

Parental care sex differences in the brown bullhead, *Ictalurus nebulosus* (Pisces, Ictaluridae)

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Received May 15, 1985 / Accepted February 7, 1986

Summary. Males were the principal care-givers in the brown bullhead, *Ictalurus nebulosus*. Direct observations on individually tagged adults in nature revealed that males attended broods at closer distances than females and were the most frequent lone care-givers. However, females often participated in parental care and in some cases assumed the typical male role in the absence of the male. In the presence of her mate, females generally performed different care-giving functions than males. Females attended broods at a distance and chased other fishes more frequently than males. Males remained directly over the brood guarding. A series of mated pairs in each of three reproductive conditions were captured and examined. Different pairs were compared between reproductive conditions for body weight, body condition, gonadal-somatic index, and a gut-contents index. The initial costs of reproduction, as measured by weight loss, condition change, and gonadal-somatic index change, were more severe in females than males. During breeding and subsequent care-giving, males did little or no feeding whereas females increased their feeding during the same time period. However, males appeared to sustain only minor weight and condition losses due to care-giving. I suggest that males were the principal care-givers because the net benefits of remaining at the nest were greater than the net benefits of leaving. Males had little opportunity to mate with more than one female each season, and offspring had little chance of survival in the absence of a care-giving adult. Considerable variation in female behavior occurred which suggests that the net benefits of care-giving were nearly balanced with the net benefits of leaving the brood. The relative importance of feeding ver-

sus care-giving by females may vary with slight differences between females and the behavior of their mates as care-givers.

Introduction

Sex differences in ecology and behavior are a natural consequence of the gamete dimorphism that defines the sexes (Parker et al. 1972; Williams 1975). Among terrestrial vertebrates, (mammals, birds, and reptiles) differences between the sexes are particularly apparent in parental care. In mammals, parental care is principally a female activity and males contribute little to the next generation other than the gametes that form zygotes. The cases in which mammalian males actively perform care-giving activities are rare and usually secondary to the contribution made by the female (Kleiman 1977; Wittenberger and Tilson 1980). Monogamy and biparental care are common in birds. However, male contributions to offspring are again secondary to the care-giving exhibited by females (Lack 1968; but see Jenni 1974 for rare exceptions). This general pattern of either no male participation or a secondary role in care-giving also characterizes the reptiles (Tinkle and Gibbons 1977) and most non-anuran amphibians (Nussbaum 1985). These patterns contrast with anurans (Wells 1977, 1981) and fishes, particularly bony fishes, in which parental care by males alone is more common than female care-giving (Blumer 1979; Perrone and Zaret 1979; Ridley 1978). Care-giving by both sexes (biparental care) occurs in relatively few families of fishes (Blumer 1982a), but has been studied intensively in the Cichlidae (Baerends and Baerends-van Roon 1950; Fryer and Iles 1972; Keenleyside 1978). In the biparental

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cichlids, the female is the principal care-giver as in biparental birds and mammals (Itzkowitz and Nyby 1982; Keenleyside and Bietz 1981; Ward and Samarakoon 1981). Biparental care as it occurs in the cichlids does not, however, characterize the parental care sex differences that occur in other fishes in which both sexes participate in care-giving.

The brown bullhead, *Ictalurus nebulosus*, is a North American catfish in which there is considerable variation between the sexes in care-giving behavior (Blumer 1985a). Frequently, the male alone is the sole care-giver, as is common in fishes. However, biparental care also occurs in this species. In this paper, I detail the sex differences in care-giving behavior I observed during a 5-year field study. The causes of sex differences and variation in parental care are considered by evaluating the costs and benefits of alternative activities for each parent. This type of analysis is necessary for understanding the evolution and maintenance of behavioral sex differences (Maynard Smith 1977).

Methods

This study was conducted on a natural population of brown bullheads at Munro Lake, Cheboygan County, Michigan (N 45° 37', W 48° 41'). Details on the physical conditions in Munro Lake can be found in Blumer (1982b). Individuals were captured, sexed (Moen 1959), weighted, measured (standard length) and tagged for distant individual identification (Blumer 1984). Wet weight and standard length were used to calculate a condition variable (K) (Bagenal and Tesch 1978), the product of total body weight and 100 (a scaling factor) divided by the cube of standard length.

Fourteen pairs were dissected for examination of gut contents and gonadal tissues. Six pairs were captured in the morning (9:00–12:00) and eight pairs were captured in the afternoon hours (13:00–18:00). Gut-contents weight was adjusted for total body weight by calculating a gut-contents index: the quotient of dry gut-contents weight and total body weight. A gonadal-somatic index, the proportion of body weight represented by gonadal tissue, was calculated using the wet weight of gonads and total body weight. Different pairs were captured and examined at each of three periods during reproduction: before oviposition (gravid), immediately after oviposition (post-gravid), and later, approximately 12 days after oviposition, during parental care (late post-gravid). Ideally, pairs of nonbreeding adults captured at the same times of year as these breeding adults would serve as controls. However, I was not confident that adults captured away from breeding sites were nonbreeding individuals. I assume that nonbreeding adults would either show no change in weight and feeding, or would show increases in these variables during the normal reproductive period. Attempts to breed adults in enclosures at Munro Lake, in which nonbreeders could be compared to breeders, were of limited success.

Behavioral observations were made on adults with 89 different broods under natural conditions. In addition to frequent checks on each brood (daily in most cases), I observed 28 broods for a total of 102 h. These observations involved a continuous record of the activities of parents and offspring during

repeated one-hour periods (mean = 4 times/brood, range = 1–11 observation periods). Methods of observation are detailed in Blumer (1985a).

Statistical analyses were nonparametric (Conover 1971) and means are given with one standard error. Categorical data were analyzed with chi-square tests. Mann-Whitney U tests were used for two-sample comparisons and pairwise analyses were made with median (sign rank) tests. Multiple sample comparisons were made with Kruskal-Wallis tests.

Results

Sex differences in parental care

Among 89 broods, 50 (56.2%) were attended by both sexes. Four broods (4.5%) were attended by a female alone, and a male was the only care-giver of 35 broods (39.3%) (Blumer 1985a). The brood-attendance categories male alone and female alone were cases in which the mate of the care-giver was never observed. Broods attended by a male alone occurred significantly more often than broods attended by a female alone ($\chi^2 = 24.64$, $P < 0.001$). Males spent a greater proportion of time attending the brood (adult present at 5 m or less) than females (median test, $P = 0.0174$, $n = 18$ biparental pairs, Table 1). The care-giving behavior of lone males was similar to that of biparental males. Both biparental and lone males spent the majority of their time within 50 cm of their brood (Table 2). Biparental males spent a smaller proportion of time attending the brood than did lone males (adult at distance ≤ 5 m), but this difference was not statistically significant (Mann-Whitney U, $P = 0.0985$, 18 biparental males attended $65.2 \pm 9.0\%$ of the time and 9 lone males attended $89.6 \pm 6.4\%$ of the time).

Males spent a greater proportion of time than

Table 1. Mean proportion of time spent by each sex at given distances from their brood. Data are for 18 biparental pairs of brown bullheads observed for 78 h. Observations on different pairs were made in each of four years. Distance categories are: zero: adult directly over the brood; close: adult 50 cm or less from brood including zero; middle: adult 60 cm to 1 m from brood; far: adult more than 1 m but less than 5 m from brood; away: adult more than 5 m away from brood. Significance levels are one-tailed

Distance from Brood	Proportion of time (mean \pm SE)		Significance Median test
	Males	Females	
Zero	59.3 \pm 8.6%	14.5 \pm 6.2%	0.0038
Close	63.0 \pm 9.0%	24.5 \pm 7.0%	0.0069
Middle	0.7 \pm 0.4%	4.4 \pm 2.0%	0.0019
Far	1.4 \pm 0.7%	7.7 \pm 2.4%	0.0023
Away	34.8 \pm 9.0%	63.4 \pm 8.4%	0.0174

Table 2. Mean proportion of time spent by males at given distances from their brood. Data are for 18 biparental and 9 lone male brown bullheads observed for 102 h. The biparental males are the same as in Table 1. Observations on different lone males were made in each of four years. Distance categories are the same as in Table 1. Significance levels are one-tailed

Distance from Brood	Proportion of time (mean \pm SE)		Significance Mann-Whitney <i>U</i>
	Biparental	Lone	
Zero	59.3 \pm 8.6%	72.9 \pm 11.2%	0.1093
Close	63.0 \pm 9.0%	86.3 \pm 7.4%	0.0618
Middle	0.7 \pm 0.4%	2.6 \pm 1.3%	0.1292
Far	1.4 \pm 0.7%	0.7 \pm 0.5%	0.1190
Away	34.8 \pm 9.0%	10.4 \pm 6.4%	0.0985

females directly over the brood and at 0–50 cm from the brood (Table 1). Consequently, males did most of the fanning and oral manipulation of offspring (Blumer 1985a). Females spent a greater proportion of time at distances greater than 1 m from the brood (Table 1) and moved to distances greater than 5 m more frequently than did males (median test, $P=0.0064$, $n=18$ biparental pairs). The directions of these sex differences were consistent in each of the four years that detailed observations were made. Sex differences were also in the same direction at each stage during offspring development (Table 3). However, females chased intruding fishes, potential brood predators (Blumer 1986), more frequently than did males ($\chi^2=29.5$, $P<0.0001$, Table 4). In contrast to these sex role patterns, I observed females assume the typical male care-giving role in nine cases in which the male was continuously absent or spent little time with the brood. If a female was present, even the temporary absence of her mate resulted in her taking the typical male guarding position directly over the brood ($n=50$ biparental broods). Qualitative changes in male attendance in the absence of the female did not occur.

Among 25 of the broods at which both sexes were observed, the adults attending 15 broods remained together until the brood was lost or the termination of parental care. Among the other 10 broods, the male was the first to leave in six cases and the female was the first to leave in four cases. Males left these broods at early stages in development and females left at late stages, but this may not be a general pattern, because sample sizes are small. Furthermore, these data do not include the majority of cases in which one parent left the other during parental care. Most brood desertions occurred shortly after oviposition, at the embryonic

Table 3. Mean proportion of time spent by each sex at given distances from their brood at each of three stages in their offspring's development. Data are for 18 biparental pairs of brown bullheads observed for 78 h. Observations on different pairs were made in each of four years. Distance categories are the same as in Table 1. Significance levels are one-tailed

Distance from Brood	Proportion of time (mean \pm SE)		Significance Median test
	Males	Females	
At the embryonic stage of development $n=9$			
Zero	52.5 \pm 11.3%	43.7 \pm 10.9%	0.0618
Close	53.7 \pm 11.1%	23.1 \pm 12.0%	0.0968
Middle	0.0 \pm 0.0%	4.2 \pm 2.4%	0.0217
Far	0.5 \pm 0.3%	4.6 \pm 2.6%	0.0139
Away	45.8 \pm 11.1%	68.1 \pm 13.7%	0.2033
At the larval stage of development $n=8$			
Zero	61.2 \pm 17.9%	31.7 \pm 15.7%	0.0495
Close	61.3 \pm 17.9%	37.7 \pm 14.6%	0.2005
Middle	0.2 \pm 0.2%	2.8 \pm 1.4%	0.0217
Far	0.2 \pm 0.2%	11.6 \pm 6.3%	0.0139
Away	38.4 \pm 18.1%	47.9 \pm 12.8%	0.4721
At the juvenile stage of development $n=8$			
Zero	61.6 \pm 14.3%	14.8 \pm 7.6%	0.0344
Close	68.9 \pm 15.1%	26.3 \pm 8.9%	0.0344
Middle	1.7 \pm 1.0%	6.2 \pm 4.3%	0.0694
Far	2.7 \pm 1.4%	9.5 \pm 4.4%	0.0885
Away	26.7 \pm 14.8%	58.0 \pm 12.9%	0.0344

Table 4. Frequency of intruder chasing by care-giving adult brown bullheads and expected frequencies (in parentheses) for the null hypothesis of no interaction between sex of care-giver and intruder chasing. Data are from 102 h observations on 18 biparental and 9 male alone broods. Intruders were any fishes that approached to within 1 m of a brood (50 cm for minnows, *Notropus* and *Pimephales* spp., and juvenile yellow perch, *Perca flavescens*)

Chase given	Sex of care-giver		Total
	Male	Female	
Yes	10 (24.8)	27 (12.2)	37
No	148 (133.2)	51 (65.8)	199
Total	158	78	236

$$\chi^2=29.5 P<0.0001$$

stage of development. Among the 39 cases of single parent care-giving, 28 were first observed when the parent was attending an egg mass (four cases in which the male left first, 24 cases in which the female left first). I observed no significant chronological changes in male or female behavior corresponding to the stages of offspring development (Kruskal-Wallis tests, $P>0.10$ for all variables for each sex, Table 3).

The variations I observed in care-giving were unrelated to most potentially important physical or biotic factors. Among broods attended by both sexes and broods attended by only one sex (male alone or female alone), there were no significant differences in water depth at the nest (Mann-Whitney U , $P=0.72$, $n_2=41$, $n_1=25$), distance from nest to shore (Mann-Whitney U , $P=0.74$, $n_2=43$, $n_1=28$), distance to nearest active bullhead nest (Mann-Whitney U , $P=1.0$, $n_2=29$, $n_1=24$), number of active sunfish, *Lepomis*, nests within 5 m of the bullhead nest (Mann-Whitney U , $P>0.10$, $n_2=7$, $n_1=10$), distance to the nearest active sunfish nest (Mann-Whitney U , $P>0.10$, $n_2=6$, $n_1=8$), brood size (egg mass weight) (Mann-Whitney U , $P>0.10$, $n_2=8$, $n_1=15$), or male condition (K) (Mann-Whitney U , $P=0.21$, $n_2=29$, $n_1=26$). However, the standard lengths of males that attended a brood with a female were significantly greater than the standard lengths of males that attended a brood alone (Mann-Whitney U , $P=0.007$ [two-tailed], biparental males $SL=22.3\pm 0.1$ cm, $n=46$, males alone $SL=21.8\pm 0.1$ cm, $n=33$). The standard lengths of females that attended a brood with a male were not significantly different from those of females that gave care alone (Mann-Whitney U , $P=0.73$, $n_2=46$, $n_1=4$). These biparental females could not be compared to the mates of lone males because a female was never observed at broods categorized as "male alone". However, biparental females were slightly longer than females from the general population (Mann-Whitney U , $P=0.036$ [one-tailed], adult females in the general population $SL=21.4\pm 0.1$ cm, $n=131$, biparental females $SL=21.7\pm 0.2$ cm, $n=46$).

Costs of reproduction and parental care

Both sexes sustained costs of reproduction as measured by weight loss and condition (K) changes. These observations are based on different pairs of adults captured at one of three periods during reproduction (three reproductive conditions), so measurements are independent both within and between reproductive conditions (see Methods). All the adults (males and females) captured post-oviposition were exhibiting parental care. The total body weights of males and females decrease during the breeding period (Kruskal-Wallis tests, males $P=0.0505$, females $P<0.0001$, $n=44$ pairs, Fig. 1). Similarly, condition (K) decreased in both sexes but this trend was significant only in females (Kruskal-Wallis tests, males $P=0.0707$, females $P<0.0001$, $n=44$ pairs, Fig. 2). However, the condition of males at the late post-gravid period was

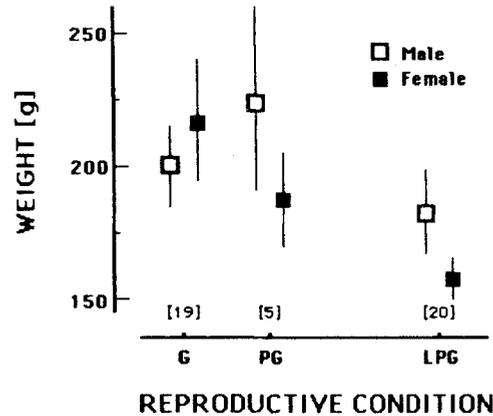


Fig. 1. Mean body weights (g) and 95% confidence intervals for adults at three reproductive conditions (G, gravid; PG, post-gravid; LPG, late post-gravid). Late post-gravid adults were captured approximately 12 days after oviposition. Sample sizes (pairs) are given in brackets

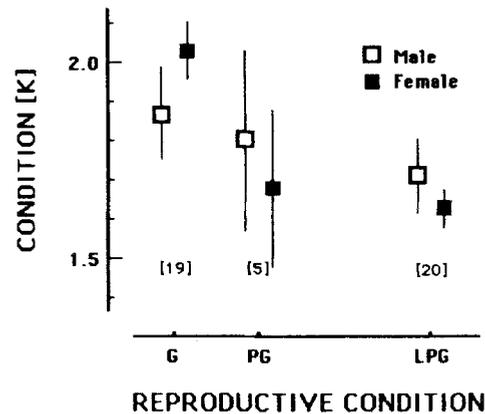


Fig. 2. Mean condition (K) and 95% confidence intervals for adults at three reproductive conditions (defined in Fig. 1). Condition (K) was calculated as the product of total body weight and 100 (a scaling factor) divided by the cube of standard length. Sample sizes (pairs) are given in brackets

significantly less than that of males prior to spawning (gravid) (Mann-Whitney U , $P=0.0316$, Fig. 2). Before oviposition there was no significant difference in the body weights of males and females (median test $P=0.32$, $n=19$ pairs), but the condition of females was significantly better than that of males (median test $P=0.01$, $n=19$ pairs). After oviposition, males were heavier and in better condition than females but these differences were not all significant (Fig. 1 and 2). Notably, changes in condition between sampling periods were significant (interpretation based on Conover 1971), only in females and only between the gravid and post-gravid periods (Mann-Whitney U , $P<0.001$, Fig. 2).

Costs of reproduction were more apparent in females than males because oviposition resulted in a considerable weight change in females. Females oviposited approximately 28 g of eggs based on wet weights of ovaries from four gravid and four immediately post-gravid females (eight different females). This represents approximately 11% of the total weight in gravid females. It should be noted that this could be an overestimate because the gravid females sampled were slightly longer than were the post-gravid females (gravid SL = 23.3 ± 0.6 cm, immediately post-gravid SL = 22.8 ± 0.4 cm). Female gonadal-somatic index decreased significantly during the entire reproductive period (Kruskal-Wallis test, $P=0.0043$) and was due to both oviposition and subsequent gonadal regression (Mann-Whitney U , $P<0.05$ in both intervals, Fig. 3). These changes in ovaries reflect parental investment by females and not, for example, weight changes due to water loss. The proportion of ovary content spawned was 85% based on weight and 93% based on dry weight (sample sizes noted above).

Similar short-term changes were not sustained by males. Dramatic changes in testes weights did not result from spawning activity (based on wet weights of testes from four pre-spawning and four immediately post-spawning males). Although there was a significant decrease in the gonadal-somatic index for males during the entire reproductive period (Kruskal-Wallis test, $P=0.0058$), the most obvious changes in testes were not due to spawning but occurred during care-giving (Mann-Whitney U , $P>0.10$, between pre-spawning [gravid] and immediately post-spawning [post-gravid], $P<0.005$ between immediately post-spawning and late post-spawning [late post-gravid], Fig. 3).

Before oviposition and immediately after oviposition, there were no statistically significant differences between the sexes in gut-content index (median tests; gravid, $P=0.06$, $n=4$ pairs; immediately post-gravid, $P=0.31$, $n=4$ pairs). However, at the late post-gravid period, the mean gut-content index of females was significantly greater than that of males (median test, $P=0.02$, $n=6$ pairs, Fig. 4). These data suggest that males fed less than did females during the late post-gravid period. As the care-giving period progressed, there was a statistically significant increasing trend in female gut-content index and a decreasing trend in male gut-content index (Kruskal-Wallis tests, males $P=0.032$, females $P=0.021$, Fig. 4). Furthermore, care-giving adults were observed mouth-ing the substrate (assumed feeding) near the nest site, and females exhibited this activity more fre-

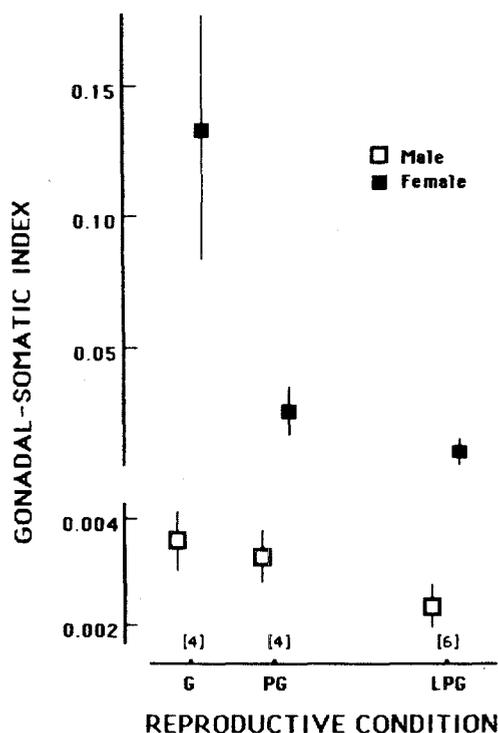


Fig. 3. Mean gonadal-somatic index and 95% confidence intervals for adults at three reproductive conditions (defined in Fig. 1). Sample sizes (pairs) are given in brackets

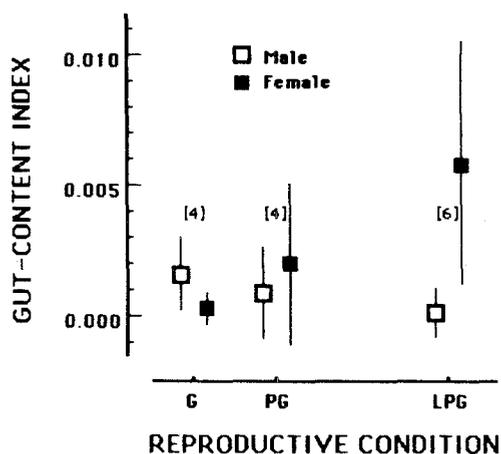


Fig. 4. Mean gut-content index and 95% confidence intervals for adults at three reproductive conditions (defined in Fig. 1). Sample sizes (pairs) are given in brackets

quently than did males (median test, $P=0.016$, $n=18$ biparental pairs).

Predation on care-giving adults was not observed although potentially predatory fishes and birds occurred at Munro Lake (fishes: northern pike, *Esox lucius*, largemouth bass, *Micropterus salmoides*; birds: osprey, *Pandion haliaetus*, great blue heron, *Ardea herodias*). Whether there were

sex differences in the risk of predation on care-giving adults could not be determined.

Discussion

Sex differences in parental care

In the brown bullhead, biparental males were slightly larger than males that gave care alone and biparental females were slightly larger than females in the general population. The biological significance of these body-size differences are unclear to me. However, large males appeared to breed earlier than smaller males, and large males were mated to large females in a nonrandom pattern (Blumer 1985a). Large females may be more likely than small females to participate in care-giving because their larger size enables them to sustain the costs of parental care more readily. This could be a function of stored fat reserves or size related differences in feeding efficiency (also see Barlow 1984). Larger females are also older females (Rubec and Qadri 1982), so experience could be a factor in the observed variation in female care-giving behavior.

Costs of reproduction and parental care

Measuring the costs of reproduction is problematic (Baylis 1981; Bell 1984). Weight changes, condition changes and gonadal weight changes are likely correlates of cost but not absolute measures. Nonetheless, these variables enabled me to compare the sexes at given times during reproduction. During the time interval that oviposition occurs, females incurred a greater cost of reproduction than did male brown bullheads (as suggested by body weight and condition changes). These initial costs of reproduction would appear to be a consequence of sex differences in gametic investment, but this need not be the case in other species if there were long complex courtships, extensive nest site preparation, or intense intrasexual competition for mates. I am also making the implicit assumption that sex differences in gonad weight changes accurately reflect total gametic costs of reproduction. In the brown bullhead, females spent a smaller proportion of time giving care than did males (Table 1), and during this time period females were feeding significantly more than males (Fig. 4). Relatively little feeding activity was observed near nest sites, so I suggest that females spent time away from their broods to feed.

In this species, recovery from reproduction (specifically oviposition) is likely to be the only

benefit of leaving the offspring that would balance or outweigh the potential costs. Furthermore, females that leave their brood immediately following oviposition and do not return are likely to sustain much greater costs of leaving than are females that participate in care-giving. Broods attended by both parents were more likely to survive to the termination of parental care than were broods attended by a male alone. This differential survival was not a consequence of obvious differences in the quality of care provided by one versus two adults (Blumer 1985b). Females deposit all their ripe eggs for one male each breeding season, and there is only one breeding season per year at Munro Lake (Blumer 1985a). The benefit of feeding immediately after oviposition must be in its effects on the future reproduction of females (survival and reproduction in subsequent years).

Evolutionary considerations

Trivers (1972) hypothesized a positive relationship between initial reproductive investments and parental care. My data do not support Trivers' hypothesis and demonstrate the absence of such a relationship, as suggested by Dawkins and Carlisle (1976). A female's investment in eggs could only be replaced at considerable cost, and in the brown bullhead, time constraints on breeding would probably delay clutch replacement until the next breeding season. Such time constraints on fecundity might often promote female participation in care-giving (Barlow 1984). Yet, it is the extreme investment of females in oviposition during a short period of time that makes the partial or complete termination of parental investment a likely event. This is contrary to the concept that large replacement costs predispose a parent to continue investing in offspring (Dawkins and Carlisle 1976). I suggest that in the brown bullhead the difference between the net benefits of care-giving and the net benefits of leaving the brood (to feed) may be near zero for most females. This net benefit difference should vary with different females (different sizes) and circumstances (reproductive histories) (see Results), and can account for the variation I observed in female brood care.

Male parental care is common in fishes, and in many families males are the only care-givers (Blumer 1982a). A major factor in the evolution of male parental care in fishes is male defense of an oviposition site at which multiple spawnings are obtained (Baylis 1981; Blumer 1979; Loiselle 1978; Ridley 1978). A male may remain at an oviposition site for the purpose of further reproduc-

tion and incidentally aid the offspring of his previous spawnings at that site (Alexander and Borgia 1979; Barlow 1964; Borgia 1979; Loiselles and Barlow 1978; Trivers 1972; Williams 1975). Attributing male parental behavior in the brown bullhead to this phenomenon may be incorrect because there is no evidence of multiple spawning by males in Munro Lake or elsewhere (Blumer 1985a). There is little information on this subject for other catfishes, but channel catfish (*Ictalurus punctatus*) males spawn with more than one female in a given breeding season (Nelson 1957). Even if brown bullhead males had an evolutionary history of multiple spawning, this alone might not account for the maintenance of male care-giving in the absence of positive selection.

Although costs of parental care to males do not appear dramatic, there are measurable decreases in male weight, condition and gonadal-somatic index which are not a consequence of gametic investment (Fig. 1, 2, and 3). The biological significance of these costs, the effect of parental care on male survival and future reproduction, was not determined. The fact that male reproductive costs are less than those sustained by females should have no direct effect on male behavior. Males could avoid the costs of parental care by leaving immediately after spawning. The fact that most males remain at the nest and give parental care suggests that the net benefits of leaving the nest are small compared to the net benefits of care-giving. This cost-benefit model parallels the discrete breeding seasons model of Maynard Smith (1977). In his model, the behavior of each sex depends on the number of offspring that survive when one or two parents are care-givers and the probability of a deserting adult finding a mate in the same breeding season. In the brown bullhead, the benefits of leaving are increased feeding and the potential of increased future reproduction. The costs are almost certain brood mortality and decreased current reproduction (Blumer 1986). The benefits of care-giving are increased brood survival, and the costs are weight loss and negative effects on survival and future reproduction. Predation was a major source of brood mortality, and parental care in brown bullheads has an anti-predation function (Blumer 1986, 1985b). Although males would be able to replace their current reproductive investment more readily than females if leaving a brood resulted in its failure, males would be unlikely to find another gravid female with whom to spawn in the current season (Blumer 1985a).

Males invest in their mate's offspring because the costs of care-giving are small and the potential

benefits of leaving the brood are also small. Here, I view the predisposition of males to remain with their broods as independent of female "decisions" to leave or give care (but see Blumer 1985b). Dawkins and Carlisle (1976) hypothesized that in fishes with external fertilization, males are predisposed to parental care because females oviposit and leave before the male can fertilize the eggs. I made no observations on oviposition and fertilization, so the sequence of events and degree of synchrony between the sexes is not known. Regardless of which sex spawns first, this hypothesis cannot account for paternal care when females remain at the nest site after oviposition as frequently occurs in this species (also see Loiselles 1978; Loiselles and Barlow 1978). The cost-benefit analysis described above is the same that would apply if males were put into a "cruel bind" by females that left the nest first (Trivers 1972; Dawkins and Carlisle 1976).

A female is likely to behave differently in the presence or absence of her mate at the nest. Unlike males, females can gain considerable benefits from both care-giving and leaving. The cost of brood predation before the termination of parental care is probably greater for females than males. Females make the majority of their investment early in the reproductive period (oviposition) whereas males invest in offspring more evenly throughout this time. Brood predation is most likely to occur before a male has fully invested in that brood, but after a female has made most of her investment. Thus, a female is truly in a "cruel bind" when her mate leaves the brood. Under these circumstances, a female may assume the typical male care-giving role as I observed in nine cases.

Acknowledgements. This work was supported by awards from the Museum of Zoology Hinsdale Scholarship, Rackham School of Graduate Studies, and the Division of Biological Sciences at the University of Michigan, the University of Michigan Biological Station, Sigma Xi, the Theodore Roosevelt Memorial Fund of the American Museum of Natural History, and the Raney Fund of the American Society of Ichthyologists and Herpetologists. I thank my field assistants, John Findley, Alan Rudolph, Craig and Noreen Flory, Todd Paddock, Fred Koelher, Tony Hainault, John Hutto, Mark Southern, and Chris Wood for their hard work and patience. I also thank the Michigan Department of Natural Resources for permission to tag fishes, the staff of the University of Michigan Biological Station, Mr. Herb Billings of F.W. Ritter Sons Co., Gilbert-Bennett Manufacturing Co., McArthur Bros., Mr. and Mrs. R.J. Gifford, and the residents of Munro Lake, Michigan. I am indebted to R.D. Alexander, G.W. Barlow, W.J. Dominey, J.F. Downhower, W.G. Holmes, B.M. Johnson, R.A. Nussbaum, G.R. Smith, R.A. Stein and students, and an anonymous referee for comments and criticisms. Special thanks to K.F. Keyes.

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