ORIGINAL ARTICLE

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Differential parental care behaviors of arboreal and terrestrial microhylid frogs from Papua New Guinea

Abstract I studied the ecology of parental care behaviors displayed by two closely related sympatric species of microhylid frogs in Papua New Guinea that occupy different microhabitats. Adult removal experiments on the terrestrial frog *Hylophorbus rufescens* and the undescribed arboreal frog *Oreophryne* sp. "A" demonstrate a significant positive effect of parental attendance on offspring survivorship and differential causes of egg mortality between microhabitats. Desiccation was the primary cause of egg mortality for the arboreal frog, whereas predation was the main source of mortality for the terrestrial frog. These selection pressures (desiccation and predation) are comparable to two of Wilson's "prime movers" of the evolution of parental care (harsh environment and predation) and may have driven and/or are maintaining the evolution of parental care behaviors in these Papuan microhylid frogs. These results highlight microhabitat-specific selection pressures in the evolution and maintenance of parental care behaviors.

Keywords Frogs · Microhabitat · Papua New Guinea · Parental care · Selection

Introduction

Parental care, by definition, is any parental behavior that increases offspring survivorship. It is a complex behavioral link among reproduction, development, ecology, and evolution. Care for eggs and offspring takes many forms and has different functions across taxa. Protection from pathogens and predators may be the most important function of parental care of eggs, but there are other functions as well. Maintenance of egg temperatures, hydration of terrestrial eggs, aeration of aquatic eggs, and jostling of eggs have also been presumed functions of egg attendance (Clutton-Brock 1991 and references therein; Crump 1996).

Although we have much to learn and novel modes of parental care are still being described (e.g., Bickford 2002), biologists have recently been able to focus research on the costs and benefits of parental care (e.g., Montgomerie and Weatherhead 1988; Owens and Bennett 1994; Smith 1995; Johnstone et al. 1996; Shaffer and Formanowicz 1996; Thiel 1997; Reguera and Gomendio 1999), defining and/or quantifying the function(s) of different care behaviors (e.g., Ketterson and Nolan 1994; Smith 1997) and characterizing the ecological and demographic situations that promote the evolution of parental care (e.g., Rosenheim et al. 1996; Wynne-Edwards 1996; Filippi et al. 2001).

Like many other areas of biology, however, there are sampling biases in the studies of parental care because only certain taxa have been well studied (mainly birds, insects, and mammals). Inferences based on a limited sample will be incomplete, and conclusions will not have great explanatory power outside those well-studied taxa. Amphibians in general, and frogs in particular, are excellent targets for research into the evolution and ecology of parental care.

Although parental care is found across many frog families (in 17 of 27; Crump 1996), the behavior is relatively rare, displayed in <10% of all frog species (McDiarmid 1978). The generality of parental care in more than half of the frog families is probably due to parallel evolution in response to the same selection pressures (e.g., predation, desiccation, competition) in similar habitats but in different areas and taxa (see McDiarmid 1978; Salthe and Mecham 1974). The overall rarity of species with parental care, however, is most likely because the behaviors are the culmination of many factors along complex evolutionary pathways, reaching the acme of parental care only under specific conditions.

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The most recent review of parental care in amphibians (Crump 1996) considered six modes of parental care in frogs: egg attendance, egg transport, tadpole attendance, tadpole transport, tadpole feeding, and internal gestation. Here, I compare the egg-attendance behaviors of two species of closely related frogs occupying sympatric terrestrial and arboreal microhabitats. Specifically, I will determine whether differences in parental care behaviors exist and infer reasons why that variation occurs between frogs in distinct microhabitats.

Papuan microhylid frogs have direct development, lacking a free-living tadpole stage. Having evolved independently in at least 10 families of frogs (data compiled from Duellman and Trueb 1986 and Hay et al. 1995), direct development exemplifies a key adaptation and probably explains the overwhelmingly successful radiations of the most species-rich group of extant terrestrial vertebrates (i.e., >600 species in the genus *Eleutherodactylus*) and the study group's diverse mono-phyletic radiation (>170 species in >20 genera of Australo-Papuan microhylids).

Parental care of eggs has been documented in 35 species from New Guinea (Zweifel and Tyler 1982; Simon 1983; Bickford 2001) and is likely to be present in all Australo-Papuan microhylids. Very little is known about the ecologies, life histories, and parental care behaviors of these frogs. I speculate that there are differences in parental care behaviors for frogs that live in separate microhabitats and hypothesize that selection pressures specific to the different microhabitats where these frogs perform parental care play a critical role in the differentiation of their parental care behaviors.

These selection pressures should presumably fall under Wilson's "prime movers" of parental care (Wilson 1975), the driving forces behind their evolution and/or mainte-nance. These prime movers include (1) high levels of predation, (2) limited or rare food supplies, (3) unusually harsh conditions for the eggs and/or offspring, and (4) a stable or well-structured habitat.

Of Wilson's (1975) four prime movers, predation may be the most important selection feature that explains any difference(s) between parental care behaviors of frogs in terrestrial versus arboreal microhabitats. There are many potential arthropod and vertebrate predators in the leaf litter (Bickford 2001), but the arboreal microhabitat (at the distal end of live leaves) has fewer potential predators. Both terrestrial and arboreal microhabitats are harsh for anamniotic eggs since the eggs would probably desiccate quickly without parental care, and harshness of habitat is therefore unlikely to explain any difference in parental care behaviors. Likewise, the stability or structure of the habitat is not likely to be pertinent because both microhabitats may be considered stable and/or structured. The last of Wilson's prime movers, limited or rare food, does not appear to be applicable for lecithotrophic froglets because they have very large yolk stores in the eggs. Hence, I predict that the predation pressures of the terrestrial microhabitat will explain any differences in parental care behaviors in these two microhabitats. If predation is an important selection pressure, I predict that significantly more clutches will be lost due to predation in the terrestrial microhabitat and that there may be higher survivorship (with or without the attending adult) in the arboreal microhabitat.

Methods

Study site

I studied the parental care behaviors of microhylid frogs from March 1997 to December 1998 at the Crater Mountain Biological Research Station (CMBRS) at Wara Sera. The station is located in the Crater Mountain Wildlife Management Area (CMWMA), Chimbu Province, Papua New Guinea (6°43′ S and 145° 05′ E). The CMWMA comprises over 2,600 km^2 of remote rainforest. The CMBRS-Wara Sera study site is a middle elevation (800–1,350 m a.s.l.), 12-km^2 area of nearly continuous primary forest. The study site is located near the center of the CMWMA in an area of extreme topography, with many rivers and streams dissecting the area.

Rainfall is aseasonal and variable, ranging from under 200 mm in atypical drought months (e.g., during the El Niño southern oscillation event), to almost 1,000 mm in a wet month. The mean annual rainfall recorded for CMBRS-Wara Sera is 6.4 m (Wright et al. 1997). Temperatures ranged from 14°C to 28°C daily.

Forty-one species of frogs have been recorded from the CMBRS-Wara Sera, although it is likely that more species await discovery (Bickford 2001). Nineteen frog species are microhylids, one is a myobatrachid, two are ranids, and the remaining 19 species are hylid frogs. Of the 19 microhylid species, 11 are recognized species and 8 are undescribed species. The two species included in this account are two of the most common frogs at the site and live in different microhabitats, making them excellent candidates for a comparative study of parental care behaviors.

Study species

The terrestrial frog *Hylophorbus rufescens* is found on the ground, never climbing on vegetation above the ground. These frogs are relatively slender and have large eyes and long arms and legs, falling into Emerson's (1988) "walker-hopper" locomotor mode. *H. rufescens* lay their eggs on the soil surface, under the leaf litter, in shallow depressions padded out of the soil by the male parent (Fig. 1).

The undescribed arboreal frog, *Oreophryne* sp. "A" (undergoing description, see Appendix for type specimens), is found on vegetation above the ground. They have expanded toe pads, large eyes, and a relatively wide head. These frogs can be classified to Emerson's (1988) "jumper-walker" locomotor mode, and they lay their eggs adherent to the axial (under-) side of live leaves 10–350 cm above the ground (Fig. 2).

Terminology

To simplify this report, I specify parental care terms based on my own experience with the microhylid frogs of New Guinea and according to previous workers. I follow part of Trivers' (1972) definition of parental care as any post-zygotic parental investment that increases offspring survivorship. It is important to designate differences between pre- and post-zygotic investment because pre-zygotic parental investment is not parental care. However, I chose to differ from the classic definition of Trivers (1972), who states that parental care must be at the cost of investing in other offspring. I think that this unnecessarily limits parental care and do not agree with Trivers' general supposition that contemporary investment necessarily limits future investment or that different individuals

Fig. 1 An attending male of *Hylophorbus rufescens* on a clutch of eggs. The clutch is in a cup-like, shallow depression constructed by the attending male. *Hylophorbus* has constant egg attendance

Fig. 2 An attending male *Oreophryne* sp. "A" with a clutch of eggs. This clutch is approximately 2.4 m aboveground on an epiphytic aneroid leaf. This *Oreophryne* species has nocturnal egg attendance

within the same clutch do not equally benefit from the same parental care behaviors.

I use the terminology of Crump (1996) to specify types of behavior for frogs. She used the terms "brooding" and "attending" for different types of parental care behaviors. Following Crump, brooding implies the carrying or transport of eggs by the care-giving adult, whereas attending simply means that the adult is found with or on the eggs. Simon (1983) uses brooding for the behavior defined as attending by Crump. None of the frogs I observed in Papua New Guinea carry eggs, and the most basic and ubiquitous parental care is egg attendance.

Hydrating is a function of attendance that has been shown to be extremely important in the survivorship of terrestrial frog eggs (Simon 1983; Taigen et al. 1984). The difference between preventing desiccation and hydrating is that hydrating is the active addition of water to the eggs, and this action has been shown to occur in frogs that lay terrestrial eggs (e.g., Taigen et al. 1984). Preventing dehydration is also an important feature of parental care in terrestrial eggs but may be hard to differentiate from hydrating.

All frogs choose an oviposition site, but not all construct nests. A nest is a type of oviposition site that is physically changed by the parent(s). An example from the terrestrial microhabitat is the shallow, cup-shaped depression made by *H. rufescens*. The arboreal *Oreophryne* sp. "A" that I studied does not construct nests.

Many frogs at this site ate the eggs that they had been attending. I differentiate this oophagy into two separate types: disturbance-induced oophagy and pathogen-removal oophagy. My reasons for separating these types of oophagy stem from their entirely different biological causes and the presumptive selection pressures that drive these behaviors. Moreover, only one of these can realistically be labeled as a parental care behavior (pathogen removal), whereas the other (disturbance induced) is a parental behavior that does not appear to increase offspring survivorship. Simon (1983) uses conspecific oophagy not as a parental care behavior, but as a selective pressure that leads to the evolution of parental care since it appears to be a major source of mortality in the closely related microhylid *Cophixalus parkeri*. Although there are many examples of oophagy in frogs, from obligate larval oophagy (e.g., Pramuk and Hiler 1999) to conspecific cannibalism (e.g., Simon 1983), disturbance-induced filial cannibalism has only recently been described and appears to be present in only Papuan microhylids (Bickford 2001).

Egg guarding and egg defense are two other terms that have been widely interchanged. Here, I specify egg guarding as any behavior that prevents attack by predators. This can be inflating the body and readjusting posture to block eggs from predators, striking or biting predators, or any other physical intervention preventing attack by egg predators. Egg defense is a subset of egg guarding where the attending adult kills and/or eats predators as a form of preventing depredation. It is the most extreme and effective form of egg guarding.

Clutch observations

Field assistants and I used 5×5 m leaf litter quadrats (Scott 1976; Jaeger and Inger 1994) and nocturnal visual encounter survey (VES) transects (Crump and Scott 1994), as well as opportunistic observations and haphazard tree climbing (up to 35 m), to discover clutches. Once clutches were found, we characterized the micro-habitat of the clutch site; identified, sexed, and measured the attending adult (to the nearest 0.1 mm with a dial calipers); and, where possible, counted, measured the diameters, and recorded the approximate developmental stage of the eggs (based on Gosner 1960). To ensure accuracy, two different observers counted eggs and measured the diameter of the egg capsules. In normal (i.e., non-voucher and non-experimental) clutches, we monitored the development of each clutch in two ways. We used scan sampling observations (5 min per day and/or per night) to track the development of the clutch and any changes in parental care behaviors. For some individuals of both species, we changed to focal clutch observations (constant nocturnal and crepuscular observation up to 14 h) after hatching until all parental care behavior ceased. We used the focal clutch method for a few (3–5) clutches until we were certain that the attending frog remained at the initial clutch site and that we had observed all parental care behaviors and responses to our manipulations. Each focal clutch observation was conducted by one or two people (with low

intensity, red filtered lights, or candles at night) staying at least 3 m from the parent frog at all times.

We elicited guarding and defensive responses from attending adults by introducing 5–15 ants and gently prodding the adult with the eraser-end of a pencil. We recorded any manipulation of the eggs or movement of the adult in response to these stimuli.

Adult-removal experiments

To determine whether parental care provided direct benefit to the offspring and why any behavioral differences in parental care might exist between these species, I measured how adult attendance affected egg survivorship and determined the causes of egg mortality. I removed the attending adult frog from 23 experimental clutches of *H. rufescens* and 7 experimental clutches of *Oreophryne* sp. "A" in the field. Each experimental clutch was selected because a suitable control clutch was located proximately (<500 m apart) and contemporarily (<24 h apart). By default, I chose the second clutch to be discovered as the experimental adult-removal clutch of the pair. Experimental clutches were paired with control clutches based on similar developmental stage of the clutches and similar number of eggs in the clutches. I used paired experimental and control clutches only to avoid effects of differential parental care based on stage of development and clutch size (<15% difference). Pairing clutches based on geographic proximity allowed me to control for microhabitat and/or drainage differences. Both clutches in a pair were routinely checked each day. If clutches were being depredated, I observed the predation until satisfied that the entire clutch was or would be lost and then collected both the predators and the remainder of the clutch (if any) as vouchers. In cases where the clutch was obviously terminated (missing, discolored, or covered by fungal hyphae or had no embryo movement or visible heartbeat), I concluded the observations and collected and preserved the remainder of the clutch. Clutches that were collected intact or nearly intact were stored as a single unit in either 10% buffered formalin or 75% ethanol. If already disarranged by predator disturbance, I split clutch constituents into a formalin aliquot for preservation and an ethanol aliquot for preservation and potential future molecular data retrieval.

Hydration

Whenever possible, we measured the capsular diameter of each egg in the clutch daily. Additionally, for *Oreophryne* sp. "A" clutches with nocturnal attendance, we measured the egg capsules' diameter twice daily (at approximately 0700 and 1800 hours). I chose these times to obtain measurements before the attending adult returned at night (after 1600 hours) and after he departed the next morning (before 0700 hours). Measurements were taken with dial calipers to the nearest 0.1 mm and crosschecked by two different people. Diagrams of egg clutches were made to ensure that we compared the same eggs through time. I compared the mean egg size per clutch before and after attendance in *Oreophryne* to see whether there were significant differences in egg size before and after attendance. I used a Student's paired *t*-test (one-tailed) to determine whether the eggs were significantly larger after attendance. For *H. rufescens*, I compared egg capsule diameters in a repeated-measure ANOVA since there were no discrete periods of attendance to compare.

Voucher specimens

In the voucher clutches, I removed the attending adult and/or the eggs and prepared them as specimens (Appendix). Adult specimens were euthanized in a weak chlorobutanol solution and dissected for DNA-rich tissues (liver and cardiac muscle) for molecular genetic studies. Some males were further dissected to remove the testes (stored in 3% glutaraldehyde) for studies of sperm morphology (Scheltinga et al. 2002). The carcasses were fixed in either a 7% formalin solution or an 85% ethanol solution, depending on the size of the specimen (formalin for adults >30 mm SVL, ethanol for any frog <30 mm SVL). All specimens were labeled with the Biological Survey Field Series (BSFS) tags from the U.S. National Museum of Natural History in Washington, D.C., where most specimens are deposited. Voucher specimens are also deposited at the National Museum of Papua New Guinea in Port Moresby.

Results

We located 118 total egg clutches for these two species (Table 1). Most *Hylophorbus rufescens* clutches were discovered through leaf litter plot sampling, and most *Oreophryne* sp. "A" clutches were found during visual encounter surveys at night. Males were almost exclusively the care-giving sex for these two species (in 97% of *H. rufescens* and 98% of *Oreophryne* sp. "A" clutches).

Egg attendance

Egg attendance was different between species. The terrestrial species, *H. rufescens*, had 24-h attendance of eggs until hatching, whereas the arboreal species, *Oreophryne* sp. "A", had nocturnal egg attendance (approximately 2000–0430 hours) with the attending adult seeking refuge away from the clutch during the day.

Table 1 Summary of methods, clutch size ($\bar{x}\pm$SD), snout-vent length (SVL), and sex of attending adult for *Hylophorbus rufescens* and *Oreophryne* sp. "A" clutches found at the CM-BRS-Wara Sera

Species	*n*	Method	Clutch size	Attending adult sex[a] and SVL
Hylophorbus rufescens	65	52 plot[b]; 13 opp[c]	13±6	F=2 (39–42 mm) M=62 (28–32 mm)
Oreophryne sp."A"	53	3 plot; 46 ves[d]; 4 opp	7.8±1.5	F=1 (32–34 mm) M=52 (21–26 mm)
Totals	118			F=3 M=114 ?=1

[a] *M* Male, *F* female, *?* escaped/unverified
[b] *plot* 5×5 m leaf litter plot
[c] *opp* Opportunistic fieldwork
[d] *ves* Visual encounter survey

Egg guarding

Egg-guarding behaviors differed dramatically between *H. rufescens* and *Oreophryne* sp. "A". The terrestrial *H. rufescens* had extreme reactions to predators and disturbance, whereas the arboreal *Oreophryne* seemed to be almost unaffected by predators and disturbance.

The terrestrial *H. rufescens* had variable but typical guarding and defensive behaviors: posturing (raising the body off the clutch), inflation of the body (to nearly spheroid), lunging at or striking and biting an offending pencil, and eating ants that were placed near the clutch. They typically postured and inflated their bodies only after contact with a pencil. During normal clutch observations, they often lowered themselves directly on top of the clutch, effectively covering most of the eggs. *H. rufescens* lunged or struck at an introduced pencil after repeated prodding. Almost half of the ant introductions (6 out of 15 trials, or 40%) resulted in the attending adult eating ants before the ants made contact with any eggs, and in every instance (*n*=4) when the ants bit an egg or tried to remove an egg, the adult *H. rufescens* ate the offending ant(s).

In contrast, the *Oreophryne* sp "A" were almost uniformly unresponsive to ants and pencils. All individuals simply readjusted their positions after being prodded by the pencil, never striking. In only 1 of 11 cases of ant introductions (after the ant crawled on top of the clutch directly in front of the adult) was there a defensive response elicited from the attending adult. Six other times, the attending adult simply ignored the ants but repositioned itself if disturbed.

Oophagy

We observed two types of oophagy in the microhylid frogs at CMBRS-Wara Sera. The first type of oophagy was simple removal of infected or unfertilized eggs. I call this pathogen-removal oophagy. A second type of oophagy exclusive to attending adults also occurred: disturbance-induced oophagy. We never saw conspecific individuals that were not attending eggs or any other frogs at this site eat microhylid eggs.

Terrestrial *H. rufescens* frogs were more prone to disturbance-induced oophagy. *H. rufescens* had more than 25% of their clutches prematurely affected by disturbance-induced oophagy. In almost every case, our disturbance to the clutch during observations appeared to cause oophagy, since we witnessed the initial oophagy and attempted escape by the attending adult. Although we never observed pathogen-removal oophagy, I concluded that it happened four times based on the presence of cloudy or dull-looking eggs during daily clutch observations that were missing in the next clutch observation.

We also observed oophagy behaviors by arboreal frogs. *Oreophryne* sp. "A" may have had a very low level of disturbance-induced oophagy because our clutch observations did not result in oophagy during or immediately after our observations (as in *Hylophorbus*). For one of the 53 clutches of *Oreophryne* sp. "A", we assumed disturbance-induced oophagy because there were no previous signs of pathogens and the entire clutch disappeared. Although there was no direct observation of the oophagy, the attending adult remained on his territory and appeared distended. It is possible that the entire clutch was lost to predation and there was no oophagy by the parent.

In two other *Oreophryne* sp. "A" clutches, I assume that pathogen-removal oophagy occurred. One of these clutches was observed to have discolored eggs prior to the removal of two eggs from the clutch, and the other clutch had only a single egg removed.

Egg hydration

We were unable to measure all clutches of *H. rufescens* eggs on a daily basis for fear of inflating rates of disturbance-induced oophagy. Based on a small and incomplete sample (*n*=5 clutches), egg capsular dimensions did not change enough for us to infer any hydration effects of attendance. This is probably due to constant 24-h attendance, where the clutches never dehydrate as they do in the nocturnal-only attendance of the arboreal *Oreophryne* sp. "A". Although *H. rufescens* may decrease water loss through evaporation as a function of attendance, we were unable to detect such effects.

In arboreal frogs, however, we found significant differences in egg capsular diameters before and after adult attendance. Nineteen clutches of *Oreophryne* sp. "A" had significant differences between egg capsular diameters measured after the adult had recently left and shortly before he resumed attendance behavior. The mean egg sizes after attendance ($\bar{x}$=7.6±0.8 mm) were significantly greater than the mean egg sizes before attendance ($\bar{x}$=5.4±0.6 mm) (Student's *t*-test, *t*=27.21, *df*=18, *P*<0.0001). In some cases, the egg capsules were almost twice as wide (diameter) or approximately five times larger in volume after the adult had attended the clutch.

Adult-removal experiments

To determine the effect of parental care and the benefits accrued by offspring, I removed attending adults from clutches of *H. rufescens* and *Oreophryne* sp. "A". I found striking effects for both species. When attending adults of the terrestrial frog, *H. rufescens*, were removed, there was 100% mortality in the clutches (*n*=23). The control clutches also had mortality (5 out of 23, or almost 22%), but it was caused entirely by oophagous attending adults and was most likely a response to our disturbance. There were significantly more deaths in the clutches whose attending adults had been removed than in the control clutches (Fisher exact test, *n*=46, *P*=0.001). Likewise, the arboreal *Oreophryne* sp. "A" had significantly more mortality in the experimental clutches than in control

clutches (Fisher exact test, $n=14$, $P=0.0006$). In a total of 14 clutches in the experiment (7 removed and 7 control), there was 100% mortality in the clutches whose attending adult had been removed and 0% mortality in the control clutches.

Although both species suffered 100% clutch mortality in the absence of attending adults, the causes of mortality were different. Egg clutches of *H. rufescens* were more susceptible to predation than those of *Oreophryne*. In the 23 cases of unattended *H. rufescens* clutch mortality, 20 clutches were attacked within 24 h by ants. Mortality in the other three clutches was caused either by fungal infection (two cases) or by a combination of fungus and ants (one case). The arboreal frog *Oreophryne* sp. "A" lays its eggs on the under surface (axial side) of live leaves and had more mortality due to desiccation. All unattended *Oreophryne* sp. "A" clutches showed signs of shrinking egg capsular volumes and decreased embryo activity within 1 day of the adult's removal. All but one case of mortality was directly caused by desiccation, the other being a combination of desiccation followed by ant predation.

Discussion

Egg attendance

The general type of attendance for the microhylids in this report is similar to that reported by Simon (1983) for a related frog, *Cophixalus parkeri*, in that we found both males and females with eggs, but only one attending adult per clutch. Nearly all parental care in these two species is by the male parent (Table 1). Simon terms this type of care "amphisexual" because either sex but not both attend the clutch.

Egg guarding

Guarding of the clutch against predators is one of the most important functions of parental attendance of eggs. In insect studies where the attending adult was removed, mortality of the insect offspring approaches 100% (Edgerly 1987; Windsor 1987; Choe 1989). In anurans, guarding is a function of attendance that protects the developing eggs and offspring from predators, including conspecifics (Kluge 1981; Simon 1983; Townsend et al. 1984). Guarding also can provide a source of nutrients for an attending adult because most potential predators are consumed (Simon 1983). In the assemblage of micro-hylids at CMBRS-Wara Sera, I observed guarding behavior by attending adults only in reference to arthro-pod predators, although a closely related frog, *Cophixalus parkeri*, guards eggs from conspecific oophagy (Simon 1983).

Oophagy

Like other amphibians (e.g., Forester 1979), attending adult frogs provide protection against pathogens via oophagy. Under moist conditions where fungi are a prevalent pathogen, the simplest way for an attending adult to get rid of the pathogen and simultaneously recoup some caloric investment is to eat the fungally infected egg(s). Although pathogen-removal oophagy seems easily explained as a parental care behavior, disturbance-induced oophagy remains hard to explain with our current data. My initial hypothesis is that this behavior evolved as a response to predation pressures by relatively large terrestrial predators (e.g., cassowaries, pittas, antechinas, snakes, and dasyurids) whereby an attending adult can recoup at least some of his investment. Since *Oreophryne* appear to have a very low occurrence of disturbance-induced oophagy, and apparently have little contact with large predators, this behavior is consistent with the hypothesis that predators drive parental care behaviors of terrestrial frogs.

Egg hydration

Another function of egg attendance behavior is protection against environmental variation (e.g., desiccation). Hydration of terrestrial and arboreal eggs is an important function of attendance in amphibians (see Taigen et al. 1984 and references therein). At a minimum, sitting on top of the eggs, as most Papuan microhylid species do while attending, probably decreases evaporative loss of water from the eggs. Perhaps even more important is the active hydration of arboreal eggs.

Although *Hylophorbus* seem to decrease water loss through evaporation as a function of attendance, it would be nearly impossible to design a field experiment that would permit evaporation but not predation by ants in the absence of an attending adult. The significant differences in egg capsular diameters before and after adult atten-dance in arboreal *Oreophryne* frogs is not surprising. In some cases, the egg capsule diameters were almost twice as large (five times larger in total egg volume) after the adult had attended the clutch. Taigen et al. (1984) demonstrated that attending frogs probably prevent des-iccation of eggs by moving water osmotically from their ventral integument to the egg capsules. The osmotic difference in water potentials drives water into the egg from the attending frog. It appears that nocturnal atten-dance in *Oreophryne* sp. "A" is extremely similar to that of *Eleutherodactylus coqui* (Taigen et al. 1984) in that it also has a hydration function. Moreover, desiccation may be an important environmental force that has shaped the suite of parental care behaviors present in this arboreal species.

In contrast to Simon (1983), who studied *Cophixalus parkeri* at high elevation (2,400–2,850 m a.s.l.) in Papua New Guinea, I found 100% mortality in unattended egg clutches, suggesting obligate parental care in these frogs.

Simon found that some of his unattended experimental clutches survived (3 of 20) but still reported a significant effect of attendance on offspring survivorship. The ecosystem in Simon's study is vastly different from that of the CMBRS-Wara Sera. Not only was desiccation the main source of mortality in terrestrial clutches, but also there was also only 23% predation by arthropods, none of which were ants (spiders, millipedes, earwigs, and beetles). Moreover, Simon did not report disturbance-induced oophagy in *C. parkeri*. Interestingly, none of the attending adults he dissected had eggs in their stomachs, although he did confirm conspecific oophagy in 5.5% of non-attending adults. I suggest that there is lower predation pressure at his site (perhaps due to the absence of ants at the higher elevation) and that the montane assemblage of terrestrial microhylid frogs may show greater plasticity in parental care behaviors than do the species at CMBRS Wara Sera. Simon (1983) also reported 18% of *C. parkeri* clutches with female care, whereas we had less than 3% in the multi-species assemblage at CMBRS at Wara Sera (see Table 1).

Microhabitat-specific selection pressures

The causes of mortality in unattended clutches may reflect different selective pressures acting on terrestrial and arboreal microhabitats. Of Wilson's (1975) four ecological selectors for parental care, predation appears to be the most relevant for the terrestrial species *Hylophorbus rufescens*, and harsh environment (desiccation) seems most important for the arboreal species *Oreophryne* sp. "A". Wilson's other proposed selection pressures, limited food availability and a stable and structured environment, may not be as pertinent in the Papuan rainforest.

List of specimens and their Biological Survey Field Series (BSFS) tag numbers

All specimens are lodged at either the National Museum of Natural History in Washington, D.C., or the National Museum of Papua New Guinea in Port Moresby, Papua New Guinea.

Hylophorbus rufescens, BSFS 11633–47, 11649–50, 11668–70, 11673, 11677–78, 11692–93, 11699–700, 11704–05, 11724–28, 11740, 11762–63, 11770–71.

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