PARENTAL CARE AND MODE OF
FERTILIZATION IN ECTOTHERMIC VERTEBRATES

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Why is parental care performed by the female in some species and the male in others? Several answers have been proposed by theoretical studies (Trivers, 1972; Williams, 1975; Dawkins and Carlisle, 1976; Maynard Smith, 1977, 1978; Perrone and Zaret, 1979), but there have been few efforts to test alternative hypotheses against observed patterns of vertebrate parental behavior. The present paper attempts to (1) derive specific predictions from three alternative hypotheses which deal with mode of fertilization (internal versus external) and parental care evolution, and (2) test these predictions using a compilation of published data on occurrence and correlates of parental care in amphibians and teleost fishes.

In a recent review of species with male parental care, Ridley (1978) concluded: "The data implicate the mode of fertilization as the most important variable determining which parent is selected to care. Parental care usually correlates with external fertilization. There exists two hypotheses to explain this: certainty of paternity and order of gamete release. It is likely that each is the final (evolutionary) cause in different phylogenetic lineages." The "certainty of paternity" hypothesis stems from the assumption that a male is unlikely to care for offspring if those offspring are not his own genetic progeny (Alexander, 1974). Trivers (1972) hypothesized that reliability of paternity will be affected by mode of fertilization—since external fertilization is without oviposition delay, reliability of paternity may be greater than with internal fertilization.

Like Ridley, Perrone and Zaret (1979) and Blumer (1979) applied Triver's hypothesized dichotomy in paternity reliability to explain mating systems in fishes. Perrone and Zaret (1979) have also extended it to other animals: "Inability to assure paternity may explain why male PI (parental investment) is unknown in reptiles, rare in mammals, and . . . occurs in birds only when accompanied by considerable long-term efforts by males to keep their mates unavailable to others." Recent theoretical models (Maynard Smith, 1977; Werren et al., 1980) cast strong doubt on the validity of this hypothesis.

The second hypothesis concerns the "order of gamete release." Dawkins and Carlisle (1976) proposed that natural selection should favor desertion of the offspring by whichever parent has the earliest opportunity, thereby forcing the remaining partner into the "cruel bind" (Trivers, 1972) of providing care. They hypothesized that internally fertilized species show female care because the female is unable to desert the embryo(s), and that parental care often evolves with external fertilization because females usually spawn first (and can then desert).

There remains, however, an additional hypothesis which may account for which sex shows care. Williams (1975) has proposed that association with the embryos preadapts a sex for parental care. With internal fertilization it is usually the female which is associated with the young. External fertilization, particularly when it occurs within a male's territory, could preadapt a species to the evolution of paternal care. We term this the "association" hypothesis. In many ways it is the simplest and most parsimonious of the three hypotheses, relying only on physical proximity of the adult and offspring.

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TABLE 1. *Distribution of parental care and mode of fertilization within amphibian and teleost familial and sub-familial groups that show both internal and external fertilization. A "+" indicates parental care; references are in the Appendix.*

	Male parental care		Female parental care	
	Internal fert.	External fert.	Internal fert.	External fert.
1) Amphibians				
Leptodactylidae (*Eleutherodactylus auriculatus* species group)	—	all species except *E. jasperi*	*E. jasperi*	—
Bufonidae	—	*Nectophryne*	*Nectophrynoides*	—
2) Teleost Fishes				
Apogonidae	+	+	—	+
Characidae	—	+	+	—
Clinidae	—	+	+	—
Cottidae	+	+	—	—
Exocoetidae	—	—	+	—
Ophidiidae	—	—	+	—
Scorpaenidae	—	—	+	—
Zoarcidae	—	—	+	+

In this paper we examine the relationship between mode of fertilization and parental care in teleost fishes and amphibians. Both groups show internal *and* external fertilization, and male *and* female care. Hence, they are important groups for examining care evolution. Our analysis differs from those of Ridley (1978) and Blumer (1979) in that (1) we attempt to frame specific predictions from the hypotheses outlined above, (2) we use data from all families, including those with maternal care and with no paternal care, and (3) we test our results statistically. Our analysis confirms the existence of a correlation between mode of fertilization and which sex shows parental care (as has been suggested by others, e.g., Williams, 1975; Maynard Smith, 1977; Ridley, 1978), and enables us to reject the "gamete-order" hypothesis on several grounds. The data do not allow us to falsify either of the other hypotheses, but the "association" hypothesis predicts observed patterns of parental care more accurately than the "reliability of paternity" model.

METHODS

Our compilation of the distribution of parental care among the amphibians and the teleosts (which comprise about 95% of all living fishes and more than 99% of all bony ones) is based mainly on recent reviews which we supplemented with current literature. Although not exhaustive, the data should correctly identify any major patterns: references are given in the Appendix. Our taxonomy follows Greenwood et al. (1966) for teleosts, and Goin et al. (1978) for amphibians. We have characterized each family according to the mode of fertilization and the presence of male, female, or no parental care. Parental care was defined as investment into offspring after fertilization, such investment presumably increasing offspring survival. Hence, our definition includes all cases where the offspring and parent remain together after fertilization of the oocytes. For example, our definition includes both viviparity and egg-guarding, but excludes activities (e.g., construction of elaborate nests) prior to ovulation. The function of these latter activities is often unknown.

Maynard Smith (1978) has examined data on teleosts, and Ridley (1978) on teleosts and amphibians, but only for those families showing parental care. We included families without parental care so that our analyses could take into account the relative frequencies of modes of fertilization. Our data compilation was independent of those by Maynard Smith and Ridley; there are minor numerical discrepancies that we cannot explain.

Throughout the analysis we treat families with both internal and external fertilization (10 families) as two separate groups, divided according to the mode of fertilization (Table 1). For example, we treated the viviparous frog *Eleutherodactylus jasperi* as separate from the rest of the Leptodactylidae, because it is the only species in which internal fertilization has been reported. For the sake of brevity, sample sizes in statistical tests in this paper are reported as "families"; readers should note that this is not strictly true in the above cases. Although the division of families according to mode of fertilization was done for reasons of analysis, current taxonomic studies suggest that these divisions may be phylogenetically realistic for at least some of the teleosts.

The present state of knowledge about breeding systems is often anecdotal. Data we believe to be reasonable were obtained from 182 teleost families (approximately 44% of all teleosts). Allowing for families with both modes of fertilization and/or both sexes showing care, this provided 206 items of data. Among the amphibians parental care is generally rare (often shown by only a few species within a large family—McDiarmid, 1978), and we have assumed that care is absent from the 10 families (29%) in which it has not been recorded. There are 45 items of amphibian data. Levels of significance were calculated from the Fisher's Exact Probability Test, or the χ^2 test (Siegel, 1956).

RESULTS

The reproductive adaptations of teleosts and amphibians show many convergences, and involve both sexes. Some species build large floating foam nests into which the eggs are deposited and guarded by the male (e.g., the fish *Betta*; the frog *Adelotus*). Many other species lay eggs on the substrate, where they are guarded by the male (the fish *Lepomis*; the frog *Pseudophryne*) or the female (the fish *Anoplarchus*; the salamander *Plethodon*). In some species the developing offspring are carried around on the body of the parent,

sometimes by the male (e.g., the fish *Syngnathus*; the frog *Assa*) and sometimes by the female (e.g., the fish *Solenostomus*; the frog *Gastrotheca*). In still others, the eggs are retained inside the parent's mouth and this activity too, may be performed by either parent (males in the fish *Bagre* and the frog *Rhinoderma*; females in the fish *Haplochromis* and the frog *Hylambates*).

Overall, parental care has been described in 45% of the 182 teleost families we examined, and in 71% of the 35 families of amphibians. Among teleosts, paternal care is significantly more common than maternal care (61% versus 39%; $\chi^2 = 5.14$, $d.f. = 1$, $P < .05$). There is no statistically significant predominance of male or female care in amphibians (46% versus 54%; $\chi^2 = 0.26$, $d.f. = 1$, $P > .05$). Solitary parental care is the dominant care pattern in both groups; biparental care occurs in less than 25% of teleost and 20% of amphibian families with care.

The general pattern for families with parental care is that female care is most common with internal fertilization (86% female care), and male parental care with external fertilization (70% male care) (Table 2). The correlation between the mode of fertilization and the sex showing parental care is highly significant both for teleosts (data from Table 2; considering only those families showing parental care; 2 × 2 contingency table with internal versus external fertilization and male versus female parental care; $N = 102$ families, $P < .001$ for two-tailed tests) and for amphibians ($N = 35$, $P < .01$). This pattern is consistent with the results of Ridley (1978), and also is consistent with the three hypotheses—gamete-order, reliability of paternity, and association.

Gamete-Order

The gamete-order hypothesis proposes that parental care patterns appear as the result of differential opportunity to desert zygotes—the sex spawning last should show care. In both teleosts and amphibians with external fertilization, males rarely spawn before females. Simultaneous gamete release appears to be the most

common situation (approximately 50–70% of known cases), and prior spawning by females the next most common. Two tests are possible.

(1) When gametes are released simultaneously, the gamete-order hypothesis predicts random assortment of parental care. Of 46 teleost species (from 12 families) with mono-parental care and simultaneous spawning, 36 have solitary male care (78%); this is a non-random assortment ($\chi^2 = 16.2$, $d.f. = 1$, $P < .001$).

(2) The gamete-order hypothesis predicts that male parental care should not evolve with external fertilization when female desertion is physically impossible. This prediction is falsified by the data. For example, most anuran amphibians with male care remain in amplexus until spawning is finished. In teleosts, female desertion should be impossible when sperm are released before ova. Yet, some Callichthyidae and Belontiidae males build foam nests, release sperm first, and provide mono-parental care. For example, female Callichthyidae draw spermatic fluid into their mouth from the vent of the male, use this sperm to fertilize eggs held in their ventral fins, place the eggs into the froth nest of the male, and then leave.

Conversely, females are known to provide care when desertion is physically possible. For example, the maternal mouthbrooding cichlids (*Sarotherodon*) spawn eggs into the substratum nest of a male, then remove the eggs from the nest and swim to brooding grounds; the male remains at the nest site.

Reliability of Paternity

A test of the reliability of paternity hypothesis is possible by deriving specific predictions separately for each sex, and including *all* families in the analysis (not just those with parental care). Internal fertilization is found in 11% of teleost and 30% of amphibian families. To allow for the predominance of external fertilization, the data need to be analyzed proportionally within each mode of fertilization. Specifically, the reliability of paternity hypothesis yields two major predictions.

(1) Paternal care should be more com-

mon proportionally in families with external fertilization than in those with internal fertilization—because reliability of paternity is higher in the former group. This prediction is supported by the data on teleosts (testing 2 × 2 contingency table; internal versus external fertilization and paternal care versus no paternal care; data from Table 2: $N = 189$ families, $P < .01$ for one-tailed test) and amphibians ($N = 37$, $P < .05$).

(2) Maternal care should be equally as common proportionally in families with external fertilization as in those with internal fertilization—because reliability of maternity is near 100% in both cases. This prediction is *not* consistent with the data in Table 2, which indicate a much higher incidence of maternal care with internal fertilization (testing 2 × 2 contingency table; internal versus external fertilization and maternal care versus no maternal care; teleosts: $N = 189$ families, $P < .001$ for two-tailed test; amphibians: $N = 37$, $P < .002$ for two-tailed test).

Association Hypothesis

The association hypothesis proposes that the above correlations are explained by preadaptation due to asymmetries of association with the offspring. Three predictions result.

(1) For internally-fertilizing species in which eggs are deposited immediately after fertilization, there remains a potential association between a male and his offspring. In this respect, oviparous internally-fertilizing species are similar to externally-fertilizing forms. The association hypothesis predicts that male parental care should be equally as common proportionally among *oviparous* families of *both* modes of fertilization. This prediction is contrary to the paternity hypothesis, but is consistent with data on teleosts ($N = 177$ families, $P > .50$ for two-tailed test). No test is possible with the amphibians, because eggs are retained for long periods *in utero* in most internally-fertilizing forms (Salthe and Mecham, 1974). In the teleosts, the exclusion of viviparous and egg-retaining forms leaves only nine

TABLE 2. *Distribution of male and female parental care with respect to mode of fertilization in teleost fishes and amphibians (see text for details). The table shows number of families; a single family may appear in more than one category, but is not listed under "no parental care" unless care is completely unknown in the family. Raw data are in the Appendix.*

	♂ Parental care		♀ Parental care		No parental care	
	Internal fert.	External fert.	Internal fert.	External fert.	Internal fert.	External fert.
Fish	2	61	14	24	5	100
Amphibians	2	14	11	8	0	10
Totals:	4	75	25	32	5	110

internally-fertilizing families in the above analysis (Pantodontidae, Characidae, Auchenipteridae, Horaichthyidae, Neostethidae, Phallostethidae, Cottidae, Apogonidae and Anarhichadidae). Hence, the power of the test is reduced. A stronger analysis of teleost data at the *species* level, however, is consistent with the prediction that the incidence of male parental care is independent of the mode of fertilization within oviparous species ($N = 61$ species, 21 with internal fertilization, $\chi^2 = 0.04$, $d.f. = 1$, $P > .50$).

(2) From the association hypothesis, oviposition within a male's territory is a preadaptation for the evolution of paternal care (Trivers, 1972; Williams, 1975; Ridley, 1978). This predicts that male parental care should be more common in territorial than in non-territorial forms. Within amphibians, only 6% of externally-fertilizing species have male territoriality (using male combat as the criterion of territoriality; Wells, 1977; Shine, 1979), yet territoriality is known in 31% of the externally-fertilizing species with male parental care ($\chi^2 = 48.24$, $N = 611$ species, $d.f. = 1$, $P < .001$). We do not have similar data for teleosts, but Perrone and Zaret (1979) claimed that all "parental" teleosts show male territoriality. This apparent correlation could be explained in two ways: either parental care is more likely to evolve in the territorial sex, or else territoriality is more likely to evolve in the parental sex (Ridely, 1978). We cannot distinguish between these two interpretations, and merely note that the observed

correlation is consistent with the association hypothesis.

(3) The association hypothesis offers a possible explanation for the correlation between internal fertilization and female parental care. When eggs are fertilized internally, rather than as they float, fall or attach to the substrate, the female is potentially put in direct association with her offspring. This provides an opportunity for selection to favor increasing length of embryo retention *in utero*, a highly effective form of parental care (Williams, 1966; Shine and Bull, 1979). This idea is reinforced by the observation that live-bearing has evolved from internal fertilization independently several times within the fishes (Rosen and Bailey, 1963) and at least four times in the amphibians (Salthe and Mecham, 1974). Indeed, female care involving retention of the embryos is the dominant pattern in internally-fertilizing species of teleosts (57% of families) and amphibians (64%). We attribute this situation to internal fertilization preadapting females to parental care evolution by providing an offspring-parent association.

A final test is to examine those few teleost species with internal fertilization but immediate egg release (nine families). The association hypothesis predicts female care should be equally as common proportionally in these families, as in families with external fertilization—since females are associated with embryos on substrate to the same degree in both cases. This prediction is supported by the data ($N = 177$ families, $P > .50$ for two-tailed test).

However, this result is consistent also with the paternity hypothesis.

DISCUSSION

In both teleosts and amphibians there is a clear relationship between the sex showing parental care and the mode of fertilization. Not only is male care correlated with external fertilization (Ridley, 1978), but female care is correlated with internal fertilization. The gamete-order hypothesis (Dawkins and Carlisle, 1976) does not properly account for the parental care patterns observed. Male care remains correlated with external fertilization independent of the order of gamete release, and the physical ability of females and males to first desert the zygotes. The empirical evidence therefore repudiates the gamete-order hypothesis. A similar conclusion was reached by Loiselle (1978).

The reliability of paternity hypothesis (Trivers, 1972; Ridley, 1978) successfully predicts the observed correlation between male care and external fertilization. However, three major problems arise with this hypothesis. First, *the assumption that paternity reliability depends upon mode of fertilization may not itself be true*, especially for those internally-fertilizing species in which multiple insemination is rare. To our knowledge, no data are available to substantiate the supposed correlation. Instead, sperm competition and cuckoldry have been documented in the field with *both* external (Warner and Robertson, 1978; Gross, 1979) and internal fertilization (Birdshall and Nash, 1973; Bray et al., 1975). In the externally-fertilizing fish *Lepomis macrochirus*, for example, about 80% of the reproductive males do not build nests but show a "cuckoldry" strategy and parasitize nesting males providing brood care (Gross and Charnov, 1980).

The second objection to the paternity reliability hypothesis comes from recent theoretical models of Maynard Smith (1978) and Werren et al. (1980). These models indicate that if paternity is equivalent for all matings independent of care behavior, paternity can not itself influence

selection for care. When a paternal male "sacrifices" alternative matings, paternity could influence care evolution because level of paternity can reflect the number of opportunities for alternative matings: high paternity can mean few opportunities and therefore a low cost for paternal care (Werren et al., 1980). Because alternative mating opportunities will be determined by many ecological factors which probably are independent of mode of fertilization (e.g., breeding density, adult sex ratio, female promiscuity, breeding synchrony, dominance hierarchies), there are strong theoretical reasons to doubt any paternity explanation for an external fertilization relationship. Finally, the paternity reliability hypothesis has failed to predict or explain the observed correlation between internal fertilization and female parental care.

The third hypothesis we have considered is that physical association between adult and offspring preadapts for the evolution of parental care (Williams, 1975). This hypothesis is attractive on theoretical grounds because of its parsimony; it could serve almost as a null hypothesis against which to test other suggestions. Hence, male care is unlikely with internal fertilization because the male is unlikely to be nearby when the eggs are finally laid. If the eggs are laid immediately after insemination there should be no obstacle to male parental care, however. The data are consistent with both predictions. With external fertilization, male or female care could evolve, because both parents are present when the eggs are laid. We attribute the predominance of male care under these conditions (Table 2) to the high frequency of male territoriality in externally-fertilizing species. Male territoriality increases the association between a male and his offspring, and is itself correlated with male parental care (Ridley, 1978; and Results section above). The association hypothesis also successfully predicts a correlation between internal fertilization and female care.

We do not suggest that *all* cases of pa-

rental care are predictable from the association hypothesis. For example, some female teleosts of the genus *Sarotherodon* spawn in male territories, but then pick up the eggs and mouth-brood them elsewhere. In this case, the association hypothesis would incorrectly predict male care. There also are territorial species with external fertilization which have no care. Parental care evolution ultimately depends upon environmentally induced selection for care, and the ability of a species or sex to improve brood survivorship, outweighing costs in terms of fewer matings (or egg production). Each species (and sex) is therefore uniquely evaluated by natural selection. Nonetheless, the association hypothesis does seem to have broad predictive powers. In view of the parsimony and apparent predictive value of this hypothesis, let us examine whether it (1) can explain the high incidence of male parental care in fishes and amphibians, and (2) is consistent with patterns of parental care in other animals.

(1) Solitary male parental care is strikingly more common in fishes and amphibians than elsewhere (Ridley, 1978). A probable reason for the predominance of single parent care in these two groups is that guarding against predators (fish and amphibians rarely feed their offspring) can be done almost as well by one parent as two (Emlen, 1973; Williams, 1975; Maynard Smith, 1977; Perrone and Zaret, 1979). We believe that male care is common because the nature of oviposition behavior put males in association with the zygotes without reducing their opportunity for additional matings. Consider the evolution of parental care from primitive free-spawning fishes (with external fertilization) which produce substratum-attaching eggs. Since successful egg development is affected by substrate and other local conditions (references in Balon, 1975), natural selection should favor those females that cast their eggs into prime areas. Males should then congregate at, and probably precede females to, these oviposition sites, much as free-spawning perches do today (Pearse and Achtenberg,

1920). Fertilization success (paternity) during a spawning act will be increased by aggressive behaviors between males, eventually leading to territorial spacing such as is found in primitive darters (Winn, 1958). If territories differ sufficiently in quality, males will be selected for site-tenacity (Baylis, 1978; Loiselle and Barlow, 1978; Ridley, 1978). Males can then evolve displays to attract females and advertise their sites; males should also improve the site, which probably has led to the substrate "sweeping" and nest building of many fishes today (e.g., the families Cichlidae and Centrarchidae). Territorial males have the option of providing care (Trivers, 1972) for the eggs in their territory. This behavior would evolve through kin selection as envisaged by Barlow (1964) and Williams (1975). With the provision of care, female choice may begin to favor male "parental" characters (e.g., defensive ability) in addition to territory sites, explaining the aggressive courtship behavior of many fishes (Breder and Rosen, 1966) and possibly accelerating paternal care evolution (Trivers, 1972). The important point is that the nature of oviposition and sexual selection pressures will result in an asymmetry of association with the embryos, preadapting the male sex for the evolution of care. A similar explanation applies to amphibians (McDiarmid and Adler, 1974; Duellman and Savitzky, 1976; Wells, 1977).

(2) Is the association hypothesis consistent with patterns of parental care in other taxa? Paternal care is common in birds (Lack, 1968), but rare in mammals (Kleiman, 1977). In both groups, paternal care consists almost entirely of *biparental* care; solitary male care is known only in a few birds with "sex role reversal" (Emlen and Oring, 1977). The higher frequency of biparental care in endotherms than in ectotherms (see Results) probably reflects the fact that endothermic parents usually feed their young as well as guard them. Because two parents can provide more food than could one, biparental care evolves (Maynard Smith, 1977; Perrone and Zaret, 1979). Guarding, in contrast, can often

be accomplished by one parent because the benefits of guarding are divisible among the offspring.

Hence, we do not invoke the association hypothesis to explain the basic dichotomy in parental care patterns between ecto-thermic and endothermic vertebrates. We feel, however, that the association hypothesis may be of value in interpreting the distribution of male care *within* the endothermic vertebrates, as well as within the ectotherms which we have analyzed in the main part of this paper. Why is male parental care (in the form of biparental care) so common in birds? Female birds typically oviposit and nest in a male's territory, therefore associating the male with the clutch. Because two parents are better than one at feeding offspring, selection favors biparental care whenever a male's alternative options (other matings) are not greater (Lack, 1968; Maynard Smith, 1977). When suitable nesting sites (Selander, 1972) and/or food resources (Orians, 1969) are dispersed, males will not show resource territoriality (Brown, 1964) and therefore not be associated with oviposition. In many grouse for which breeding resources are dispersed (Wiley, 1974), females approach clumped displaying males to be mated; oviposition occurs elsewhere and there is no male parental care (see also Loiselle and Barlow, 1978).

Since most mammals are live-bearers, males are associated with the embryos only so long as they remain associated with the female. This will occur when females remain in a male's territory such as is found in many social carnivores (Williams, 1975; Maynard Smith, 1978) and some primates (Clutton-Brock and Harvey, 1977), and here male care is prevalent. As Orians (1969) and others have argued (e.g., Emlen and Oring, 1977; Maynard Smith, 1977), male care will not evolve without male ability to contribute to offspring survival. For example, lack of male care in herbivores could reflect the inability of males to contribute food resources to the gestating female (Trivers, 1972). But this does not itself explain why

few male ungulates defend new-born young from predators (Owen-Smith, 1977), such as is seen in vicūna (Franklin, 1974), and is common to females (e.g., goats, Shank, 1972; bison, McHugh, 1958). It is perhaps better argued that the nature of herbivorous feeding has curtailed social territoriality in ungulates (Wilson, 1975), thereby reducing offspring-male association, and predisposing females to solitary care.

Similar arguments may be used for other animals. For example, parental care is rare in insects (Ridley, 1978) and many internally fertilized species oviposit in areas separate from mating sites. This is particularly pronounced when larvae feed on resources different from that of adults (Jones, 1977). The Belostomatinae (Hemiptera) are a striking exception, having solitary male care with internal fertilization (Smith, 1976). Males prolong copulation with the female, which Smith (1979) has argued insures paternity of the eggs the male will carry. Imagine an ancestral bug with internal fertilization and no care. If opportunities for additional male mating are few, selection may favor maximizing the paternity of a mating, resulting in a postcopulatory passive phase during which the male remains attached to the female (Parker, 1970). When eggs are released, this places both male and female with equal proximity to the embryos (despite internal fertilization). If any adhesive eggs fortuitously attach to the male's body, this could mark the beginning of paternal care evolution. That is, initial selection for paternity may indirectly result in male-offspring association which then leads to paternal care. A similar argument may apply to marine spiders (pycnogonids, Nakamura and Sekiguchi, 1980) and possibly the Syngnathidae (pipefish and seahorses, Herald, 1959).

SUMMARY

In both fishes and amphibians, paternal care correlates with external fertilization and maternal care with internal fertilization. Three different hypotheses have been proposed to explain these relation-

ships: (1) "gamete-order" (Dawkins and Carlisle, 1976; Ridley, 1978); (2) "reliability of paternity" (Trivers, 1972; Ridley, 1978); and (3) "parent-offspring association" (Williams, 1975). We have attempted to test these hypotheses by drawing specific predictions and using detailed data on teleost and amphibian parental care.

We reject the gamete-order hypothesis because male care remains correlated with external fertilization independent of the physical ability of females and males to first desert the zygotes.

Although the reliability of paternity hypothesis predicts the correlation between male care and external fertilization, the hypothesis is not supported by the distribution of female care. Two further objections are that the assumption of differences in paternity reliability with mode of fertilization is questionable, and that theoretical models cast doubt on the generality of the basic hypothesis (Maynard Smith, 1978; Werren et al., 1980).

Overall, the association hypothesis is most consistent with the available data. This hypothesis successfully predicts patterns of both male and female parental care, and offers possible explanations for differences in the incidence of male versus female parental care in different vertebrate groups. We interpret the prevalence of male parental care with external fertilization as resulting from male territoriality, which in turn results from female discrimination of oviposition sites. Internal fertilization preadapts females to selection for embryo retention, leading to live-bearing.

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APPENDIX 1. *Parental care and mode of fertilization in amphibians and teleost fishes. Taxonomic arrangement follows Goin et al. (1978) and Greenwood et al. (1966). An "X" in any of the first four columns means that the relevant combination of parental care and mode of fertilization has been recorded in that family; however, in many cases parental care may occur in only a small proportion of species within the family.*
References: 1. Albrecht (1969), 2. Allen (1972), 3. Anderson et al. (1971), 4. Balon (1975), 5. Barlow (1964), 6. Barlow et al. (1968), 7. Barlow (1974), 8. Bell (1978), 9. Bellomy (1969), 10. Bhatt (1968), 11. Bolin (1947), 12. Breder and Rosen (1966), 13. Brothers (1975), 14. Carlander (1977), 15. Chapman (1978), 16. Colin (1978), 17. Constantz (1975), 18. Corben et al. (1974), 19. Daniels (1979), 20. DeMartini (1976), 21. Dmitrenko (1970), 22. Drewry and Jones (1976), 23. Echelle (1973), 24. Fitzsimons (1976), 25. Forester (1979), 26. Fryer and Iles (1972), 27. Garnaud (1962), 28. Garnaud (1963), 29. Goldberg (1976), 30. Gosline (1966), 31. Gross (1980), 32. Hart (1973), 33. Hirshfield (1977), 34. Hoar (1969), 35. Hoedeman (1974), 36. Ihering (1937), 37. Inger (1966), 38. Itzkowitz (1974), 39. Jackson (1978), 40. Jubb (1967), 41. Kodolov (1968), 42. Kramer (1973), 43. Krekorian and Dunham (1972), 44. Kumai and Nakamura (1978), 45. Lake (1978), 46. Lake and Midgley (1970), 47. Lamotte and Lescure (1977), 48. Lastein and Van Deurs (1973), 49. Ledrew and Green (1975), 50. Lowe-McConnell (1975), 51. Lubbock (1975), 52. Marliave and DeMartini (1977), 53. Martin and Martin (1971), 54. McDowall (1978), 55. Mochek (1973), 56. Moore (1970), 57. Morris (1952), 58. Moyle (1976), 59. Myrberg (1976), 60. Nelson (1964), 61. Nelson (1976), 62. Nelson and Krekorian (1976), 63. Newdick (1979), 64. Nishida (1978), 65. Ozeti (1979), 66. Peden (1972), 67. Phillips (1977), 68. Pietsch (1976), 69. Pietsch and Grobecker (1980), 70. Placida (1979), 71. Porter (1972), 72. Qasim (1957), 73. Reese (1975), 74. Roberts (1971), 75. Robertson (1973), 76. Robertson and Hoffman (1977), 77. Robertson and Warner (1978), 78. Robertson et al. (1979), 79. Rosen and Bailey (1963), 80. Ross (1978), 81. Sakamoto and Suzuki (1978), 82. Salthe and Mecham (1974), 83. Scott and Crossman (1973), 84. Sjölander et al. (1972), 85. Smith (1945), 86. Soltz and Naiman (1979), 87. Sterba (1962), 88. Sturm (1978), 89. Suzuki and Hioki (1978), 90. Thakur et al. (1977), 91. Thomson et al. (1979), 92. Timms and Kennleyside (1975), 93. Wake (1977), 94. Wake (1978), 95. Wake (1980), 96. Warner and Robertson (1978), 97. Wells (1977), 98. Wells (1978), 99. Westenhagen (1974), 100. Westin (1969), 101. Wheeler (1969), 102. Wheeler (1975), 103. Wheeler (1978). 104. Winn (1958), 105. Woodruff (1977), 106. Wootton (1976), 107. Wourms and Bayne (1973), 108. Wourms and Cohen (1975), 109. Wourms and Evans (1974), 110. Xavier (1977).

| | ♂ Parental care | | ♀ Parental care | | No parental care | | |
	Internal fertilization	External fertilization	Internal fertilization	External fertilization	Internal fertilization	External fertilization	References
Amphibians							
(i) Caecilians							
Caeciliidae			X				82, 93
Ichthyophiidae			X				82, 93
Scolecomorphidae			X				82, 93
Typhlonectidae			X				82, 93
(ii) Caudates							
Ambystomatidae			X				82
Amphiumidae			X				82
Cryptobranchidae		X					82
Hynobiidae		X					82
Plethodontidae	X		X				25, 82
Proteidae	X		X				82
Salamandridae			X				65, 82
Sirenidae						X	82
(iii) Anurans							
Allophrynidae						X	82
Ascaphidae						X	82
Brachycephalidae						X	82
Bufonidae		X	X				47, 95, 110
Centrolenidae		X					47
Dendrobatidae		X		X			47, 98
Discoglossidae		X					82
Heleophrynidae						X	82
Hylidae		X		X			82
Hyperoliidae						X	82
Leptodactylidae		X	X	X			22, 47, 94

APPENDIX *Continued.*

| | ♂ Parental care | | ♀ Parental care | | No parental care | | |
	Internal fertilization	External fertilization	Internal fertilization	External fertilization	Internal fertilization	External fertilization	References
Liopelmatidae		X					8, 47
Microhylidae		X		X			47
Myobatrachidae		X		X			18, 105
Pelobatidae						X	82
Pelodryadidae						X	82
Pipidae				X			82
Pseudidae						X	82
Ranidae		X		X			37, 71, 97
Rhacophoridae				X			71
Rhinodermatidae		X					47
Rhinophrynidae						X	82
Sooglossidae		X					82
Teleosts							
(i) Elopiformes							
Elopidae						X	12
Megalopidae						X	12
Albulidae						X	12
(ii) Anguilliformes							
Anguillidae						X	12, 83
Moringuidae						X	12
Muraenidae						X	12
Nettastomatidae						X	12
Nessorhamphidae						X	12
Congridae						X	12
Ophichthidae						X	12
Synaphobranchidae						X	12
Serrivomeridae						X	12
Saccopharyngidae						X	12
Eurypharyngidae						X	12
(iii) Notacanthiformes							
Halosauridae						X	12
Notacanthidae						X	12
(iv) Clupeiformes							
Clupeidae						X	12, 58
Engraulidae						X	12
Chirocentridae						X	12
(v) Osteoglossiformes							
Osteoglossidae	X		X				4, 12
Pantodontidae				X			48
Hiodontidae						X	12
Notopteridae	X						12, 102
(vi) Mormyriformes							
Gymnarchidae	X						4
(vii) Salmoniformes							
Salmonidae				X			12, 83
Plecoglossidae						X	12, 64
Osmeridae						X	12, 83
Argentinidae						X	12
Salangidae						X	102
Retropinnidae						X	45
Galaxiidae	X						53

APPENDIX *Continued*.

| | ♂ Parental care | | ♀ Parental care | | No parental care | | |
	Internal fertil-ization	External fertil-ization	Internal fertil-ization	External fertil-ization	Internal fertil-ization	External fertil-ization	References
Esocidae						X	12, 83
Umbridae				X			12, 103
Gonostomatidae						X	12, 70
Sternoptychidae						X	12
Melanostomiatidae						X	12
Stomiatidae						X	12
Idiacanthidae						X	12
Synodontidae						X	102
Chlorophthalmidae						X	12
Alepisauridae						X	12
Myctophidae							
(viii) Cetomimiformes							
Giganturidae						X	12
(ix) Gonorynchiformes							
Gonorynchidae						X	12
Chanidae						X	12
Kneriidae						X	12
Phractolaemidae						X	12
(x) Cypriniformes							
Characidae	X	X					12, 60, 87
Erythrinidae	X						12
Hepsetidae	X			X			40
Lebiasinidae	X						4, 43, 62
Anostomidae	X						4
Hemiodontidae						X	102
Citharinidae						X	102
Cyprinidae	X						4, 83, 101
Catostomidae						X	58, 83
Cobitidae						X	12, 35
(xi) Siluriformes							
Ictaluridae	X			X			12, 83
Bagridae	X						34, 102
Cranoglanididae	X						4
Siluridae	X						12, 63, 101
Schilbeidae						X	12
Clariidae	X						4, 12
Heteropneustidae						X	10, 90
Ariidae	X						12, 21, 46
Doradidae	X			X			12
Auchenipteridae					X		36
Aspredinidae				X			12, 34
Plotosidae	X			X			12, 45
Callichthyidae	X						12, 35
Loricariidae	X						12, 35, 87
(xii) Percopsiformes							
Amblyopsidae				X			4, 12
Aphredoderidae	X			X			12
Percopsidae						X	12
(xiii) Batrachoidiformes							
Batrachoididae	X						4, 12, 56
(xiv) Gobiesociformes							
Gobiesocidae	X			X			53, 91

APPENDIX *Continued*.

| | ♂ Parental care | | ♀ Parental care | | No parental care | | |
	Internal fertil-ization	External fertil-ization	Internal fertil-ization	External fertil-ization	Internal fertil-ization	External fertil-ization	References
(xv) Lophiiformes							
Lophiidae						X	12
Antennariidae		X					69
Ceratiidae						X	12, 68
Caulophrynidae						X	12
(xvi) Gadiformes							
Muraenolepididae						X	12
Gadidae						X	12, 83
Merlucciidae						X	102
Ophidiidae			X			X	12, 91, 107, 108
Carapidae						X	12
Zoarcidae			X	X			12, 101
Macrouridae						X	12
(xvii) Atheriniformes							
Exocoetidae			X			X	12, 61, 85
Belonidae						X	12
Scomberesocidae						X	12
Oryziatidae				X			12, 23
Adrianichthyidae			X				12
Horaichthyidae					X		4, 12
Cyprinodontidae		X					23, 38, 83, 86
Goodeidae			X				24, 34, 35, 87
Anablepidae			X				12, 34
Jenynsiidae			X				12, 34
Poeciliidae			X				17, 66, 79
Atherinidae					X		58
Neostethidae					X		4, 12
Phallostethidae					X		12, 74
(xviii) Beryciformes							
Holocentridae						X	12
(xix) Zeiformes							
Zeidae						X	12
(xx) Lampridiformes							
Lampridae						X	12
Trachipteridae						X	12
Regalecidae						X	12
(xxi) Gasterosteiformes							
Gasterosteidae	X						106
Aulorhynchidae	X						12
Fistulariidae						X	12
Solenostomidae				X			12, 34
Syngnathidae	X						9, 101
(xxii) Channiformes							
Channidae	X		X				4, 12
(xxiii) Synbranchiformes							
Alabetidae	X		X				12
Synbranchidae	X						12
Amphipnoidae	X						12
(xxiv) Scorpaeniformes							
Scorpaenidae			X			X	12, 61, 101

APPENDIX *Continued.*

	δ Parental care		♀ Parental care		No parental care		
	Internal fertilization	External fertilization	Internal fertilization	External fertilization	Internal fertilization	External fertilization	References
Triglidae						X	12
Hexagrammidae		X					12, 20
Anoplopomatidae						X	12, 41
Cottidae	X	X					11, 57, 100
Comephoridae			X				4, 12, 61
Cyclopteridae		X					12, 55, 101
(xxv) Perciformes							
Centropomidae						X	12, 45
Serranidae		X					12, 30
Pseudochromidae		X					51
Plesiopidae		X					12
Theraponidae		X					12
Kuhliidae						X	45
Centrarchidae		X					14, 31
Apogonidae	X	X		X			12, 27, 28
Percidae		X					4, 58, 104
Sillaginidae						X	44
Echeneidae						X	12
Carangidae						X	12, 99
Lutjanidae						X	12
Pentapodidae						X	89
Sparidae		X					12, 101
Sciaenidae						X	29
Ephippidae						X	15
Chaetodontidae						X	73
Nandidae		X					5, 6, 35, 61
Embiotocidae			X				12, 34
Cichlidae		X		X			7, 26, 35, 92
Pomacentridae		X		X			1, 2, 59, 75, 80
Gadopsidae		X					39
Mugilidae						X	12
Sphyraenidae						X	12
Polynemidae						X	12
Labridae		X					49, 76, 84, 96
Scaridae						X	16, 77
Opisthognathidae		X					12
Nototheniidae			*				19
Blenniidae		X					12, 67, 101
Anarhichadidae			X				12, 32
Tripterygiidae		X					54
Clinidae		X	X				12
Chaenopsidae		X					91
Stichaeidae		X		X			32, 49, 52, 109
Pholidae		X		X			12, 52, 72, 109
Ammodytidae						X	49
Callionymidae						X	12
Gobiidae		X		X			3, 13, 45, 54, 101
Kurtidae		X					12
Acanthuridae						X	7, 78
Scombridae						X	12, 88
Istiophoridae						X	12
Stromateidae						X	12
Anabantidae		X					12, 35, 50
Belontiidae		X		X			35, 42
Helostomatidae						X	35

APPENDIX *Continued.*

	δ Parental care		♀ Parental care		No parental care		
	Internal fertilization	External fertilization	Internal fertilization	External fertilization	Internal fertilization	External fertilization	References
Osphronemidae	X		X				4
Mastacembelidae						X	12
(xxvi) Pleuronectiformes							
Scophthalmidae						X	49
Bothidae						X	12, 101
Pleuronectidae						X	12, 101
Soleidae						X	12, 101
Cynoglossidae						X	12
(xxvii) Tetraodontiformes							
Balistidae				X			91
Ostraciontidae						X	12
Tetraodontidae	X						12, 102
Diodontidae						X	12, 81
Molidae						X	12

* = Female parental care known; mode of fertilization unknown.