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The cost of polygyny and the evolution of female care in poison frogs

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Previous research on a variety of organisms indicates that polygyny can impose a cost on the reproductive success of females. Some authors have hypothesized that this cost may have caused the evolution of female parental care from paternal or biparental care in some lineages, particularly in poison frogs of the genus *Dendrobates*. In this paper, we evaluate the assumptions and theoretical implications of this hypothesis and present several game-theoretic models that clarify some of the issues. We conclude that a cost of polygyny is unlikely to drive a female care strategy to fixation on its own; however, if caring males suffer a cost of lost mating opportunities then a cost of polygyny may destabilize male care and result in the evolution of uniparental female care. A cost of polygyny on its own may be able to drive a transition from male care to biparental care. We also discuss other factors that may have influenced the evolution of parental care in the poison frogs, including results from recent field and laboratory research, and we evaluate the possibility that female care evolved from biparental, as opposed to male care.

ADDITIONAL KEYWORDS:—parental care – *dendrobates* – game theory

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INTRODUCTION

Parental care is a central feature in the life histories of many animals. How and why one type of parental care evolves from another is a controversial issue of central importance in evolutionary ecology (Maynard Smith, 1977; Lazarus, 1990; Clutton-Brock, 1991). Research on a variety of taxa suggests that several factors may affect the trajectories and equilibria of parental care evolution, including the cost of parental care to male mating success (Trivers, 1972; Maynard Smith, 1977; Wells, 1981), the effect of parental care on female fecundity (Maynard Smith, 1977; Gross & Sargeant, 1985; Balshine-Earn 1995), the relationship between parental care and confidence of paternity (Alexander & Borgia, 1979; Westneat & Sherman, 1993), and costs of male polygyny to female reproductive success (Weygoldt, 1987; Clutton-Brock, 1991).

Weygoldt (1987) addressed the evolution of female parental care in poison frogs of the genus *Dendrobates* (Wagler, 1830), in which males or females carry tadpoles from terrestrial oviposition sites to small pools of water. Most of the research he reviewed involved captive frogs. He hypothesized that males in species with biparental care might frequently deposit eggs from one mate in pools containing tadpoles from a previous mate, resulting in cannibalism and a cost of polygyny to the second female. He further hypothesized that this high cost of polygyny could cause the evolution of female care in a lineage derived from the biparental care lineage (see below). In this paper, we attempt to evaluate the assumptions and theoretical implications of this argument. We also discuss other factors which may have influenced the evolution of parental care in poison frogs and results from recent field and laboratory research relevant to this issue.

NATURAL HISTORY

The poison frogs, a neotropical group of toxic, diurnal, terrestrial frogs (Myers & Daly, 1983), exhibit a diversity of parental care strategies (Wells, 1978, 1981; Weygoldt 1987; Zimmermann & Zimmermann, 1988; Crump, 1995, 1996). The *D. tinctorius* species group, which includes *D. auratus* (Girard, 1855), *D. leucomelas* (Steindachner, 1864), *D. azureus* (Hoogmoed, 1969), *D. tinctorius* (Schneider, 1799), and *D. truncatus* (Cope, 1861), deposits small (2–8 eggs) clutches in the leaf litter that are attended by the male (Wells, 1978; Weygoldt, 1987; Summers, 1989). Once the eggs have developed into mature tadpoles (10–14 days), they are typically carried by the male to small pools of water that form in treeholes (Eaton, 1941; Dunn, 1941; Wells, 1981). Additional tadpoles may be placed in the same pool, and these may be cannibalized by larger tadpoles (Summers, 1990).

In the *D. histrionicus* species group, which includes *D. histrionicus* (Berthold, 1845), *D. speciosus* (Schmidt, 1857), *D. granuliferus* (Taylor, 1958), *D. pumilio* (Schmidt, 1857) and *D. arboreus* (Myers, Daly & Martinez, 1984), females deposit the young in small accumulations of water that form in the leaf or stem axils of plants (e.g. bromeliads). The female then returns to the pools periodically and lays infertile eggs that are eaten by the tadpole (Weygoldt, 1980; Zimmermann & Zimmermann, 1981; Brust, 1993). This form of feeding is obligatory in *D. pumilio*; the tadpole will neither grow nor survive if not provisioned with trophic eggs (Brust, 1993). Although the male performs some egg attendance in some of these species (e.g. *D. pumilio*; Weygoldt, 1980), the female is the main care provider (Weygoldt, 1987). In this paper, we will classify these species as having female parental care.

In captive *D. ventrimaculatus* (previously classified as *D. quinquevitattus* (Steindachner, 1864); the name *D. ventrimaculatus* was resurrected by Caldwell & Myers, 1990), Zimmermann & Zimmermann (1984) observed that both parents attend the clutch, which is oviposited above a pool in the leaf axil of a bromeliad. The male then carries the tadpoles (usually one at a time) to a different pool and returns periodically to call, thus attracting his mate who lays infertile eggs to nourish the young. However, recent field research suggests that biparental care does not occur in *D. ventrimaculatus* in amazonian Ecuador. Briefly, the mating system is promiscuous, unrelated individuals oviposit in the same axil, and females do not return to pools to feed tadpoles (Summers & Amos, 1997; Summers, in preparation). The frogs studied by Zimmermann and Zimmermann (1984) were from Peru, and may eventually be classified as belonging to a different species from those in Ecuador (Caldwell & Myers, 1990).

Biparental care has also been observed in captive *D. reticulatus* (Boulenger, 1883; Zimmermann & Zimmermann, 1984), and in other similar species from amazonia (Zimmermann & Zimmermann, 1988). Biparental care has been observed in the field in *Dendrobates vanzolini* (Caldwell, 1997). In this species, males carry tadpoles individually to small pools of water in treeholes, and females feed tadpoles with nutritive eggs. Males and females maintain an intimate association or pair bond throughout the period of parental care (Caldwell, 1997).

Studies of birds have revealed extrordinary variation within and between populations of a single species in the mating system and parental roles (e.g. Davies, 1985). It is possible that similar levels of variability occur in poison frogs, so there may be variation in parental roles even among populations of the same species.

THE EVOLUTION OF PARENTAL CARE

Male parental care was hypothesized to be the ancestral state in *Dendrobates* (Weygoldt, 1987) based on studies of parental care in species of *Phyllobates* (Dumeril & Bibron, 1841), *Minyobates* (Myers, 1987) and *Epipedobates* (Myers, 1987). Four of five species of *Phyllobates* have been studied in captivity, and all exhibit male parental care (Weygoldt, 1987: Zimmermann & Zimmermann, 1988). Fourteen of 22 species of *Epipedobates* have been studied, and all exhibit male parental care (Weygoldt, 1987; Zimmermann & Zimmermann, 1988). In *Minyobates minutus* (Shreve, 1935), recent research has demonstrated that this species also exhibits male parental care (Summers, in prep.). The genus *Colostethus* (Edwards, 1974) is thought to be basal to the toxic dendrobatids (Myers *et al.*, 1991). In most *Colostethus*, the males provide care for the tadpoles (Weygoldt, 1987), although females provide care (tadpole transport) in a few species (Wells, 1981). Tadpoles are transported to streams (not axil pools) and tadpoles are never fed nutritive eggs by females in these species (Weygoldt, 1987). The genus *Aromobates* is believed to be the most basal taxon (Myers *et al.*, 1991); it is not known whether or not this species has parental care. The most parsimonious interpretation of the information currently available is that male parental care is the primitive state within *Dendrobates* (Weygoldt, 1987).

Zimmermann and Zimmermann (1984) suggested that the *D. ventrimaculatus* group (with biparental care) is intermediate between the male and the female care group in *Dendrobates* (see above), and suggested that parental care evolved in a transition series from male to biparental to female parental care. Weygoldt (1987) suggested that *D. ventrimaculatus* males may mate with more than one female, but will use the eggs from some of their mates to feed tadpoles from previous mates. He said that males do this by mating with the second female on bromeliad leaves above the axil where previously carried offspring were placed. The male then pushes the eggs or embryos into the axil pool, and they are eaten by the tadpole. He argued that secondary females of this species experience a high cost of polygyny (see below), and that this may have favoured the evolution of female parental care. Zimmermann & Zimmermann (1988) constructed a phylogenetic hypothesis for 32 species of poison frogs, using behaviours observed in terraria as characters. Based on this phylogeny, they suggested that female parental care evolved from biparental care, which in turn evolved from male parental care. However, some of the behavioral characters that Zimmermann & Zimmermann (1988) used were not independent of the behaviours of interest (parental care behaviours), and some behaviours apparently differ between the field and terraria (Summers, 1989).

In order to derive an independent estimate of the evolution of parental care in poison frogs, Summers *et al.* (1999) used molecular methods to construct a phylogenetic hypothesis for representative species of these frogs. Using the polymerase chain reaction, DNA sequences were obtained from the cytochrome oxidase 1 region (521 base pairs) and cytochrome b region (292 base pairs) and the 16s rRNA region (536 base pairs) of the mitochondrial genome of poison frogs. A phylogenetic analysis of these data yielded a phylogeny which differs from that presented by Zimmermann & Zimmermann (1988). This phylogenetic hypothesis (Fig. 1) supports the monophyly of female care, but suggests that female and biparental care evolved independently from male parental care, in contrast to Zimmermann & Zimmermann's (1988) hypothesis. Hence, the pattern of parental care evolution in the genus *Dendrobates* is somewhat controversial.

In this paper, we have constrained hypotheses of the process of parental care evolution with the assumption that male parental care is ancestral in the genus *Dendrobates*. We have not assumed that female parental care evolved from biparental care (rather than male parental care), as this remains controversial.

THE COST OF POLYGYNY: INTERSEXUAL AND PARENT-OFFSPRING CONFLICT

Selection may often favour multiple mating by males, but polygyny may impose a cost on some or all of the male's mates, resulting in intersexual conflict (Dawkins, 1976; Davies, 1985). In order to evaluate Weygoldt's hypothesis, it is important to

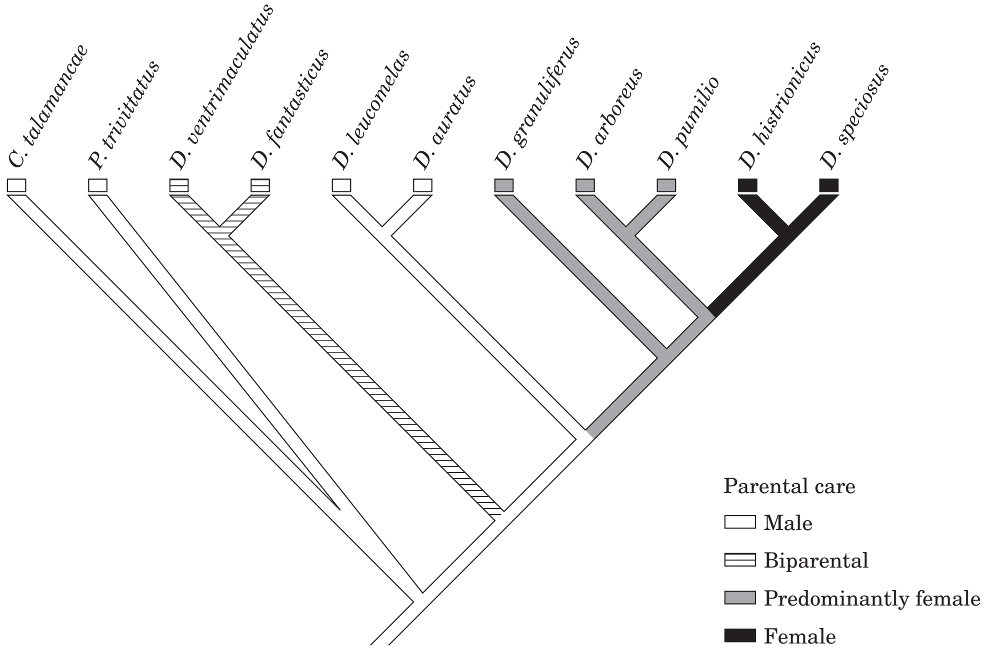

Figure 1. The most parsimonious reconstruction of the evolution of parental care in poison frogs of the genus *Dendrobates*, based on a hypothesis of evolutionary relationships derived from an analysis of mtDNA sequences (Summers *et al.*, in press). The reconstruction was carried out with the program MacClade (Maddison & Maddison, 1992).

describe how polygyny can impose costs on female poison frogs. The cost of polygyny in these frogs is likely to derive from the deposition of multiple tadpoles in a pool (Summers, 1990), or from the deposition of eggs and/or embryos with tadpoles (Weygoldt, 1987). The cost arises because tadpoles are cannibalistic, and because tadpoles have a negative effect on each other's growth rate (Weygoldt, 1987; Summers, 1990; Brust, 1993).

The most obvious cost arises when a male mates with two females and deposits one or more offspring from each female in the same pool. If the tadpole of one female eats its half-sibling, then the direct fitness of the victim's mother is reduced, and her indirect (inclusive) fitness is not increased, because she is unrelated to the cannibal (assuming the two females are unrelated). Such cannibalism may or may not be in the interests of the father, depending on the tradeoff between increased growth and survivorship of the cannibal and reduced total number of offspring. However, because the male controls the placement of tadpoles, cannibalism is likely to coincide with the inclusive fitness interests of the father, given constraints on pool availability.

A less obvious cost of polygyny may occur if tadpoles refrain from eating half-sibs. This may engender an unusual type of parent-offspring conflict. Usually, parent-offspring conflict is expected to occur when offspring are selected to take more resources than parents are selected to provide, or to take a higher proportion of the resources provided to all offspring than is in one or both parent's interests (Trivers, 1974). Parent-offspring conflict may occur over siblicide if it is in an offspring's interest to kill its sibling, but not in the interest of one or both parents (Mock & Parker, 1986).

A different type of parent-offspring conflict may occur if offspring are more altruistic toward each other than is in one or both parents' interests for them to be. Even if tadpoles can recognize half-sibs, and the inclusive fitness of tadpoles that refrain from eating half-sibs is higher than those that do not, there is still likely to be a cost to the mother. This is because the conditions favouring altruism between two half-sibs are less stringent for the half-sibs than for a female that is closely related to only one of those tadpoles.

In species with male parental care, it is unlikely that females could influence tadpole interactions directly, because eggs are not deposited near the pools used for deposition, and males, rather than females, transport tadpoles and choose the deposition site. In these species, a female's only opportunity to reduce such conflict may be to prevent her mate from mating with other females. Mate guarding by females has been observed in the field in two species of *Dendrobates* with male parental care: *Dendrobates auratus* and *Dendrobates leucomelas* (Summers, 1989, 1992).

MATING SYSTEMS: POLYGYNY THRESHOLD VERSUS DECEPTION

It is not necessarily the case that polygyny will impose a cost on females. Polygyny could be beneficial or neutral to females. For example, if the value of feeding tadpoles is very high, and the cost of polygyny is evenly distributed (see below), then some degree of polygyny might actually represent a net benefit to females. This argument is analogous to the argument used to explain the evolution of polyandry in tamarins (Terborgh & Goldizen, 1985). In saddle-backed tamarins, two males frequently care for the offspring of a single female, apparently because the importance of triparental care to offspring survival outweighs the lowered probability of paternity suffered by each male.

In poison frogs, it is possible that enhanced growth and survivorship experienced by tadpoles in pools provisioned by eggs and embryos from two females is high enough that it outweighs costs to each female that result from 'uncertainty of maternity'. This might occur if there is a premium on fast growth. By breeding synchronously, each of two females may ensure that at least some of her offspring have a chance of reaching large size quickly (by cannibalizing poolmates) before any other eggs, embryos, or tadpoles can be placed in the pool by other individuals.

In order for a cost of polygyny to produce selection for some females to care on their own, there must be no better option for those females. That is, females must achieve higher reproductive success by caring for their own offspring than by leaving them to be cared for by an already mated male (who may not spend much time caring for his latest mate's young) or by a male who has not mated in the recent past (who may have low territory quality or poor parental ability). This situation is analogous to the polygyny threshold hypothesis (Orians, 1969), except that females opt to care themselves rather than leave their offspring under the care of a single male. Alternatively, females may not be able to distinguish between mated and unmated males, and so be unable to avoid the cost of polygyny (e.g. deception hypothesis; Alatalo, Lundberg & Ratti, 1990). Polygyny does occur in species with male and biparental care (Summers, 1989; Caldwell, 1997; Summers & Amos, 1997), but at present there are insufficient data to say with certainty whether

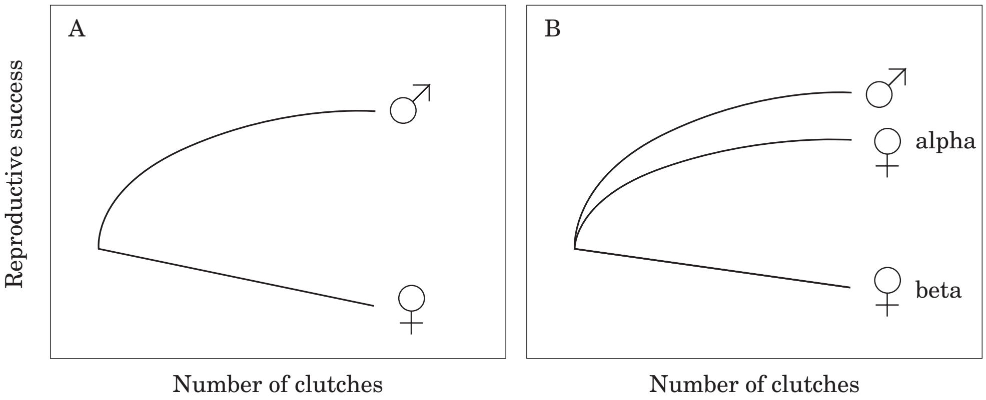

Figure 2. Hypothetical relationships between the number of offspring (from different females) cared for by a male and his reproductive success relative to that of his mates. Under an egalitarian distribution of the cost of polygyny (A), all females suffer equally from multiple tadpole deposition by their mate, whereas under a despotic distribution (B), primary (alpha) females benefit from multiple deposition, whereas secondary (beta) females suffer a cost.

polygyny typically occurs as a result of deception or because of polygyny threshold effects in species with either type of parental care.

Weygoldt (1987) suggested that the cost of polygyny is highest in members of the *D. ventrimaculatus* group with biparental care, and that it predisposed these species towards the evolution of female parental care. However, it is not clear that a high cost of polygyny will cause the evolution of a pure female parental care strategy, or that there is a higher cost of polygyny to females in the *D. ventrimaculatus* group (with biparental care) than in the *D. auratus* group (with male parental care). First, we will present some general considerations regarding the effect of a cost of polygyny on the evolution of female parental care, then we will discuss specific differences between species with male and female parental care.

EGALITARIAN VERSUS DESPOTIC DISTRIBUTIONS OF THE COST OF POLYGYNY

The costs and benefits of polygyny may be distributed in an egalitarian manner (costs and benefits accrue to each female equitably), or a despotic manner (some females suffer most of the cost, other females do not suffer, or even gain from polygyny). The distribution of the these costs and benefits may affect the probability that female parental care will evolve.

Figure 2A illustrates the effect of male polygyny on female fitness, under the assumption that all females experience equivalent costs and benefits of polygyny (an egalitarian distribution). If we introduce an element of despotism into the system, then the situation changes (Fig. 2B). If some females (here referred to as primary or alpha females) are able to ensure that their offspring are fed, and not eaten, then they gain the full benefit of male feeding behaviour, but do not suffer the cost of having offspring eaten. Females on the other end of the hierarchy (here referred to as secondary or beta females) now suffer a high cost from male polygyny because their offspring are being fed to those of the primary females.

Under either distribution of the costs and benefits of polygyny, it is possible that selection will favour a female that cares for her own offspring. The threshold at which selection favours female parental care will depend on the fitness of caring females relative to secondary non-caring females if female parental care is a condition dependent strategy (i.e. a female's size, nutritional status, health, etc. influences whether or not she will perform care), but will depend on the fitness of caring females relative to all non-caring females if the strategy is not condition dependent (Maynard Smith, 1982).

SIMPLE FREQUENCY DEPENDENT MODELS

Can the emergence of polygyny and an associated cost to females (through cannibalism of their young) cause evolution from pure male care (MC) to pure female care (FC)? To address this question, we begin with a simple game-theoretic model that ignores the distinction between primary and secondary females and any corresponding effects on males.

Egalitarian model

We estimate fitness by reproductive rate, which is the product of the number of eggs produced (and fertilized) per unit time and the probability that a fertilized egg survives to become a tadpole and eventually a mature frog.

In this section, we assume for simplicity that only one parent provides parental care; if a female deserts then her mate will provide the required parental care and if she cares then her mate will desert. We denote the probability of survival under uniparental care by P_1, in keeping with the notation of Maynard Smith (1977, 1982). In the absence of polygyny, a proportion P_1 of fertilized eggs survives to become adult frogs.

The number of eggs a female can produce per unit time (her fertility) depends on whether she cares or deserts. We denote the fertility of caring and deserting females by v and V, respectively ($V > v$). The (absolute) fertility cost of caring is $V - v$.

Thus, in the absence of polygyny, caring females have fitness vP_1 while deserting females have fitness VP_1.

Polygyny can impose a cost on a deserting female because she is not present to prevent her mate from feeding her young to the offspring of another female. The severity of this cost depends on the frequency of female desertion (male care) in the population, because a male probably cannot feed the offspring of deserting females to those of caring females (he is unlikely to know where the tadpoles of caring females are). We let c and C denote the cost of polygyny relative to the maximum fertility V, in populations of caring and deserting females, respectively ($0 \leq c \leq C \leq 1$). The effective fertility of deserting females is reduced by a factor $1 - c$ in a caring female population and by $1 - C$ in a deserting female population.

The benefit of polygyny to a female is to increase the survival probability of her offspring by nutritional supplements in the form of tadpoles (or embryos) of other females. This benefit also depends on the frequency of female care in the population, since males have the opportunity to facilitate cannibalism only if some of their mates

Table 1. Fitnesses of females in the egalitarian model

		Population	
		Care	Desert
Mutant	Care	vP_1	$vP_1\,(1 + b)$
	Desert	$V\,(1 - c)\,P_1$	$V(1 - C)\,P_1\,(1 + B)$

desert. Thus polygyny has no benefit for females in a population of caring females. We let b and B denote the benefit of polygyny to caring and deserting females, respectively, in a population of deserting females. In such a population, survival probability is enhanced by a factor $1 + b$ or $1 + B$, depending on whether the female in question cares or deserts. The benefit of polygyny to a mutant caring female (b) is probably negligible since her mate is unlikely to find the pond where she placed their tadpoles. In any case, $B \geq b \geq 0$, and $B \leq (1 - P_1)/P_1$ (since the maximum possible benefit of polygyny is to make survival certain, i.e. to make the survival probability unity).

These considerations yield the fitnesses given in Table 1. This game is a version of ‘playing the field’ (Maynard Smith, 1982, §2.C).

In the absence of polygyny ($C = c = 0$ and $B = b = 0$) Table 1 shows that the unique evolutionarily stable strategy (ESS) is desertion (i.e. male care) since $V > v$. Desertion remains an ESS if the cost of polygyny is sufficiently small. More precisely, if

$$C < 1 - \frac{v}{V}\frac{1 + b}{1 + B} \tag{1}$$

then $V(1 - C)(1 + B) > v(1 + b)$, so female desertion is an ESS.

Caring (FC) is an ESS if the cost of polygyny is sufficiently large,

$$c > 1 - \frac{v}{V}. \tag{2}$$

Note here that $1 - (v/V) = (V - v)/V$ is the (relative) fertility cost of caring. Thus, FC is an ESS if the cost of polygyny for caring females in a population of caring females (c) exceeds the fertility cost of caring. Given that c is probably small or negligible, FC is very unlikely to be an ESS.

If the benefit of polygyny is greater for deserting females than for caring females ($B > b$, as is almost certainly the case) then in principle it is possible for both conditions (1) and (2) to hold, i.e.

$$1 - \frac{v}{V} < c \leq C < 1 - \frac{v}{V}\frac{1 + b}{1 + B}. \tag{3}$$

In this case, both FC and MC are ESSs.

In order for a cost of polygyny to drive an evolutionary transition from MC to FC, it is essential that the introduction of this cost destabilizes MC. Thus, to evolve from MC to FC, we require the opposite of condition (1), namely

$$C > 1 - \frac{v}{V}\frac{1 + b}{1 + B}. \tag{4}$$

If, in addition to this condition, FC is an ESS (condition (2)), then female care will become fixed in the population.

After a cost of polygyny evolves, if neither female desertion (MC) nor female care (FC) is an ESS, i.e.

$$c < 1 - \frac{v}{V} \text{ and } 1 - \frac{v}{V}\frac{1 + b}{1 + B} < C, \tag{5}$$

then evolution will lead to an ESS that is a mixture of female care and male care. We now discuss this relevant but more complicated case.

The resulting evolutionarily stable frequency of female care in a mixed ESS depends on the relations between the costs and benefits of polygyny and the frequency of female care. Since these relations are unknown, we consider a simple, illustrative example. We assume that if the frequency of female care is f then the cost of polygyny for deserting females is $fc + (1 - f)C$; we also assume that the benefit of polygyny is $(1 - f)b$ for caring females and $(1 - f)B$ for deserting females. If the frequency dependences of the costs and benefits of polygyny are different from these forms then the ESS frequency of female care will be different from the value we derive below, but it is only the frequency of female care at equilibrium that depends on our specific assumptions: condition (5) for the existence of a mixed ESS does not depend on the detailed frequency dependence of the costs and benefits of polygyny (only on the costs and benefits in the extremes of pure MC or FC).

Continuing with our simple example, the fitness of a caring female is

$$W_c(f) = vP_1\,[1 + (1 - f)\,b] \tag{6}$$

while the fitness of a deserting female is

$$W_d(f) = V\,[1 - (fc + (1 - f)\,C)]\,P_1\,[1 + (1 - f)\,B]. \tag{7}$$

These frequency-dependent fitness functions agree with the fitnesses given in Table 1 when female care is fixed in the population ($f = 1$) and when female desertion is fixed ($f = 0$).

At a mixed equilibrium, the fitnesses of the caring and deserting strategies must be the same. Setting $W_c = W_d$ we obtain a quadratic equation in f, which can be solved for the equilibrium frequency f^*. The expression for f^* is unwieldy in general, so we concentrate on the most realistic special case, $b = c = 0$. In this case,

$$W_c - W_d = BC\,(1 - f)^2 + (C - B)\,(1 - f) - \left(1 - \frac{v}{V}\right), \tag{8}$$

and the solutions of $W_c - W_d = 0$ are

$$f_{\pm} = 1 + \frac{1}{2BC}\left[C - B \pm \sqrt{(C - B)^2 + 4BC\left(1 - \frac{v}{V}\right)}\right]. \tag{9}$$

Now, with $b = c = 0$, condition (5) reduces to

$$0 < 1 - \frac{v}{V} < C - B + BC, \tag{10}$$

which implies that $0 < f_- < 1 < f_+$. Since any frequency of female care must be between 0 and 1, the equilibrium frequency cannot be f_+. Thus,

$$f^* = f_-. \tag{11}$$

For $f = 1$, $W_c - W_d = -(1 - v/V) < 0$; so since f_- and f_+ are the only zeros of $W_c - W_d$, it follows that $W_c > W_d$ if $f < f^*$ and $W_c < W_d$ if $f^* < f \leq 1$.

It is now easy to prove that the mixed equilibrium is stable. Suppose that the population mean frequency of female care is not equal to the equilibrium value, $f \neq f^*$, and consider a mutant that cares with a frequency different from the mean, $f' \neq f$. The fitness of this mutant is

$$W(f', f) = f' W_c(f) + (1 - f') W_d(f), \tag{12}$$

where W_c and W_d are given in Eqs. (6) and (7), respectively. The fitness payoff to this mutant is

$$W(f', f) - W(f, f) = (f' - f)\,[W_c(f) - W_d(f)]. \tag{13}$$

If $f < f^*$ then $W_c(f) > W_d(f)$ (we proved this above for the case $b = c = 0$), so this fitness payoff is positive if and only if $f' > f$. Similarly, if $f > f^*$ then the payoff is positive if and only if $f' < f$. Thus selection always favours mutants whose behaviour will bring the population mean closer to the equilibrium frequency f^*; the mixed equilibrium is therefore stable. The same equilibrium caring frequency is stable as a polymorphism in the population, with a fraction f^* of females always caring and a fraction $1 - f^*$ always deserting. If $f \neq f^*$ then it will pay some caring individuals to desert, or some deserting individuals to care, until the frequency of female care in the population reaches f^*.

Despotic model

A despotic distribution of the cost of polygyny is plausible if rainfall (and hence breeding) is not continuous. In this case, healthy (primary) females can guard males for a short time after each rainfall until they have laid a clutch. They can therefore ensure that their tadpoles are carried first, and hence are placed first in any pool that the male uses for tadpoles of other mates. Females do guard their mates in some species with male care, and there is anecdotal evidence that this guarding is stronger before a female mates with a male than afterwards (Summers, 1989).

We now consider the effects of condition-dependent despotism, assuming that

Table 2. Fitnesses of females in the despotic model

		Population	
		Care	Desert
Mutant	Care	vP_1	$vP_1(1 + hb)$
	Desert	$VP_1[1 - (1 - h)c]$	$VP_1[1 + hB - (1 - h)C]$

females are healthy with fixed probability h and unhealthy with fixed probability $1 - h$. Healthy females are strong enough to guard their mates; unhealthy females are too weak to guard, and if they desert then their clutches may be fed to those of healthy females. In contrast to the egalitarian model, we are now assuming that it is not possible for a given female to encounter both a cost and benefit of polygyny in the same breeding cycle.

Since we assume the probability h is a fixed parameter (it does not evolve), we do not specify an explicit dependence of the costs and benefits of polygyny on h (which is also the frequency of healthy females). Of course, the costs and benefits of polygyny must be different for different h. For example, in the extreme limit that females are always healthy ($h = 1$), they can always mate-guard so cannibalism is prevented altogether and there can be no costs or benefits of polygyny. Interesting effects can occur only when there is a mixture of healthy and unhealthy individuals, so we assume $0 < h < 1$.

As in the egalitarian model, the costs and benefits of polygyny do depend on our evolutionary variable, the frequency of female care (f). The fitness of a caring female in a population with pure FC ($f = 1$) is not affected by polygyny, so her fitness is vP_1, as in the egalitarian model. However, when playing against a population of deserting females ($f = 0$), the fitness of a mutant caring female ($f' = 1$) depends on her condition (good with probability h, bad otherwise) and can be written

$$h\,[vP_1\,(1 + b)] + (1 - h)\,vP_1 = vP_1\,(1 + hb). \tag{14}$$

In a population of caring females ($f = 1$), a deserting female ($f' = 0$) has fitness

$$h[VP_1] + (1 - h)\,[V(1 - c)\,P_1] = VP_1\,[1 - (1 - h)\,c]. \tag{15}$$

If all females desert ($f' = f = 0$) then each has fitness

$$h[VP_1\,(1 + B)] + (1 - h)\,[V(1 - C)\,P_1] = VP_1\,[1 + hB - (1 - h)C]. \tag{16}$$

Table 2 summarizes these fitnesses. The egalitarian and despotic models are, of course, identical in the absence of polygyny ($b = B = 0$ and $c = C = 0$).

In the despotic model, the condition for the MC ESS to be destabilized by the cost of polygyny is

$$C > \frac{1}{1 - h}\left[(1 + Bh) - \frac{v}{V}(1 + bh)\right]. \tag{17}$$

If the probability of being in good health is below a critical level, $h < h_{\text{crit}}$, then this

TABLE 3. Fitnesses of males and females in the asymmetric game

		Female	
		Care	Desert
Male	Care	$vP_2\alpha'_r$ $vP_2\alpha'_r\,(1 + r)$	$VP_1\alpha_r$ $VP_1\,(1 + r)\,\alpha_r$
	Desert	vP_1 $vP_1\,(1 + R)$	$VP_0\alpha_R$ $VP_0\alpha_{\mathrm{R}}\,(1 + R)$

condition (17) is weaker than condition (4) for the egalitarian model, i.e. the threshold cost of polygyny that causes some frequency of FC to evolve is lower in the despotic than in the egalitarian model. The critical probability of good health is

$$h_{\mathrm{crit}} = \frac{B - b}{(V/v)\,(B + 1)^2 - (Bb + 2b + 1)}. \tag{18}$$

Note that if $V \geq v$ and $B \geq b$, as we have assumed, then h_{crit} is always a meaningful probability, i.e. $0 \leq h_{\mathrm{crit}} \leq 1$. If $h < h_{\mathrm{crit}}$ then, relative to an egalitarian distribution of the costs of polygyny, despotism increases the probability that some frequency of female care will evolve from MC. However, if $h > h_{\mathrm{crit}}$ then despotism actually makes it harder for FC to evolve. If $h = h_{\mathrm{crit}}$ then despotism has no effect.

ROLE ASYMMETRY AND THE COST OF LOST MATING OPPORTUNITIES

Weygoldt (1987) considered the evolution of FC only from the female's perspective. This is the approach we took in the previous section, where females played against the female population but not against their mates. In this section, we make essentially the opposite approximation: we consider the effects of polygyny (cannibalism) when females play against males—generalizing the model of Maynard Smith (1982, §10.B)—but we ignore the frequency dependence of the costs and benefits of polygyny.

Our notation is identical to Maynard Smith's, except that we use r and R to denote the probabilities of remating (during the care period for the current clutch) for caring and deserting males, respectively. In Maynard Smith's notation, $R = p$ and $r = p'$; our notation is chosen to make the relationship between these two quantities more obvious ($R \geq r$). P_0 and P_2 denote survival probabilities with no care (NC) and biparental care (BC), possibilities that were excluded in the models of the previous section (normally $P_0 \leq P_1 \leq P_2$). All the other symbols that we use have the same meaning as in the population games in the previous section.

The asymmetric payoff matrix for this game is given in Table 3. Note that the entries of this table give the fitnesses of males and females when the relevant care strategy is fixed in the population (as in the asymmetric games of Maynard Smith [1977, 1982], Yamamura & Tsuji [1993] and Balshine-Earn & Earn [1997, 1998]). Fitnesses of mutants are not given here, unlike the tables in the previous section. The only corresponding entry in Table 1 and Table 3 is the fitness of females in a

Table 4. ESS conditions in the asymmetric game

ESS	Conditions		
Biparental care	$vP_2 > VP_1 \cdot \alpha_r/{}'_r$	and	$P_2\,(1 + r) > P_1\,(1 + R)/\alpha'_r$
Male care	$VP_1 > vP_2 \cdot \alpha'_r/\alpha_r$	and	$P_1\,(1 + r) > P_0\,(1 + R)\,\alpha_R/\alpha_r$
Female care	$vP_1 > VP_0 \cdot \alpha_{\mathrm{R}}$	and	$P_1\,(1 + R) > P_2\,(1 + r)\,\alpha'_r$
No care	$VP_0 > vP_1/\alpha_{\mathrm{R}}$	and	$P_0\,(1 + R) > P_1\,(1 + r)\,\alpha_r/\alpha_R$

population in which all females desert and all males care: the bottom right hand entry in Table 1 and the top right hand entry (for females) in Table 3.

Since we now assume that males remate only with some probability r or R (rather than with certainty as in the previous section) there are costs and benefits of polygyny only on occasions when males remate. Therefore, in Table 3, a factor r or R is included in the costs and benefits of polygyny: in the benefits this is the probability that the male will remate before the care period for his current clutch is completed, while in the costs this is the probability that the current brood was conceived before the end of the care period of the male's previous clutch.

Under BC the male certainly knows the location of all his tadpoles, so he may have opportunities to facilitate cannibalism; whether or not he is able to do this depends on whether caring females actively prevent their partners from taking away some of their young. Since the costs and benefits of polygyny may not be the same under BC and MC, we use B' and C' for the case of BC and B and C for the case of MC. There are no costs or benefits to polygyny under FC in this model because deserting males do not know the locations of the tadpoles of caring females. If both parents desert, we assume that the male first carries the young to a pool of water, where they may be eaten by a previous brood or where they may survive by cannibalizing other tadpoles brought to the pool later. In practice, the probability of survival without care is likely to be very small ($P_0 \ll P_1$).

As in Maynard Smith's model, there are exactly four possible ESSs. Mixed equilibria are not possible in asymmetric games of this type because the role asymmetry (male vs female) is known with certainty to both players (Selten, 1980; Maynard Smith 1982:107). It is easiest to describe the ESSs if we define

$$\alpha_x \equiv (1 - xC)\,(1 + xB), \tag{19a}$$

$$\alpha'_x \equiv (1 - xC')\,(1 + xB'). \tag{19b}$$

Note that factors of α_r, α_R and α'_r occur in Table 3. The present model reduces to Maynard Smith's if $\alpha'_r = \alpha_r = \alpha_R = 1$ (e.g. if the costs and benefits of polygyny vanish). Conditions for each of the four ESSs are given in Table 4.

Suppose now that we begin with a non-cannibalistic species of frogs that is fixed at an ESS with male care. Thus, initially $B = C = 0$ and $B' = C' = 0$ so $\alpha'_r = \alpha_r = \alpha_R = 1$.

From the second line of Table 3 it follows that

$$\frac{v}{V}\frac{P_2}{P_1} < 1 \quad \text{and} \quad \frac{P_0}{P_1} \cdot \frac{1 + R}{1 + r} < 1. \tag{20}$$

If cannibalism evolves (after which $B > 0$ and $C > 0$) then MC will be destabilized if and only if the condition in the second line of Table 4 no longer holds, i.e.

$$\frac{\alpha_r}{\alpha'_r} \leq \frac{v}{V}\frac{P_2}{P_1} \quad \text{or} \quad \frac{\alpha_r}{\alpha_R} \leq \frac{P_0}{P_1} \cdot \frac{1 + R}{1 + r}. \tag{21}$$

The second condition will not be satisfied if P_0 is sufficiently small, but one of these conditions is sufficient to destabilize MC. If we define

$$\beta \equiv \frac{v}{V}\frac{P_2}{P_1} \cdot \frac{1 + rB'}{1 + rB}, \tag{22}$$

and use (19), the first condition in (21) can be written

$$C - \beta C' \geq \frac{1}{r}(1 - \beta). \tag{23}$$

We now consider two special cases.

If the costs and benefits of polygyny are the same under MC and BC ($B' = B$ and $C' = C$) then $0 < \beta < 1$ and condition (23) reduces to

$$C \geq \frac{1}{r}. \tag{24}$$

Since $C \leq 1$ and $0 \leq r \leq 1$, condition (24) can be satisfied only in the extreme that $r = 1$ (certain remating for caring males) and $C = 1$ (the cost of polygyny is complete loss of the clutch). This is impossible in practice because if $r = 1$ and $C = 1$ then *all* tadpoles get eaten, hence none survive. Thus MC cannot be destabilized by the evolution of cannibalism if the costs and benefits of polygyny are the same under MC and BC.

If under BC females actively prevent their mates from using the young as food for other tadpoles, then the situation is quite different. If females are perfectly successful in protecting their young from bad intentions by their mates then $B' = C' = 0$ and condition (23) becomes

$$C \geq \frac{1}{r}(1 - \beta). \tag{25a}$$

From the first part of (20) and the assumption that $B' = 0$, it follows that $\beta < 1$ so the right hand side of (25*a*) is positive and this condition is not necessarily satisfied. Since $C \leq 1$, condition (25*a*) can never be satisfied unless the right hand side is less than or equal to 1, i.e.

$$B \leq \frac{1}{r}\left(\frac{v}{V}\frac{P_2}{P_1} \cdot \frac{1}{1 - r} - 1\right). \tag{25b}$$

Since $B \geq 0$, this condition can in turn be satisfied only if the right hand side is non-negative, i.e.

$$r \geq 1 - \frac{v}{V}\frac{P_2}{P_1}. \tag{25c}$$

From the first part of (20), the right hand side of (25*c*) is between 0 and 1, so this criterion may be satisfied. If conditions (25*a*), (25*b*) and (25*c*) are all satisfied—the cost of polygyny is sufficiently large, the benefit of polygyny is sufficiently small and the probability of remating for caring males is sufficiently high—then the evolution of cannibalism will destabilize MC.

If MC is destabilized in this way, what evolutionary outcome should we expect? If P_0 is sufficiently small then selection will not favour the complete absence of care. We must therefore end up with either FC or BC. Table 4 shows that the ESS conditions for FC and BC are mutually exclusive, so a dynamical argument is not required to determine where parental care evolution will lead. (Such an argument would be necessary if there was no ESS at all after MC was destabilized, but we shall see below that within our framework there must be an ESS.)

If inequality (25*a*) is strict then it is equivalent to the first condition for a BC ESS in Table 4. The second condition for a BC ESS can be written

$$\frac{P_2}{P_1} > \frac{1+R}{1+r} \cdot \frac{1}{\alpha'_r}. \tag{26}$$

Thus we expect BC to evolve if the benefit of BC relative to uniparental care is sufficiently great. Note that if $B' = C' = 0$, as we assumed above to destabilize MC, then $\alpha'_r = 1$. Since $0 \leq r \leq R \leq 1$, in this case the right hand side of (26) is between 1 and 2, so survival probability under BC need not be twice as high as under uniparental care for BC to evolve in response to the destabilization of MC by cannibalism.

From the third line of Table 4, FC will be an ESS if and only if

$$\alpha_R < \frac{v}{V}\frac{P_1}{P_0} \quad \text{and} \quad \frac{P_2}{P_1} < \frac{1+R}{1+r} \cdot \frac{1}{\alpha'_r}. \tag{27}$$

The first condition here has the same structure as the first condition in (21), so we can immediately see that it will be satisfied if and only if

$$C > \frac{1}{R}\left(1 - \frac{v}{V}\frac{P_1}{P_0} \cdot \frac{1}{1+RB}\right), \tag{28a}$$

$$B < \frac{1}{R}\left(\frac{v}{V}\frac{P_1}{P_0} \cdot \frac{1}{1-R} - 1\right), \tag{28b}$$

and

$$R > 1 - \frac{v}{V}\frac{P_1}{P_0}. \tag{28c}$$

If P_0 is sufficiently small then conditions (28*a*), (28*b*) and (28*c*) will all be satisfied. The second condition in (27) is the opposite of (26).

Thus, provided P_0 is sufficiently small, one of BC or FC will be an ESS after MC has been destabilized in the way hypothesized above. Which of the two evolves depends on whether it is condition (26) or the second condition of (27) that holds, i.e. whether survival enhancement under BC is sufficiently great. Note, however, that FC cannot be stable in this model unless males acquire more matings if they desert ($R > r$). A cost of polygyny can drive evolution from MC to FC only if the cost of lost mating opportunities for caring males ($R - r$) is sufficiently large.

In practice, the cost of lost mating opportunities ($R - r$) is probably frequency dependent (like the costs and benefits of polygyny). Our present model does not take this into account but it does provide us with a framework within which to speculate on the influence of frequency dependent costs. If the proportion of caring females in the population increases, then $R - r$ will probably increase, because caring females give males a higher return per mating, in terms of reproductive rate; this is why male competition is most intense when females provide all of the investment required by offspring (Trivers, 1972). There is, therefore, potential for synergism between the cost of polygyny and the cost of lost mating opportunities for males, as follows. Suppose the population is at first fixed at the MC ESS. If a cost of polygyny evolves and destabilizes MC then caring females may start to emerge in the population. Even if there was no cost of lost mating opportunities in the pure MC population ($R = r$), the introduction of caring females may introduce such a cost, making $R > r$. If $R - r$ becomes sufficiently large then males will start to desert, which will tend to put more pressure on females to care. In this way, female-only care may eventually become fixed in the population. This is a possible evolutionary pathway from MC to FC in poison frogs. We will explore this with a rigorous model in future work.

ALTERNATIVE HYPOTHESES

It is, of course, possible that selection in favour of male desertion alone could lead to uniparental female parental care. This is particularly likely in species with biparental care, because females already perform care in these species. Male desertion in the absence of any tendency by females to perform care on their own could come about as a result of changes in the monopolizability of resources critical to female reproduction. For example, if the distribution of pools was patchy such that some males could defend clumped patches of pools, then it might pay males to guard territories encompassing those pools, at the expense of parental care. Females would presumably achieve higher reproductive success with the help of a male, but would have no choice but to care on their own in the face of male desertion.

Brood parasitism

Female parental care may have evolved for reasons having more to do with reproductive parasitism than with any particular cost of mating with a polygynous male. For example, in *D. ventrimaculatus*, since both males and females are intimately associated with the pools used for egg and tadpole deposition, members of each sex have opportunities to practice reproductive parasitism (male feeding of embryos from some mates to tadpoles of others is a special case of such parasitism). Recent research on *D. ventrimaculatus* suggests that multiple deposition of eggs and tadpoles in axils is common in the field, and that cannibalism is more the rule than the exception (Summers & Amos, 1997). Genetic analysis indicates that eggs, embryos, or tadpoles from the same pool but different clutches are frequently not full-sibs, suggesting that reproductive parasitism may be common (Summers & Amos, 1997).

In order for reproductive parasitism by females to be effective it is probably necessary for them to transport tadpoles. This is because it is necessary to place a tadpole into a pool where there are no older (i.e. larger) tadpoles, but where there are eggs or embryos developing in the axil. Females could parasitize the reproductive effort of others by placing tadpoles in pools being used by other individuals before the offspring of those individuals had reached the tadpole stage. Hence, any tendency for tadpole carrying on the part of females might be favored by selection. This would explain the evolution of tadpole carrying by females, but would not explain why males would stop carrying. Again, some benefit to males for desertion must be invoked (see above).

Pool size and distribution

Changes in pool size or distribution may have driven the evolution of female parental care, independent of any effect of the cost of polygyny or selection in favour of male desertion. After colonization of an environment with only small pools by a species with male parental care, adapted to using large pools, selection may have favored regular offspring provisioning, because of low nutrient availability in small pools. Biparental and female care appear to be alternative strategies for such provisioning. The key difference that caused these two alternatives to evolve may have to do with pool distribution. Hence, if pools were small, but located near the habitats where the frogs normally live (as in *D. ventrimaculatus* in Ecuador), this may have selected for biparental care, because it is relatively simple for males and females to coordinate provisioning. Alternatively, if pools were located far from the areas where the frogs normally live (i.e. a terrestrial species that lives on the forest floor but utilizes bromeliad pools in the canopy), then coordination of provisioning between males and females may become difficult and inefficient. In this case, female parental care would have an advantage because no coordination between the male and female is required. In this scenario, female parental care evolves because of the increased efficiency of tadpole provisioning, not because of a cost of polygyny to females.

Competition between species of different overall size might have the same effect. If two species that have diverged in body size (for reasons having nothing to do with parental care) become sympatric over part of their ranges at some point after they diverge, the larger tadpoles of the larger species will eat those of smaller species, potentially forcing the smaller species to use pools of marginal size and nutrient availability that are unexploited by the larger species. Here we might find a powerful selection pressure for the evolution of efficient feeding, and hence of female parental care.

This hypothesis is more likely to explain a transition from male to female care than from biparental to female care, as female provisioning already occurs in species with biparental care. It might also explain a transition from male to biparental care.

MALE VERSUS BIPARENTAL CARE

Which type of species (paternal or biparental) was more likely to have given rise to a lineage with female parental care? Ecological and behavioral differences between species with male and biparental care may affect the cost of polygyny, the probability of male desertion, the frequency of reproductive parasitism, and the size of pools typically utilized, among other things. We will briefly review two differences that might be important.

Biparental and female care

The most obvious difference between species with male and biparental care is that females are already providing substantial care for offspring in species with biparental care. Hence the evolution of female care from biparental care is a simpler process, requiring only the loss of male parental care, not both the loss of male care and the evolution of female care. Also, male desertion may impose a lower cost on offspring survival in species with biparental care than in species with male parental care, causing factors favouring male desertion to have a stronger effect in biparental species.

Pool size: food versus time limitation

There appears to be a difference between species of *Dendrobates* with male care and species with biparental and female parental care in the size of pools used. Species with male care tend to use larger pools, though some species with male care do utilize small pools (e.g. *Minyobates minutus*). Even so, pool size may affect the value of feeding (cannibalism) to tadpoles in the different species. Species with female parental care typically use small pools such as those that form in the leaf axils of *Heliconia* plants. Field experiments on *D. pumilio*, a species with female care which uses small leaf and stem axil pools, have shown that tadpoles will not grow and survive in these pools unless they are provided with eggs to eat (Brust, 1993). Zimmermann & Zimmermann (1984) observed that *D. ventrimaculatus* (from Peru) utilize small bromeliad axil pools, and frequently feed their tadpoles with eggs in captivity, suggesting that feeding may be critical in this species. Tadpole feeding (with nutritive eggs) has also been observed in *D. vanzolinii*, which also utilizes small pools (Caldwell, 1997).

In species of *Dendrobates* with male parental care, as exemplified by *D. auratus*, males carry individual tadpoles to pools of water that form in treeholes, or husks (e.g. calabash husks or palm leaf husks), which fall to the forest floor and fill with water. These pools vary considerably in size, but usually contain more than 200 ml of water (pers. obs.). Field experiments have demonstrated that tadpoles of *D. auratus* can survive and grow to metamorphosis in these pools without receiving smaller tadpoles to eat (Summers, 1990). Males were observed to carry tadpoles from a single clutch to different pools, suggesting that dispersing tadpoles is the optimal strategy (Summers, 1989, 1990). However, males may place more than one tadpole in a pool. In focal observations of marked individuals, about one quarter of the depositions observed were cases where the male placed a tadpole in a pool where he had placed a tadpole previously (Summers, 1990).

Minyobates minutus, a species of poison frog with male parental care, shows a similar strategy. This frog typically places a single tadpole in a pool, but places more than one tadpole in the same pool in a small percentage of pools (approximately 15%; Summers, unpublished results).

Why some males place more than one tadpole in a pool is unclear. It is possible that returning to a pool days or weeks later with another, small tadpole is a form of tadpole feeding. This possibility was supported by experiments comparing the growth rates of large *D. auratus* tadpoles placed in experimental pools with and without small tadpoles (Summers, unpublished results). The small tadpoles disappeared (apparently eaten by the large tadpoles), and the large tadpoles with small tadpoles showed higher growth rates than similarly sized control tadpoles without small tadpoles (Mann-Whitney U Statistic $= 40.00$, N with tadpole $= 7$, N without tadpole $= 7$, $P < 0.05$). On the other hand, it is important to carry out experiments on kin recognition in this species before concluding that younger half-sibs are consumed by older half-sibs (as pointed out above, females are likely to experience a cost of polygyny in either case).

The pool use strategy employed by *D. auratus*, and probably by other species that use similar types of pools (*D. leucomelas*, *D. tinctorius*, *D. galactonotus*, *D. azureus*, and *D. truncatus*), may be a facultative feeding strategy in which feeding is rare relative to species with female or biparental care. Males do not always place more than one offspring in a pool, but may do so when time limitations constrain their ability to find pools. That is, each male presumably has a limited amount of time in which to carry out all of its activities (courting, feeding, searching for mates, searching for pools, etc.). Each male will find a certain number of pools in the time it spends searching for pools, and apparently this is not always enough to allow the male to place a single tadpole in each pool. If this description is correct, then searching time limits tadpole dispersion in species of *Dendrobates* with paternal care.

Hence, a key difference between species with male and biparental care may be the importance and frequency of feeding. Both the costs and the benefits of polygyny may be higher in species with biparental care. Reproductive parasitism may also be more common in species with biparental care.

CONCLUSIONS

Model results

Our models indicate that the cost of polygyny on its own is unlikely to drive the evolution of a pure female parental care strategy, although it might drive a female care strategy to some non-zero frequency in a population. However, the existence of a cost of lost mating opportunities for caring males makes it possible for a cost of polygyny to destabilize male care and drive the evolution of a pure female care strategy. A cost of polygyny could instead cause the evolution of biparental care from male care.

Hypotheses

To date there are four hypotheses that might explain the evolution of a pure female care strategy in poison frogs: (1) The cost of polygyny in combination with selection favouring male desertion. (2) Changes in the monopolizability of resources critical to reproduction, favoring a shift from parental to mating effort by males, leading to female care by default. (3) Selection favouring reproductive parasitism by females, again accompanied by selection in favour of male desertion. (4) Changes in the size or distribution of pools utilized, making feeding necessary and female care more efficient.

Key questions and suggestions for empirical research

Do males face a tradeoff between mating and parental effort? This prediction could conceivably be tested by adding females or removing males from a local population, thus causing the operational sex ratio to be become biased towards females. This manipulation would not directly simulate the evolutionary change which was modelled in this paper (i.e. an increasing investment per offspring by females, making them more valuable as mates), but would test the hypothesis that males face a tradeoff between the allocation of effort to parental care versus courtship and mating.

Does polygyny impose a substantial cost on the reproductive success of females? Observational and experimental evidence from the green poison frog (*Dendrobates auratus*) suggests that it does (Summers, 1990). This hypothesis could be further tested by removal experiments designed to enhance the polygyny levels of males in a local area (by reducing the availability of males). If there is a cost of polygyny, increased levels of polygyny should reduce the reproductive success of females, relative to females in unmanipulated control sites.

Are females capable of influencing the cost of polygyny in species with biparental care? This question can only be answered by studying the responses of females to polygyny by their mates in biparental species, either in the field or terraria.

The despotic model presented in this paper suggests that condition (health and vigor) will affect the ability of females to influence the parental care of their mates (i.e. to prevent cannibalism of their own offspring). This prediction could be tested by experimentally manipulating the condition of females through supplemental feeding of secondaries and by restricting the diet of primaries. This type of manipulation should enable secondary females to become primary, and cause them to benefit from polygyny.

The hypothesis that pool size has been an important influence on the evolution of female parental care predicts that tadpole feeding is critical when a species utilizes small pools. The idea is that males will have evolved to feed their offspring in small-pool species (through feeding small tadpoles to large ones), and that tadpole growth and survival rates will be lower than in species with female parental care. This hypothesis could be tested by comparing female caring species with species that have male parental care and utilize small pools (e.g. some species of *Minyobates*).

The hypothesis that the potential for resource monopolization may influence the cost of lost mating opportunities to males could be tested by manipulating the concentration of resources critical for reproduction, such as *Heliconia* pools in *D. ventrimaculatus*. The prediction is that males should attempt to monopolize such resources as their defence becomes more economical.

Finally, if in certain species there are opportunities for brood parasitism that provide important fitness benefits to females, then we might expect females in these species to carry tadpoles occasionally. This has not been reported from the field, but few species have been studied.

Final comments

With regard to the cost of polygyny in species with male parental care compared to species with biparental care, we need more information on the reproductive strategies of both types of species. The considerations presented in this paper suggest that the cost of polygyny in poison frogs will depend on the value of feeding (cannibalism), the degree of despotism by primary females, and the options available to secondary females. Evidence to date suggests that the value of feeding in biparental species (e.g. *D. vanzolini*) is quite high, but further investigation is required. The degree of despotism is unknown.

The observation that captive females in species with biparental care (e.g. *D. vanzolinii*) feed their offspring may be considered a pre-adaptation for the evolution of female parental care. Hence, any selection pressure that favoured female parental care (cost of polygyny, male desertion, reproductive parasitism, small pools) is more likely to have encountered appropriate variation in species with biparental care than in species with male parental care. Even so, recent evidence suggests that both types of care may have evolved independently from male parental care (Summers, *et al.* 1999).

Clutton-Brock (1991: 118) specifically referred to cases in which females remained within a male's territory. While a cost of polygyny might explain the evolution of biparental care in such species, it does not explain male desertion. However, once females begin to care, this might alter the cost/benefit ratio of care to males, making it more profitable for males to invest in mating effort than in parental care. Male desertion is unlikely to provide any benefit to females, but may benefit males if reproductive gains from pursuit of additional mates outweigh reproductive gains from allocating similar effort to parental care of offspring.

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