

The ecology of parental care in a terrestrial breeding frog from New Guinea

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Summary. *Cophixalus parkeri* is a terrestrial breeding microhylid frog from the montane moss forests of northeastern New Guinea. The pattern of parental care in this species and its adaptive significance was studied in the field and in the laboratory. Egg brooding, is performed by the male in most cases, and much less frequently by the female. The parent remains with the clutch throughout the 85–100 day prehatching period. Egg removal experiments demonstrated that survivorship of embryos significantly decreased in the absence of the attending parent. Mortality of unattended embryos may be caused by a variety of factors, including fungal infection, egg cannibalism, predation by arthropods, and abnormal development.

Brooding adults can provide protection to their developing offspring via several possible mechanisms eg. aggressive defense of territories on which eggs are deposited, ingestion of potential arthropod predators, and egg turning (Fig. 2).

Several differences were found in the quality and quantity of food ingested by brooding versus non-brooding adults collected in the same locality during the same period. On average, brooding adults consumed less food and of lower quality than non-brooding adults (Table 1). These differences in diet were correlated with length of time parents had attended their eggs before they were examined (Fig. 3). The reduced food intake during egg brooding is reflected by significantly smaller fat bodies and less carcass fat in egg brooders relative to nonbrooding adults (Table 1). These results are discussed in terms of relative costs and benefits of parental care in this species.

Introduction

The parental association of adult anurans with their offspring is relatively uncommon. Only 10

to 15% of the 2,700+ species of frogs have been observed to exhibit parental care, but this behavior is widely distributed among the taxa, occurring in 70% of the families of frogs (McDiarmid 1978). Several recent papers have reviewed parental care patterns in anurans (Salthe and Mecham 1974; McDiarmid 1978; Lamotte and Lescure 1977; Ridley 1978; Wells 1981). With a few exceptions, e.g. Woodruff (1977), McDiarmid (1978), Kluge (1981), and Townsend (in press), the literature consists largely of descriptions of various associations of an adult with its offspring, with little documentation of advantages to the offspring.

Twelve New Guinea microhylid frogs have been reported in the literature (Tyler 1963; Zweifel and Tyler 1982) or observed by me to associate with eggs or hatchlings. Probably most if not all of the 70 other described and dozens of undescribed species also perform parental care (Tyler 1976). *Cophixalus parkeri* a small microhylid frog from the montane areas of eastern New Guinea was chosen for a detailed study of parental care.

The objectives of this paper are to describe parental egg brooding in the New Guinea microhylid frog, *Cophixalus parkeri*, and to determine the adaptive significance of parental care in this species by answering the following questions: To what extent does this behavior affect the offspring's survivorship? Which factors decrease the survivorship of the unattended offspring? How can the parent reduce the mortality of its offspring? What are the potential costs of parental care?

Materials and methods

Study area

The study area consisted of a gradually inclining 10 km segment of a montane cloud forest in the northeastern portion of Papua New Guinea (146°40' east, 7°10' south; elevation 2,400–2,850 m). Average annual rainfall (1974–1978) was 2,959 mm (range: 2,677–3,492). The mean minimum monthly

temperature for the same period was 7 °C (range: 2.5–12 °C), and the mean maximum monthly temperature was 16 °C (range: 12.5–25.5 °C). In addition to *C. parkeri*, other anurans occurring in the general vicinity of my study area are 4–6 species of Hylidae and 8–12 species of described and undescribed species of Microhylidae. For a more detailed description of floral and faunal characteristics of the general area, refer to Gressitt and Nadkarni (1978).

Field and laboratory observations

I found clutches of *Cophixalus parkeri* eggs in the field from November 1975 to October 1978 and recorded details of the microhabitat characteristics of the oviposition sites and the developmental stage of the eggs. In some cases I collected attending adults and their eggs or hatchlings. The specimens were killed with chloroform and fixed by abdominal injection of buffered 10% formalin solution and later preserved in 70% ethanol. Snout-vent lengths of preserved specimens were measured using a dial caliper. Sex was determined by internal examination of gonads. Stomachs were excised and contents examined under a binocular dissecting microscope. The size of food items, eggs, and gonads were measured using an ocular micrometer.

Field and laboratory experiments

Removal of brooding parent in the field. Forty clutches of *Cophixalus parkeri* were uncovered during a 6 day period in April 1978. In 20 clutches the attending parent was removed. The clutches were then covered with moss. Twenty other clutches, found in the same area were used as controls, and the parents were left with their eggs. The locations of both experimental and control clutches were marked. Both groups of clutches were reexamined 2, 6, and 10 weeks after initiation of the experiment. Determination of egg mortality was based on discoloration and decomposition of eggs and of egg capsules and, absence of movement or heartbeat of embryos. The presence of mold, arthropods, and other potential mortality agents also was noted.

Egg turning in the laboratory. Fifteen clutches of early stage embryos were collected in the field and transported to the laboratory. The eggs were kept near normal conditions of temperature (16 ± 3 °C). Each clutch was divided into two groups of equal numbers of eggs. Both experimental and control clutches were rinsed in sterilized distilled water and placed between two layers of sterile cotton gauze, soaked in sterile distilled water. The experimental clutches were turned manually with a small nylon spatula once a day for approximately 1 min. The control clutches were uncovered for 1 min, but not turned. Viability of eggs in both sets of clutches was monitored at 10 day intervals for 60 days.

Determination of feeding and nutritional state. Twenty-seven brooding and 37 non-brooding specimens were all collected during the same 6 week period in the same general locality and microhabitat (underneath the moss-leaf litter) at the same time of the day (1000–1600 h) and examined in the laboratory. The stage of embryonic development of the eggs in each nest was recorded at the time of collection. The 64 specimens were killed and injected abdominally with 10% formalin within 4 h of collection. Stomach contents were examined, and the total length of prey items was determined using an ocular micrometer. Plant and animal material were separated manually under a microscope dried, and weighed. The carcasses and abdominal fatbodies were excised, dried, and then weighed. The dried car-

casses were placed in Soxhlet Extractors for 48 h. The carcass fats and ether-soluble fats were removed using anhydrous ethyl-ether as a solvent.

Results

Life history and parental care patterns of Cophixalus parkeri

Cophixalus parkeri spends the daylight hours 10–30 cm underneath the moss-leaf litter layer on the forest floor. At night individuals climb to nearby perches on low growing vegetation. All individuals are highly philopatric and remain near the same perch site for most or all of their lives. Individuals actively defend perch sites against intrusion by conspecifics.

Female *Cophixalus parkeri* deposit an average of 18 large (3.0–4.0 mm), heavily yolked eggs in a depression within the moss layer or, less frequently, in decaying leaf litter. I have found eggs throughout the year, suggesting that breeding is aseasonal. Development is direct; the eggs hatch as tailless miniature adults. Of 135 clutches observed in the field 132 had a single adult associated with eggs or hatchlings, and three of the 135 clutches were found without an attending adult. The adult invariably was found in contact with a tightly packed egg mass, usually lying directly on top of the eggs. Based on repeated observations of clutches throughout the developmental period it was evident that the parent remained close to its eggs during the 85–100 day prehatching period. In 86% of 72 clutches examined in detail, the male was the attending parent. Females were found with eggs in the remaining 14% of the clutches. Except during oviposition, the male and female were never observed with the same clutch of eggs. In those cases where I made repeated observations of the same clutch, I always observed the same parent tending the eggs. The froglets remained with the parents during the 30–40 day period of absorption of the abdominal yolk mass and then dispersed. I observed newly hatched froglets sitting on top of the attending adult *C. parkeri* (Fig. 1), but actual transport of the young was not observed.

Effects of egg brooding on survivorship of offspring

The results of parent removal field experiments clearly indicate that the presence of an adult enhances offspring survivorship. In only 3 of the 20 clutches in which the parents were removed did

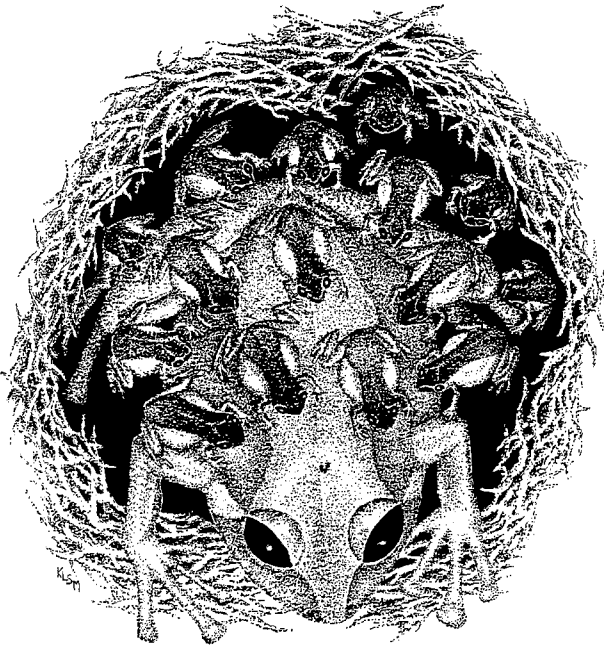


Fig. 1. An adult *Cophixalus parkeri* with hatchlings. Note the large light-colored yolk masses of the hatchlings. (Drawing made by K. Manly from photographs of individuals in situ.)

the embryos hatch compared to 19 of 20 control clutches in which the parents remained with the clutch ($\chi^2 11.64$; $P < 0.005$).

Causes of egg mortality in Cophixalus parkeri

Arthropod predation. Insects (Coleoptera and Dermaptera) were seen feeding on eggs and egg capsules in two of the three clutches with which no adult was found. Experimental removal of the parent was followed by predation on the eggs by arthropods (spiders, millipedes, earwigs, and carabid and staphylinid beetles) in 23% of the clutches.

Intraspecific oophagy. The stomachs of 5.5% of 325 non-guarding *C. parkeri* contained one to three relatively intact *C. parkeri* eggs. No *C. parkeri* eggs were found in the stomachs of brooding individuals.

Fungal infestation. Fungal hyphae were seen on and inside eggs of *C. parkeri* found without parents. The parent removal experiments revealed a similar pattern; in 70% of the clutches, removal of the parent was followed by fungal growth on the embryos and egg capsules.

Abnormal development. An examination of unattended eggs in the laboratory and the field revealed that many of the embryos were obviously mal-

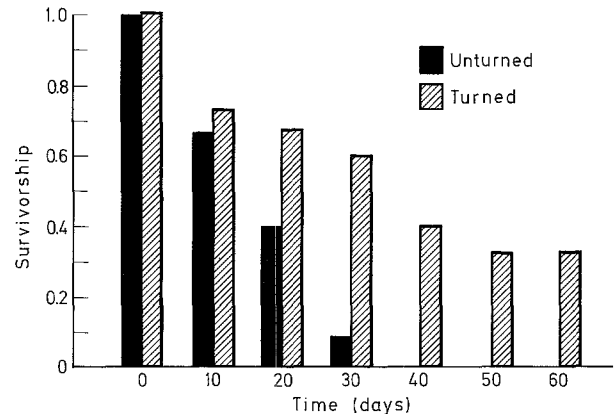


Fig. 2. Survivorship of turned and unturned *Cophixalus parkeri* eggs kept under laboratory conditions

formed at the time of death. In many of the eggs the yolk had settled into one hemisphere of the egg capsule. These observations suggest that yolk adhesion and stratification may be the cause of the observed abnormal development and subsequent death of unattended embryos.

Mechanisms of protecting offspring

Anti-arthropod predation. Direct observation of attending adults toward potential arthropod predators was difficult due to the cryptic nature of their oviposition sites. However, analysis of the stomach contents of guarding and non-guarding adults demonstrates that many of the same types and sizes of arthropods found eating the eggs were also found in the stomachs.

Egg turning. The results of the egg-turning experiment are shown in Fig. 2. The survivorship of the turned eggs was significantly higher than the unturned eggs ($P < 0.05$). Field observations of the activity of brooding adults indicate that eggs are jostled during the movement of the parents in the nest.

Stomach content analysis of guarding and non-guarding individuals

Several differences were found in the amount and type of material ingested by guarding versus non-guarding adults. Guarding adults had less animal material by dry weight and less total material in their stomachs than did non-guarding individuals. Guarding individuals, however, had a significantly higher amount of plant material in their stomachs than did non-guarding individuals. There also was a significant relationship between the relative

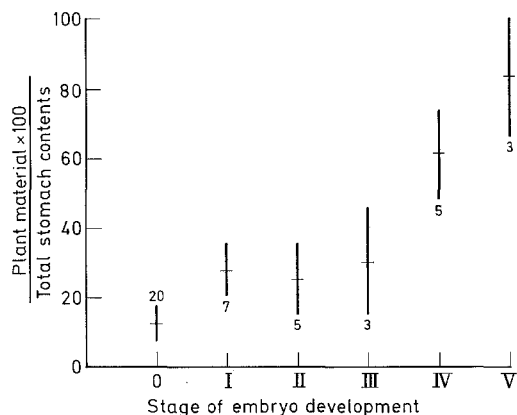


Fig. 3. Relationship of the relative amount of plant material found in brooding male *Cophixalus parkeri* stomachs and the stage of development of its embryos at the time the brooding adult was collected. The horizontal bars represent the mean values; vertical bars \pm one standard error. Numbers in parentheses signify the sample size. Each stage of development is of 20–25 days duration. Stage 0 represents the stomach contents of non-brooding males; stage V represents individuals found with newly hatched froglets in the nest

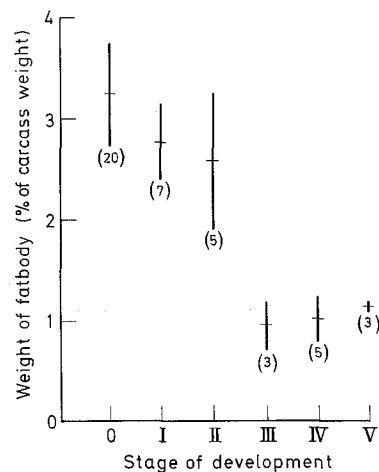


Fig. 4. The relationship between dry weight of fatbodies found in brooding *Cophixalus parkeri* males and the stage of development of the embryos at the time the adults were collected. The number of individuals used for analysis are in parentheses. The horizontal bar represents the mean; vertical bars \pm one standard error. The stages of development are the same as that of Fig. 3

amount of plant material ingested and the stage of development at the time the brooding individuals were collected (Fig. 3; $r = 0.62$, $P < 0.001$). The average prey size in guarding individuals was significantly smaller than non-guarding individuals (4.35 mm vs. 5.60 mm) ($t = 2.20$; $P < 0.025$). The relative prey size distributions were also significantly different (Kolmogorov-Smirnov Contingency-test; $P < 0.025$). On average, the non-guarding frogs ingested a higher number of prey types

Table 1. Stomach contents and stored fat in brooding and non-brooding adult *Cophixalus parkeri*. The values for stomach contents and stored fat are presented as the percent of dried frog carcass weight (mean \pm one standard error). Significance values (P) are based on t -tests of transformed data (arcsin). NS not statistically significant ($P > 0.05$); sample sizes are given in parentheses

	Brooding adults (27)	Non-brooding adults (37)	
Snout-vent length (mm)	26.7 \pm 0.39	26.8 \pm 0.36	NS
Stomach contents (% of carcass weight)			
Total	1.35 \pm 0.17	2.17 \pm 0.29	$P < 0.025$
Animal material	0.83 \pm 0.16	1.99 \pm 0.32	$P < 0.005$
Plant material	0.52 \pm 0.15	0.18 \pm 0.08	$P < 0.01$
Stored fat (% of carcass)			
Carcass fat	1.72 \pm 0.41	3.98 \pm 0.73	$P < 0.05$
Fatbodies	1.62 \pm 0.21	2.52 \pm 0.23	$P < 0.025$

(14 vs 10). Also, a comparison of the H's (Shannon-Weaver Indices) of both groups demonstrates that the diet of the non-guarding individuals is more taxonomically diverse than the diet of the guarding group of frogs ($t = 2.15$; $df = 36$; $P < 0.025$).

Carcass fat and fatbody analysis

Guarding individuals had significantly smaller fatbodies (dry weight), and less carcass fat than did non-guarding adults. There was no significant difference in fat-free dry carcass weight between the two groups (Table 1, Fig. 4).

Discussion

Amphisexual parental care

An unusual characteristic of *C. parkeri* parental care is that either sex, but not both, will care for a given clutch of eggs. To distinguish this pattern of parental care from biparental care in which both parents care for the same clutch of offspring, I propose use of the term *amphisexual parental care*. The distinction of biparental and amphisexual parental care is required because the two modes reflect two different strategies of parental investment (Maynard Smith 1977; Gittleman 1981).

Amphisexual parental care occurs only rarely in vertebrates, and most of the examples in anurans are poorly documented or have been observed only under laboratory conditions (Zweifel 1956; Mudrack 1969; Vaz-Ferreira and Gehrau 1975; Silverstone 1976; Woodruff 1977).

Adaptive significance of parental care

The results of the field and laboratory experiments demonstrated that the brooding behavior of *C. parkeri* provides large advantage to its offspring. Recently, other workers have also begun to examine the effects of egg brooding on pre-hatching survival of offspring. McDiarmid (1978) studied the reproductive behavior of two closely related species of neotropical centrolenid frogs, and found that the species which continuously brooded its eggs had a higher prehatching survivorship than did the species which deserted its clutch during part of the day. Townsend (in press) in his study of *Eleutherodactylus coqui* concluded that prehatching mortality increased from less than 25% to over 50% when the attending male was experimentally removed from his clutch. Woodruff (1977), on the other hand, has shown that in three species of Australian *Pseudophryne* egg attendance has no apparent effect on egg survivorship. He concluded that egg attendance in these species may be incidental to territorial attachment by males attempting to attract additional gravid females.

Causes of mortality

Arthropod predation. Arthropods are the most frequently mentioned predators of frog eggs (Salthe and Mecham 1974). Both the observational and experimental data I collected suggest that the eggs of *C. parkeri* are highly vulnerable to predation by many groups of moderately-sized carnivorous arthropods. There is no evidence, however, that any arthropod predators specialize on the eggs of this species, as is the case for other tropical anurans (Villa 1977).

Fungus. The results of my field and laboratory studies demonstrate that the eggs of *C. parkeri* are susceptible to attack by fungi. There is considerable doubt that fungi will infect eggs while the embryo is alive (Salthe and Mecham 1974). Under both field and laboratory conditions fungus grew on *C. parkeri* eggs in which the embryos were alive, as indicated by visible heartbeat and/or movement of the embryo. The ability of fungus to attack and destroy living amphibian eggs has also been observed by Villa (1979).

Intraspecific oophagy. Intraspecific oophagy is known for both salamanders and frogs (see Simon, in press, for a review), and, has been suggested by Salthe and Mecham (1974) to be an important selection pressure in the evolution of parental care

in amphibians. The presence of conspecific frog eggs in the stomachs of non-brooding *C. parkeri* but not in brooding individuals suggests that there is little likelihood of filial cannibalism (Rowher 1978) occurring in this species.

Abnormal development. Salthe and Mecham (1974) have proposed that large, heavily-yolked eggs may be susceptible to yolk stratification, which would then lead to abnormal development of the eggs. The appearance of many of the unattended *C. parkeri* embryos at the time of death suggests that yolk stratification in unattended eggs may be an important cause of mortality of eggs at early stages of development.

Desiccation. Death of terrestrial eggs due to desiccation is one of the most commonly suggested causes of mortality in amphibian eggs (Salthe and Mecham 1974; Taigen et al., in press). Desiccation does not, however seem to be an important problem for *C. parkeri* due to the fact that parents use extremely wet microhabitats as oviposition sites.

Mechanisms of protection

Given that egg brooding in frogs contributed significantly to the survival of its offspring and, the major factors of potential egg mortality can be identified, what then are the specific mechanisms used by the parent to counter these mortality factors? Ways in which amphibians increase the survivorship of their offspring have been reviewed recently by Salthe and Mecham (1974), Woodruff (1977), and Forester (1979).

Protection from predators. Woodruff (1977) used the absence of potential egg predators in the stomachs of egg-brooding adults of three species of Australian myobatrachid frogs as evidence to dismiss the hypothesis that protection from arthropod predators is a function of egg brooding in these species. Using this same criterion for *C. parkeri*, it is clear that egg predation is reduced because brooding parents eat potential arthropod egg predators. It may well be that this protection of eggs by parents is simply the result of general foraging behaviors of the adult frog, and not the evolution of specific offspring protection behaviors.

Protection from intraspecific oophagy. Territoriality and parental care have been linked both theoretically and empirically (Trivers 1972; McDiarmid 1978; Wells 1981). Defense of perches by *C. parkeri* may be a means by which brooding

adults reduce the access of potential conspecific predators to their nests which lie directly below the perches.

Fungicidal properties. It has often been hypothesized that an important function of egg brooding is to prevent fungal growth on eggs (Tilley 1972; Woodruff 1977; Forester 1979). Several activities performed by parents have been suggested to inhibit fungal growth in terrestrial amphibian eggs, e.g. movement, vibration, or jostling of the eggs, and consumption of dead or diseased eggs (Tilley 1972; Forester 1979). The observed movement patterns of brooding *C. parkeri* adults may provide an indirect means of reducing fungus growth. However, the absence of any eggs in the stomachs of brooding *C. parkeri* decreases the possibility of egg removal being a mechanism of egg protection in this species.

Egg turning. Salthe and Mecham (1974) suggest that mechanical disturbance of large, heavily yolked eggs may prevent abnormal development of the embryo due to yolk stratification. This hypothesis is supported by Forester (1979) in his study of parental care in the salamander *Desmognathus ochrophaeus*. The significant increase in survivorship of turned *C. parkeri* eggs suggests that inadvertent manipulation of eggs during movements of the parent reduce the likelihood of stratification and adhesion of its large yolk mass.

Cost of parental care

Insufficient nourishment can adversely affect an animal's ability to perform normally and ultimately results in decreased survivorship and reproductive output (Maiorana 1976; Wootton 1979; Robbins 1983). One of the many potential costs attributed to parental care is that it may result in decreases in nutrient uptake by the parent (Rowher 1978; Kryzysik 1980; Forester 1981; LeBoeuf et al. 1972; but see Kaplan and Crump 1978, for an opposing conclusion). The results of stomach content analysis of brooding and non-brooding *C. parkeri* support this idea. Not only is the total amount of food being ingested by brooding adults lower, but also the nutritional quality of the food is poorer, having a much higher percent of plant material in their diet. Plants are much lower in protein and fat than a comparable amount of arthropod food items (Golley 1961, 1969).

The ability of *C. parkeri* to assimilate plant material is not known. However, a comparison of the energy balance of brooding and non-brooding in-

dividuals may provide some information on the long term costs, if any, of increased proportion of plants in the diet of brooding *C. parkeri*. One widely used measure of an animal's overall energy balance is the amount of its stored fat reserves (Robbins 1983). In frogs, the abdominal fatbodies are among the most important storage sites of accumulated fat (Fitzpatrick 1976). The fact that the amount of fat stored in the fatbodies and the carcass is significantly reduced during egg brooding suggests strongly that brooding *C. parkeri* are incurring a substantial nutritional cost.

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