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ORIGINAL ARTICLE

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Paternity and condition affect cannibalistic behavior in nest-tending bluegill sunfish

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Abstract Theory of parental care evolution predicts that a parent should invest more in a brood when its fitness value is greater than alternative investments such as the parent's own survivorship or future broods. In fish, filial cannibalism (eating one's own offspring) is widespread and represents a challenge to parental care evolution. In this study, I investigated filial cannibalism in bluegill sunfish (*Lepomis macrochirus*). Bluegill are characterized by alternative mating tactics referred to as "parentals" and "cuckolders". Parentals delay maturation, construct nests, court females and provide sole parental care for the developing offspring. Cuckolders mature precociously and parasitize parentals using two tactics called "sneakers" and "satellites". I found that parentals that obtained fewer eggs during spawning appeared more likely to completely cannibalize their brood (total filial cannibalism: P=0.07), regardless of their condition. Among parentals that provided care, partial cannibalism was greater during the egg phase as compared to the fry phase of care, but it was unrelated to brood size. Throughout the care period, parentals in better condition were less likely to partially cannibalize their brood, indicating that parentals use cannibalism to replenish energy reserves. Independent of condition, parentals that were cuckolded more were more likely to eat part of their brood. This relationship was evident only after the eggs had hatched, which is consistent with data showing that parentals can use olfactory cues produced by fry but not eggs to assess their paternity. This latter result proposes that parentals may be selectively culling cuckolder offspring from their nest. These data provide empirical support for parental care theory, and the first evidence for the importance of paternity on cannibalistic behavior.

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Introduction

Parental care theory predicts that the degree of genetic relatedness between parent and offspring should affect the amount of care provided (e.g., Trivers 1972; Whittingham et al. 1992; Sargent and Gross 1993; Westneat and Sherman 1993; Kokko 1999). When relatedness to a brood is decreased by cuckoldry or intraspecific parasitism, the evolutionary value of investing in those young is decreased. Cuckolded or parasitized parents should reduce effort toward the current brood in favor of alternative investments (e.g., their own survivorship and future broods) whenever the alternatives are expected to provide greater reproductive success. This is known as "Williams's principle" (Sargent and Gross 1993).

Considerable support for the theory has come from correlational studies of paternity and parental investment (e.g., Burke et al. 1989; Dixon et al. 1994; Neff and Gross 2001). However, there is controversy about how to interpret these studies because they may be confounded by phenotypic or life history correlates (Lessells 1991; Kempenaers and Sheldon 1997). Experimental manipulations of paternity have been advocated and conducted (e.g., Møller 1988; Davies et al. 1992; Sheldon and Ellegren 1998; Hunt and Simmons 2002), and when the manipulation effectively alters a male's perceived paternity these studies have supported the theory (see Neff and Sherman 2002).

In some mating systems, parental care also involves cannibalism, whereby a parent will consume some (partial filial cannibalism) or all (total filial cannibalism) of the young within its nest (reviewed by Fitzgerald 1992; Manica 2002a). This extreme behavior appears to challenge parental care theory. However, cannibalism could be adaptive when the consumed young are unrelated to the parent, sickly and not likely to survive, or required by the parent to replenish energy reserves which are needed

to provide care to the remaining offspring (Rowher 1978; Sargent 1992; Sargent et al. 1995). Furthermore, it has recently been shown in the beaugregory damselfish (*Stegastes leucostictus*) that partial cannibalism may be used by care-providing males when oxygen is in low concentration to reduce the overall requirements of the brood and thereby ensure hatching of the uneaten eggs (Payne et al. 2002). Thus, in some cases, cannibalistic behavior can be adaptive and total filial cannibalism can be viewed as investment by the parent into future offspring, while partial filial cannibalism can be viewed as investment into future offspring as well as investment into current offspring (those that are not cannibalized). In the case of partial filial cannibalism, parental care theory predicts that the number of offspring cannibalized should decrease as the genetic relatedness to a brood increases, as the independence of the young increases (i.e., the probability that they will survive to maturity), or as the parent's own condition increases. In systems where parental care is non-sharable, for example in fish species that actively oxygenate eggs, offspring number is expected to have less of an effect on parental care decisions such as cannibalism (Williams 1975). Particularly, larger broods will be affected the least by offspring number because of the increasing marginal cost of an additional offspring, leading to diminishing returns to offspring number (see Manica 2002a).

In this paper, I examine the cannibalistic behavior of nest-tending bluegill sunfish (*Lepomis macrochirus*). Bluegill provide an ideal system to test some predictions of filial cannibalism theory because they display both total and partial filial cannibalism, parental care is costly, offspring number varies widely from brood to brood, there is cuckoldry, and it has been previously documented that individuals are capable of making adaptive parental investment decision. Bluegill males are characterized by alternative life histories termed "parental" and "cuckolder" (Gross and Charnov 1980; Gross 1982). In Lake Opinicon (southeastern Ontario: 44°16′N, 76°30′W), parentals mature at age 7 or 8 years and compete to construct nests in densely packed colonies during their breeding season (May–July). Nesting males court and spawn with females over the course of a single day, and then provide sole parental care for the developing eggs and fry in their nests (Gross 1982). By contrast, cuckolders mature precociously and steal fertilizations in the nests of parentals through two tactics: "sneakers" (age 2–3 years) dart into nests during female egg releases; and "satellites" (age 4–5 years) express female color and behavior and appear to deceive parentals into identifying them as a second female in the nest (Gross 1982; Neff and Gross 2001).

The care period lasts about 7 days and has two distinct phases. The egg phase involves parentals fanning and defending the eggs until they hatch (about 3 days). During this phase parentals expend about 75% of their total investment into parental care as measured by changes in body weight (Coleman and Fischer 1991). Because oxygen requirements by the eggs increases with number, a large portion of the care is non-sharable. After hatching, the parentals stop fanning, but the developing fry are defended from predators until they leave the nest. Parentals do not forage during the parental care period and may expend up to 15% of their body weight (see also Colgan and Gross 1977; Gross 1982). Males often abandon their broods during the care period and they sometimes cannibalize the brood prior to leaving (total filial cannibalism), presumably because the young have energetic value to the male and they are unlikely to survive on their own (Sargent and Gross 1993). Other males cannibalize some of the brood during the care period (partial filial cannibalism), but continue to defend and care for the other young in the nest. After the fry have dispersed from the nest, parentals return to deeper waters to feed and replenish their energy reserves before re-nesting in subsequent spawning bouts. Parentals in better condition are able to re-nest sooner (Cargnelli and Gross 1996, 1997).

It has previously been shown that parentals make dynamic adjustments in their parental behavior during the care period in response to information on paternity. Neff and Gross (2001) examined the response of nest-tending parentals to a brood predator during both the egg and fry phases of parental care. They found that during the egg phase, a parental uses the conspicuous intrusions of sneakers as an indirect cue of their paternity when making investment decisions. During this phase they do not seem to use cuckoldry by satellites in their assessment of paternity. Thus, only males that were heavily cuckolded by sneakers were less likely to defend their brood from the predator. However, once the eggs hatch parentals can use olfactory cues to assess their actual paternity (Neff and Sherman 2003), and males adjust their level of care according to cuckoldry by both sneakers and satellites. It is not yet known whether parentals also adjust their cannibalistic behavior in response to their perceived paternity or their own energy reserves (condition).

Methods

The colony

In June 1996, a bluegill colony was carefully selected to represent several characteristics of the many that have been studied in Lake Opinicon. For example, the colony was of average size and depth, and had egg scores, vegetation and substrate characteristic of areas occupied by other colonies (see Gross 1982, 1991; Phillip and Gross 1994). Once spawning began, a large enclosure was constructed by placing a 100-m net (ca. 6×6 mm mesh size) across the mouth of the bay containing the colony. The enclosure prevented dispersal of breeding individuals. The colony occupied less than 15% of the enclosure and the net did not appear to interfere with the breeding dynamics of the colony. Furthermore, the enclosure contained numerous natural brood predators including non-nesting bluegill and pumpkinseed sunfish (*Lepomis gibbosus*).

The day after spawning, brood size was ranked by a single observer using qualitative egg scores ranging from 1 to 5. Claussen (1991) has shown that these egg scores correlate with the actual number of eggs in a nest [r_s=0.96, P<0.001, n=32; 1 (range: 27–

4,889 eggs), 2 (4,666–28,806), 3 (27,072–53,221), 4 (49,369–86,552), 5 (82,063–112,810)], and this method has been used in other studies (e.g., Cargnelli and Gross 1996). At the end of the parental care period, dip and seine nets were used to collect all mature individuals within the enclosure, including the parentals and cuckolders, and fry were collected from each nest using SCUBA. Sneakers were differentiated from satellites based on body size and coloration (see Gross 1982). A random sample of the fry (~100) from each nest were preserved in 70% ethanol for later microsatellite DNA analysis.

Cannibalistic behavior and parental condition

Each nest-tending parental was observed during both the egg phase and fry phase of parental care. Cannibalistic behavior was quantified by counting the number of "pecking" motions a male performed. A peck involved a male angling downward toward his nest, followed by forward movement towards the base of the nest, where the eggs or fry reside. The male's mouth could typically be observed contacting the base of the nest. The male then returned to a horizontal position hovering approximately 20 cm above the nest. A pecking behavior was usually accompanied by movement of the male's mouth and gills. Analysis of stomach content of ten other nesting parentals showed that the number of pecks was correlated with the number of fry found in the stomach (Neff, unpublished data: r_s=0.73, P=0.015, n=10).

The number of pecks a male performed was quantified based on a total of four 15-min observations (60 min total per nest). Observations were taken in the morning (0800–2400 hours EST) of the second, third, fifth and sixth days post spawning. The eggs hatched after the third day post spawning. Thus, the first two observation days occurred during the egg phase of care and the last two occurred during the fry phase of care. Up to four nests were observed simultaneously by a swimmer in snorkel gear, and the order that nests were observed was altered daily. For each nest, the two observations taken during the egg phase were summed as were those taken during the fry phase.

Fulton's condition factor was calculated for each parental at the end of the care period according to: wet weight (g) / cube of total length (mm^3). Fulton's condition factor (hereafter referred to as 'condition') correlates with mobile lipids in bluegill and is commonly used in the fisheries as a measure of energetic state (Sutton et al. 2000).

Paternity

Using microsatellite multiplexing methods described in Neff et al. (2000a), genotypes at up to 11 loci (previously described in: Colbourne et al. 1996; Neff et al. 1999) were obtained for each breeding adult (mature males and females) and a random sample of fry from each nest (range: 31–46 fry). A total of 19,547 genotypes were generated from 1,777 individuals. Within the colony, the paternity of each male in each brood was calculated using the Two-Sex Paternity model developed by Neff et al. (2000b, 2000c). This model was selected because it allows for incomplete sampling of the candidate parents and young. Furthermore, when the exclusion probability is 1.0 (i.e., each parent is genetically distinct), the model simplifies to straight exclusion techniques.

Specifically, the model was used to calculate the paternity of each nest-tending parental to its brood (see Neff 2001). The paternity of each cuckolder was then calculated in each nest using the same model with the following modification. To account for the dominant genetic contribution of the nest-tending parental (typically about 80% of the young), the prior probability distribution of paternity was restricted for each cuckolder to only paternities between zero and the residual paternity — i.e., the paternity not assigned to the nest-tending parental (see Appendix 1 in Neff et al. 2000c). Overall, because of the high combined resolving power of the loci, the parentage analysis had high precision (see Neff 2001).

Statistics

Mann-Whitney U-test was used to determine if males that abandoned their brood during the care period had fewer eggs than those that stayed. Next, Spearman's non-parametric correlation and Wilcoxon's non-parametric test for two related samples were used to investigate the relationships between the number of pecks during the egg and fry phases. Spearman's correlation was also used to investigate the relationship between number of pecks (either egg phase or fry phase) and brood size (egg score), sneaker paternity, satellite paternity or parental condition. I then used partial correlation to control for parental condition while examining the effect of sneaker or satellite paternity on the number of pecks during the egg phase. For the number of pecks during the fry phase I examined the effect of the parental's overall paternity, controlling for his condition, and the effect of condition controlling for paternity.

All statistics were performed using SPSS (v.10). For parametric statistics, proportional data were first arcsine square-root transformed to control for mean-dependent variance (Zar 1999). For clarity, proportional data are displayed in their untransformed form. All means are reported plus or minus one standard error and all P-values are from two-tailed tests.

Results

The colony

At the time of spawning (12 June 1996) there were 100 parentals with nests. Forty parentals provided care until the day before swim-up (9 days post-spawning) at which time they were collected, 32 deserted shortly after spawning, 18 deserted either 1 or 2 days following spawning and the remaining 10 abandoned shortly after egg hatching. I was unable to obtain egg scores for the first 32 males that deserted because egg scores were taken the day after spawning. One non-deserter was a bluegill-

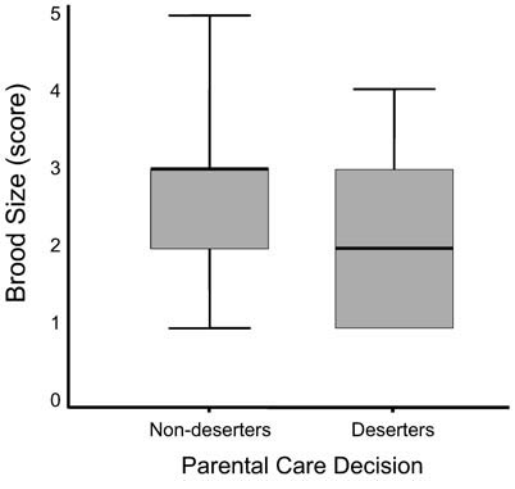

Fig. 1 Brood size and parental care decisions in bluegill sunfish (*Lepomis macrochirus*). Parentals that abandoned their brood had fewer eggs (as measured by scores) than parentals that provided care to fry maturity, although the difference was not significant (P=0.07). The *boxes* represent upper and lower quartile, the *heavy horizontal line* represents the median egg score, and the *whiskers* represent maximum and minimum values

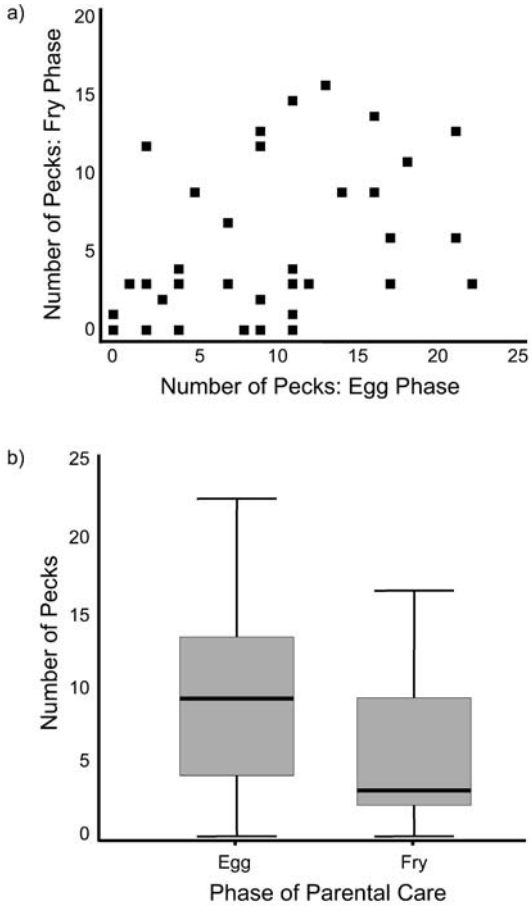

Fig. 2a, b Cannibalistic behavior during the egg and fry phases of parental care. **a** There was a positive correlation between the number of pecks during the egg and fry phases. **b** Parentals pecked at their brood significantly more times during the egg phase of care as compared to the fry phase. The *boxes* represent upper and lower quartile, the *heavy horizontal line* represents the median number of pecks, and the *whiskers* represent maximum and minimum values

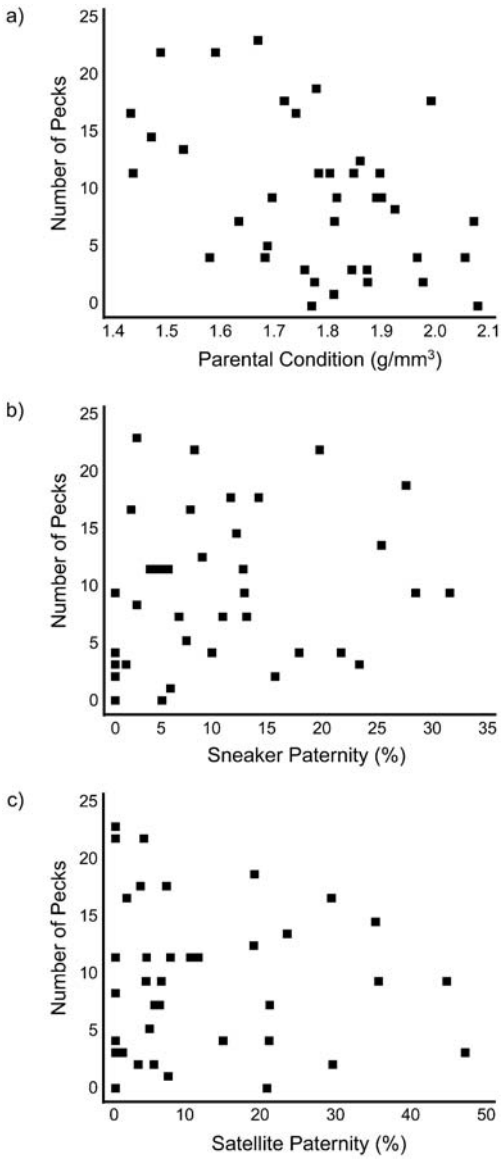

Fig. 3a–c Cannibalistic behavior during the egg phase of parental care. **a** There was a negative correlation between parental condition and the number of pecks at the brood. There was no relationship between the number of pecks and cuckoldry by **b** sneakers or **c** satellites

pumpkinseed hybrid (likely F1), which was excluded from the analyses. DNA of sufficient quality from one parental's nest could not be obtained. Thus, the sample of non-deserting parentals comprised 38 males. A total of 82 cuckolders were collected from within the enclosure, 58 of which (comprising 32 sneakers and 26 satellites) had paternity within the colony.

Paternity, condition and cannibalistic behavior

Details of the paternity analysis are presented in Neff and Gross (2001) and Neff (2001). Briefly, the genetic analyses revealed that parentals providing care through to fry maturity fertilized on average of 79% of the young in their nests (range: 26–100%, n=38). Sneakers fertilized 10% (range: 0–31%, n=32) and satellites fertilized 11% (range: 0–45%, n=26). We could not calculate paternity in the broods that were abandoned because all of the offspring were cannibalized (presumably by the nest-tending parental prior to leaving). However, behavioral observations of cuckolder intrusions during spawning showed that these parentals were cuckolded more heavily by sneakers as compared to parentals that did not abandon their brood (see Neff and Gross 2001). Parentals that remained on their nest throughout the care period obtained more eggs, although this difference was not significant (Mann-Whitney U=410, P=0.07, n=67; Fig. 1).

Overall parentals pecked an average of 14.3±1.5 times (range: 0–34) in the 60 min of observation per nest. They pecked an average 9.1±1.0 times (range: 0–22) during the egg phase of care and 5.3±0.8 times (range: 0–16) during the fry phase of care. Although the number of pecks in the two phases were positively correlated (r_s=0.46, P=0.003,

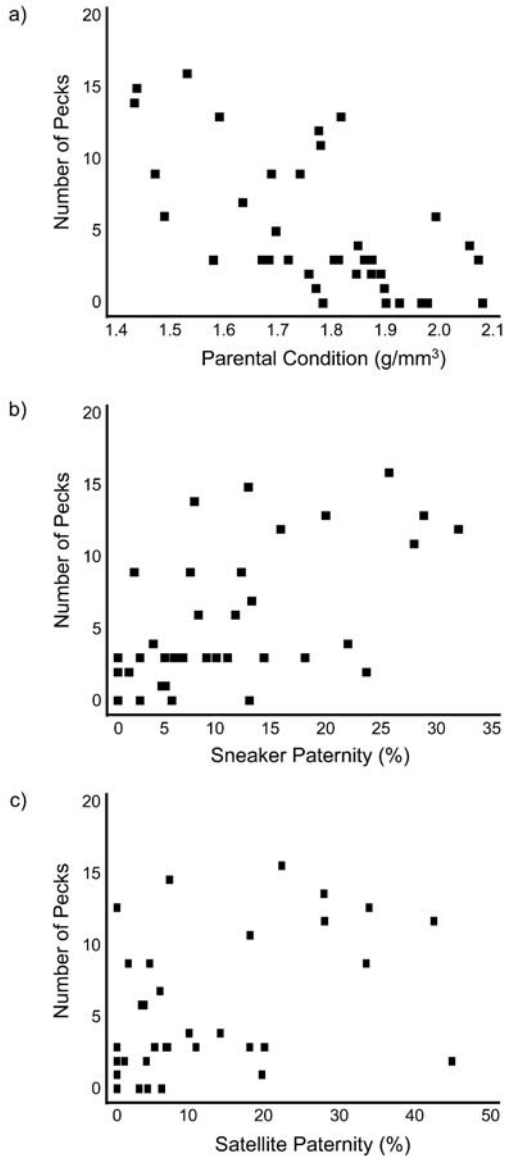

Fig. 4a–c Cannibalistic behavior during the fry phase of care. **a** There was a negative correlation between parental condition and the number of pecks at the brood. There was a positive correlation between the number of pecks and cuckoldry by **b** sneakers and **c** satellites

n=38; Fig. 2a), parentals pecked significantly less during the fry phase as compared to the egg phase of care (Wilcoxon Z=–3.27, P=0.001, n=38; Fig. 2b).

There was no relationship between brood size (egg score) and the number of pecks in either the egg or fry phase of care (egg: r_s=0.23, P=0.17, n=38; fry: r_s=0.12, P=0.48, n=38). There was also no relationship between parental condition and brood size (r_s=–0.17, P=0.30, n=38). During the egg phase, I found a negative relationship between the number of pecks and parental condition (r_s=–0.40, P=0.01, n=38; Fig. 3a). Neither sneaker paternity (r_s=0.29, P=0.08, n=38; Fig. 3b) nor satellite paternity (r_s=0.01, P=0.99, n=38; Fig. 3c) were significantly associated with the number of pecks. Partial correlation controlling for condition confirmed that there was no significant effect of either sneaker or satellite paternity (P>0.10 for both).

During the fry phase of care there was also a negative relationship between the number of pecks and parental condition (r_s=–0.62, P<0.001, n=38; Fig. 4a). Furthermore, there was a significant positive relationship between sneaker paternity and the number of pecks (r_s=0.61, P<0.001, n=38; Fig. 4b) as well as satellite paternity and the number of pecks (r_s=0.47, P=0.003, n=38; Fig. 4c). Partial correlation controlling for condition revealed a significant negative relationship between parental paternity and the number of pecks (r=-0.45, P=0.005, n=38). Similarly, partial correlation first controlling for paternity revealed a significant negative relationship between condition and the number of pecks (r=–0.54, P<0.001, n=38). Thus, both condition and paternity have independent effects on the pecking behavior of parentals.

Discussion

This study investigated the effect of paternity, condition and offspring number on the cannibalistic behavior of parental bluegill sunfish. The data confirm many predictions made by parental care theory, and provide the first evidence for the role of genetic relatedness on cannibalism during parental care.

First, I found that parentals that deserted their brood (many of whom cannibalize the young first: total filial cannibalism) appeared to have fewer eggs as compared to parentals that remained throughout the care period (P=0.07; Fig. 1). This is consistent with several other field studies on fish (e.g., Dominey and Blumer 1984; Lavery and Keenleyside 1990a; Lindström and Sargent 1997; Manica 2002b). It is possible, however, that the deserting parentals were also inferior males because, although they were of similar size, weight and condition to non-deserting parentals, they had significantly more parasites (Neff and Gross, unpublished data). Furthermore, behavioral observations showed that deserting parentals were cuckolded more than non-deserting parentals. Thus, parentals may cannibalize and desert their brood because there are fewer eggs, the parental requires the extra energy to compensate for heightened parasite load, or fewer of the young are actual offspring of the parental.

Second, I found that among the parentals that remained on their nest throughout the care period, there was no effect of brood size on the number of pecking behaviors performed by a male. Theory suggests that partial cannibalism should increase with brood size, at least until some asymptotic value is approached (see Manica 2002a). However, because smaller broods typically are completely cannibalized, it can be difficult to examine partial cannibalism in small broods where brood size is predicted to have its strongest affect. I found that

parentals that deserted their nests had fewer eggs. However, among the remaining parentals there was still significant variation in egg number. For example, there were broods of all different sizes (i.e., egg scores of 1–5). Most other studies on fish have similarly found no relationship between brood size and partial cannibalism (e.g., Sargent 1988; Lindström and Sargent 1997). Thus, currently empirical data seems largely inconsistent with the theory.

Third, I found that parentals were less likely to consume parts of their brood during the fry phase as compared to during the egg phase of care (Fig. 2). This relationship may reflect the decreased nutritional value of the fry as compared to the eggs (Gilbert 1985). It also may reflect the increased evolutionary value of the fry relative to the parental's expected future reproductive success (Sargent and Gross 1993). Coleman et al. (1985) manipulated past investment in nesting parental bluegill by experimentally reducing brood sizes either early or late in the care period. They showed that males that had made large past investment (late brood reduction) were more willing to invest in their brood as compared to males that had made only small past investment (early brood reduction), presumably because males with large past investment had consequently lower future reproductive success. Coleman et al. (1985) thereby provided empirical support for the resolution of the "Concorde Fallacy" (Sargent and Gross 1985; see also Jennions and Polakow 2001). Thus, the longer a parental remains on his nest caring for the brood (e.g., fanning the eggs to oxygenate them), the lower his future reproductive success will be. Furthermore, older young are more likely to survive to maturity and therefore the present value of the brood should increase with its age (Sargent and Gross 1993). Increased present value and reduced future value will both select for parentals to invest more in a brood during the fry phase as compared to the egg phase. This could account for the reduced cannibalism observed later in the care period (see also Lavery and Keenleyside 1990b).

Fourth, a parental's condition was also correlated with the amount of partial cannibalism he performed (Figs. 3a, 4a). Parentals in good condition were less likely to peck at their brood, especially during the fry phase of care. I could rule out several other potential confounding factors, including brood size because there was no relationship between parental condition and brood size, or between brood size and the number of pecks. I could also largely rule out cuckoldry because, although parentals in better condition experience less cuckoldry (Neff and Gross 2001; Neff 2001), partial correlation analysis revealed independent effects of both cuckoldry and condition. However, experimental manipulation of paternity and condition is required to definitely quantify the independent effects of each on cannibalistic behavior. Other correlative studies in fish provide similar support for the theory (e.g., Marconato et al. 1993). Furthermore, experimental studies of cortez damselfish (*Eupomacentrus rectifraenum*) (Hoelzer 1995) and common gobies (*Pomatoschistus microps*) (Kvarnemo et al. 1998) that fed some care-providing males showed that these males were less likely to cannibalize their broods as compared to non-supplemented, control males. However, no effect of food supplementation was found on cannibalize rate in the threespine sticklebacks (*Gasterosteus aculeatus*) (Belles-Isles and Fitzgerald 1991) or the fantail darter (*Etheostoma flabellare*) even though cannibalism did increase condition of the care-providing male (Lindström and Sargent 1997). Nevertheless, accumulating empirical data provide strong support for the importance of a parent's condition on the rate of partial cannibalism.

Finally, I found a significant effect of paternity on the cannibalistic behavior of parental bluegill. This relationship was independent of a parental's condition (and the number of offspring in his brood). Presumably parentals can assess their paternity using olfactory cues emitted by the offspring once they have hatched (Neff and Gross 2001; Neff and Sherman 2003). It has been suggested that this cue may reside in the urine that the fry excrete (e.g., Moore et al. 1994). Neff and Gross (2001) showed that during the egg phase of care, satellites go undetected by parentals. Thus, parentals can not determine their paternity as accurately during this phase of care. This may partly explain why there was no effect of paternity on the rate of pecking prior to the eggs hatching. To my knowledge, only one other study has investigated the relationship between paternity and partial cannibalism. Studying the common goby, Svensson et al. (1998) introduced smaller males (presumably sneaker males) into aquariums containing a mated pair during spawning. After spawning was complete they removed the sneaker male and compared the rate of cannibalism between the mated males and control males that spawned in the absence of a sneaker male. Results revealed no difference in the cannibalistic behavior of the males in either treatment. Thus, the current study on bluegill provides the first empirical support for the effect of paternity on partial cannibalism.

It will be interesting to determine if parental bluegill are actually cannibalizing cuckolded offspring and not their own. Given that parentals can distinguish their offspring from unrelated offspring (Neff and Sherman 2003), parentals may be able to selectively forage on the latter. Such behavior would seem adaptive and should be favored by natural selection. In the context of foraging, it has been shown that cannibals in certain salamanders and toads avoid associating with and eating their genetic relatives (Pfennig et al. 1993, 1994). However, in the context of parental care, DeWoody et al. (2001) found no evidence that nest-tending tessellated darter males selectively cannibalized unrelated young. The possibility remains to be investigated in bluegill.

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