by Guardab,

4 (1960),

Kreiner (1954) snd Pilkington and Sinkias (1966). The Latter study

showed conclusively that endolysphatic calcius carbonate is resorbed

during wetenorphic climax to provide calciun for akeletal ossification

Pilkington and Simkiss suggested that the process of early storage and

ater mobilization vas an adaptation to allow contiqued skeletal

ossification during the extensive morphological changes of metazorphic

cli

mx, whon no feeding occure, My observations of the early formation and Later dissolution of ECD in E. cogut suggest a similar cateiun storage and mobilization scenario for these terrestrial embryos. The EoD first appear early in development (Stage § in ay scheme), Long defore ossification begins in any Eleutherodactylus (Lynn, 1942; Lynn ?and Lute, 1946; Yailett and Janeson, 1961). They enlarge during the

ext one-third of development, and begin to d

ntegrate coincident

With the beginning of skeleral ossification. te gpbic.

eesification begins in the Liabs at -12 days, im the vertebral coluan

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at -11 days and in the heat at 10 days (Lyse, 192). These times are

equivalent to late Stage 12 and Stage 13 in E. cogui, vhen the ECD are

starting to disintegrate. tn E.

jotmetonet (Adanson et al. 1960),

ification of the Linbs begins in Stage VII (equivalent to ay Stage

12).

While the calciua storage functinn of the entolymphatic organ is probably similar in aquatic anuran Larvae and direct-developing embryos, the source of the caiciun is probably different. cateiua

stored by aquatic larvae alaost

tainly is derived from larval food.

In eggs with direc: development, the calciua must be invested in the

eam by tne fesal> prio co oviposition.

Temperature and Devel opment

Teapot

ure has @ strong effect on the developmental rate in embryos and Larvae of aquatic-dreeding anphivians (Moore, 1939, 1942; Pettus and Angleton, 1967; Licht, 1971; Howard, 1978; Seith-Gill and Berven, 1979). t have found 4 significant inverse relationship between aabient tenperature and developmental rate for the terrestrial eggs of

E. coqui. Over the range of teupcracures encountered in the field

(approxinately 15-28 6), £1 ¢ drop in sean daily temperature caused

change in mean developmental period of 2.5 days. This strong

relationship between temperature and developaratal rate results in an

average winter developmental period (Jan-Feb: 26.3 d) which is 1.57

times the sumer suamer developaental period (June: 16.8 A)(Table 19).

Two principal effects of groving amphibian Larvae at lower

Yeaperatures are longer larval periods and Larger size at aetasorphosia

(untenutn, 1519;

wart, 1955; Ekin, 1964; Kollros, 1961; Smith-Cill

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ase

land Bervon, 1979). Because she to

y developuertal period of E. coqui

whieh re

WES fro lower teapsrs.ures ie spent wholly vithia che egg,

there is no reason co exsnst that ?itcMings should be Larger at lover

tesperatures, Unlike free

sis Lacvae, E. cogui eabryos

cannot fred for sone sare extuviet pe?

Avaore important result of come devevopment in f.

cogui is the

longer period during vaich enge are vstneraste 69 wort ity.

Desiccation and cazaibatisn are waios causos of epg mortality in E.,

g0qui (Townsend et al,, 19841. Altaough vais parental care significantiy recuces ogg aoeeslicy, 1.57% increase in developmental Period could revi: in much Tow: hatching success despite full-term

pareneaL

Wis Walaerabit sty of sags Sue to leager developmental Periods aay be further comprunied by che Ueier conditions during the vincer months

Abchough fh2 lowes tenpersrures ond deter conditions of the winter mouths may have a direct effeer on tue physiclogy and reproductive

behavior of atts 2. cogat, 9. co

vsed vulnerability and hence lower

hatching seccess cf pgs laid dicise shat auvton say be a selection

?eased Level of

Feproductive activity which | roseevad during chat season. There ie

arked searonatity vraading insene!ty of

cogui, with less

than one-third the murder of clutches being Laid in Jan-Feb as are

deposites in May-June (Chapter 2), i: is resonable to expect that

fensles shot de!

yed vitellogenesis oF ovucat ion during the winter and

put energy int» growth way have eucs highce reproductive success.

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