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Dynamic adjustment of parental care in response to perceived paternity

Bryan D. Neff* **and Mart R. Gross**

Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, Ontario, Canada M5S 3G5

Theories of parental care evolution predict that genetic relatedness will be an important variable in the amount of care a parent provides. However, current inferences of relatedness-based parental investment from studies in humans and birds remain challenged. No study has yet demonstrated parental care adjustment in a manner uncomplicated by life-history correlates or experimental design. We now present a unique test that controls for individual life histories and demonstrates paternity-related dynamic adjustments in parental care. Brood-rearing male bluegill sunfish (*Lepomis macrochirus*) that are cuckolded to a varying degree will either increase or decrease their parental investment in response to changing information on paternity during brood development. Specifically, as parental males detect paternity lost to cuckolders and, hence, a reduction in the value of their brood, they adaptively lower their level of parental care. Conversely, if they detect that their paternity is higher than previously assessed, they adaptively raise their level of parental care. This dynamic adjustment during brood rearing indicates the importance of genetic relatedness in parental investment decisions and provides needed empirical support for theoretical predictions.

Keywords: paternity; parental care; kin recognition; fish

1. INTRODUCTION

Evolutionary and behavioural ecologists are attempting to explain how parents make decisions about the amount of care to provide to their young (reviewed by Westneat & Sargent 1996; Wright 1998; see also Kokko & McRae 2000). A central prediction of parental care theory is that the value of the young will shape the amount of care an adult provides (e.g. Trivers 1972; Whittingham *et al.* 1992; Sargent & Gross 1993; Westneat & Sherman 1993). One important component of 'value' is genetic relatedness or the presence of the parent's genes in the brood. For example, when a male's relatedness to the young is decreased by cuckoldry, fewer of his genes are present and, thus, the evolutionary value of his investment into the current young is decreased relative to possible future young. Cuckolded males should therefore reduce their level of investment, even if this increases the mortality of the young in their care, and allocate the investment to future opportunities. However, direct empirical support for relatedness-based parental investment decisions has proven extremely difficult to obtain (reviewed by Wright 1998).

Testing of the theory requires varying the degree of genetic relatedness between an adult and their young while holding everything else constant. Experimental manipulations have been advocated for testing the theory since correlational studies may not unequivocally control for 'everything else' (Lessells 1991; Kempenaers & Sheldon 1997; but see Jamieson & Quinn 1997; Lifjeld *et al.* 1998). However, experimental manipulations also have drawbacks. For example, it is impossible to show conclusively that the manipulation has influenced the desired variable as intended (i.e. perceived paternity) and not an unmeasured third variable that could instead explain the observed response in parental behaviour (Lifjeld *et al.* 1998; Wright 1998; Kokko & McRae 2000). Thus, experimental studies suffer from a similar problem to correlational studies. Consider the following example. Detaining a male bird during his mate's fertile period may reduce the male's perceived paternity, but could also affect his hormonal levels. If a reduction in parental investment is subsequently observed, the possibility that the additional effect of the manipulation and not a reduction in perceived paternity explains the apparently adaptive behaviour cannot be ruled out (see Kokko & McRae 2000). Alternatively, when no relationship is observed, it is too easy to state that the manipulation did not have the desired influence on perceived paternity and thereby dismiss the results. Thus, neither experimental manipulations nor correlational studies can provide conclusive proof. Instead, carefully conducted studies, whether experimental or correlational, and logically interpreted data are necessary for testing the theory (see also Lifjeld *et al.* 1998; Wright 1998). For example, correlational studies can be controlled for potential confounding variables that are biologically realistic, such as male size or quality.

In this paper, we take advantage of the natural variation in perceived paternity that exists in bluegill sunfish and develop a unique testing procedure in order to demonstrate that the degree of genetic relatedness to the young in their care is an important variable in the amount of parental investment that males choose to make. Bluegill sunfish are native to the lakes and rivers of North America, but are now found throughout the world (Lee *et al.* 1980). Males are characterized by a discrete polymorphism in life histories termed 'parental' and 'cuckolder' (Gross 1982, 1991). In Lake Opinicon (Ontario, Canada), parental males mature at the age of

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*Author and current address for correspondence: Department of Neurobiology and Behavior, Cornell University, Seeley G. Mudd Hall, Ithaca, NY 14853, USA (bdtneff@netscape.net). From 1 September 2001: Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7, Canada.

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seven or eight years and compete in order to construct nests in a colony. Nesting males court and spawn with females (synchronously over the course of a single day) and provide sole parental care for the developing eggs and fry in their nests (Gross 1982). In contrast, cuckolder males do not build nests of their own or care for their offspring. Cuckolders mature precociously and steal fertilizations in the nests of parental males through two tactics: 'sneakers' (age two to three years) hide behind plants and debris near the nest edge, but are visible after darting into the nest during female egg releases, whereas 'satellites' (age four to five years) are about the size of mature females (age four to eight years) and, by expressing female colour and behaviour, are able to lead parental males into misidentifying them as a second female in the nest (Gross 1982). Parental males readily detect and attempt to chase sneakers out of their nests, but are relatively unsuccessful at detecting satellites. Thus, parental males may use the intrusion rates of sneakers but not satellites as a cue for estimating their paternity and, hence, the value of the brood when making parental investment decisions. Successful cuckolders release sperm along with the parental male during egg releases by females. This results in several thousand embryos of mixed parentage intermingled within the nest (Phillip & Gross 1994). Following spawning, females and cuckolder males leave the colony while the parental males stay at their nests to raise the young.

The care period lasts approximately seven days and has two distinct phases. The egg phase involves fanning and defending the eggs until they hatch (approximately three days). After hatching, the parental males stop fanning, but the developing fry are defended from predators until they leave the nest. Males do not forage during the parental care period and expend *ca.* 10% of their body mass (Colgan & Gross 1977; Gross 1982). After the fry have dispersed, parental males then return to deeper waters in order to feed and replenish their energy reserves before renesting in subsequent spawning bouts. Some males attempt as many as four nestings in a single breeding year and may survive to breed in two or three years (Gross 1982, 1991; Cargnelli 1995). Paternity among broods is quite variable (e.g. Phillip & Gross 1994) and can vary between each breeding attempt by a male. An interesting part of bluegill natural history is the frequent desertion of nests immediately after the eggs have hatched. Across different colonies, some 5–80% of parental males may abandon their broods to predators or even cannibalize the brood themselves. These males renest sooner or with greater energy reserves (Cargnelli 1995). Thus, parental investment in a current brood is at the expense of future broods and, as predicted by Williams' principle (Sargent & Gross 1993), these counterpoised reproductive costs and benefits generate the potential for a dynamic allocation of energy to parental care.

2. METHODS

(a) *The colony*

We quantified the paternity and parental care behaviour of bluegill sunfish in Lake Opinicon during their June to July breeding season (1996). Once spawning began we constructed a large enclosure by placing a net of *ca.* 90 m across the mouth of a bay, thereby completely enclosing it. The bay contained a naturally formed colony. The enclosure allowed all natural behaviours to occur but prevented dispersal and, thus, allowed us to capture the entire breeding unit after all reproduction was completed, including 44 females, 58 cuckolders (32 sneakers and 26 satellites) and 38 nesting and 68 deserting parental males. Divers recorded breeding behaviour, including that of sneakers and satellites intruding into the nests and the subsequent care behaviour of parental males. While satellites are rarely detected by parental males, they can be identified by experienced human observers (e.g. Gross 1980, 1982).

(b) *Parental investment*

The fanning rate of parental males was calculated from 5 min of observation on each of the three days that the eggs were present before hatching. Divers using snorkeling equipment recorded the number of fanning motions (Colgan & Gross 1977; Gross & MacMillan 1981; Gross 1982) performed by the parental male and this was later analysed as fans per minute. Brood defence was tested by presenting a live brood predator (pumpkinseed sunfish, *Lepomis gibbosus*) in a clear bag at the nest edge of each parental male (Colgan & Gross 1977; Gross & MacMillan 1981). A trial consisted of presenting the predator for 30 s followed by removal for 30 s and then presenting for another 30 s. An index of the parental male's willingness to defend his brood was calculated from the equation brood defence $= 1 \times \mathrm{LD} + 2 \times \mathrm{OF} + 3 \times \mathrm{Bi}$, where LD, OF and Bi are the total number of lateral displays, opercular flares and bites performed by the parental male during the trial, respectively. The coefficients were selected in order to reflect the apparent relative intensity of the parental male's reaction (Colgan & Gross 1977). Brood defence was tested twice, once during the egg stage (the day after spawning) and once during the fry stage (the day after eggs hatched).

(c) *Paternity analysis*

Just before the fry left the nest at the end of the parental care period, each parental male and the fry within his nest were collected by SCUBA divers ($n = 38$) and all the other bluegill sunfish from the breeding population within the enclosure were netted for DNA fingerprinting analysis. DNA samples from the adults and an average of 42 fry (range = 38–46) from each nest were analysed using 11 microsatellite loci and techniques that we have described previously (Colbourne *et al.* 1996; Neff *et al.* 1999, 2000*a*). We calculated the genetic relatedness of each parental male to the brood in his nest from these genetic profiles and our mathematical models (Neff *et al.* 2000*b*,*c*), as well as the proportions of the brood fathered by sneakers and by satellites. The paternity of parental males that had abandoned their broods could not be determined directly from the genetic analysis since all offspring were lost to predation. However, their paternity could be inferred from the intrusion rates of cuckolders (see Fu *et al.* 2001).

(d) *Dynamic adjustment*

The change in parental investment ($\Delta\mathrm{PI}$) between the egg and fry stages of care was calculated for each parental male from the following formula:

$$\Delta\mathrm{PI} = \ln(\mathrm{defence}_{\mathrm{fry}} + 1) - \ln(\mathrm{defence}_{\mathrm{egg}} + 1) - \beta. \qquad (1)$$

Therefore, positive values of $\Delta\mathrm{PI}$ represent increases in the level of brood defence (relative to the mean difference) and negative

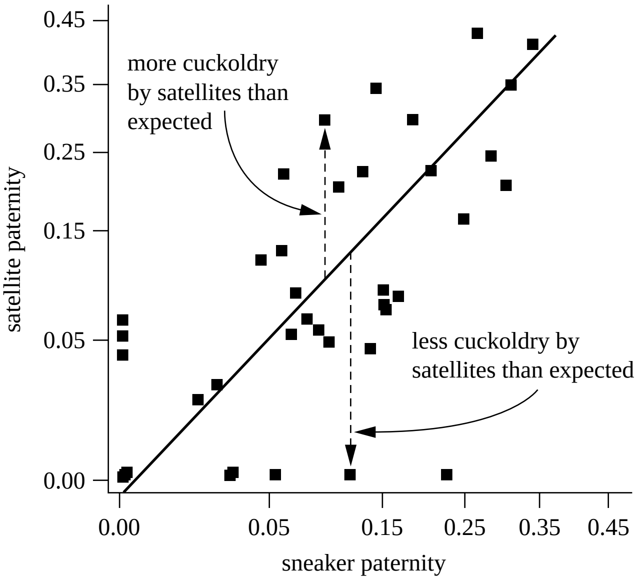

Figure 1. The relationship between sneaker paternity and satellite paternity in each of the nests of the 38 parental males. Geometric mean regression was used for calculating the residuals of satellite paternity ($r = 0.66$, $p < 0.01$ and $n = 38$). Points above the regression line represent nests with more cuckoldry than expected by satellites given the amount of cuckoldry by sneakers. Conversely, points below the line represent nests with less cuckoldry than expected by satellites. Sneaker and satellite paternities were arcsine square-root transformed prior to analysis (Zar 1999). The axes are back adjusted to the actual paternity values and, therefore, have uneven intervals.

values of ΔPI represent decreases. β is the mean difference in defence across all individuals or the differential value of brood defence between the egg and fry stages of care. By subtracting β from each value, the mean ΔPI is centred on the origin. For example, when β is greater than zero, the value of brood defence during the fry stage is greater than its value during the egg stage.

The change in perceived paternity was calculated from the residuals of the geometric mean regression of satellite paternity onto sneaker paternity (multiplied by -1 to flip the sign of the residuals). Therefore, negative residuals represent parental males that have proportionately more cuckoldry by satellites than would be predicted given the amount of cuckoldry by sneakers (which are detectable during spawning). Conversely, positive residuals represent individuals that have proportionately less cuckoldry by satellites (figure 1). While parental males can detect cuckoldry by sneakers during spawning, they may be able to detect cuckoldry by satellites only after the eggs have hatched (see § 4). As such, males with positive residuals will have an increase in their perceived paternity between the egg and fry stages and, according to theory, should increase their level of parental investment. Conversely, males with negative residuals will have a decrease in their perceived paternity and should decrease their level of parental investment.

Linear regression was used for examining the relationship between the change in parental investment and the change in perceived paternity and determining whether parental males were making adaptive adjustments in their parental investment in response to changes in their perceived paternity. All statistics were performed using either SPSS (v. 10) or Microsoft Excel (v. 2000).

3. RESULTS

The divers' observations of spawning behaviour revealed that parental males who remained to raise the young in their nests had significantly fewer intrusions by sneakers than did parental males who deserted their broods (remained $5.3 \pm 1.0\%$ (s.e.) versus deserted $16.4 \pm 3.7\%$) ($t = 4.1$, $p < 0.001$ and d.f. = 43). There was no significant difference in the rate of satellite intrusions (remained $1.7 \pm 0.7\%$ versus deserted $4.4 \pm 2.7\%$) ($t = 1.4$, $p = 0.17$ and d.f. = 43). Overall, intrusions by cuckolders were significantly lower in the nests of males who remained (remained $7.0 \pm 1.1\%$ versus deserted $20.8 \pm 5.5\%$) ($t = 3.8$, $p < 0.001$ and d.f. = 43). Since deserted nests quickly lost their young to predators, we could not confirm a paternity difference directly. However, behavioural observations of intrusions were strongly correlated with genetically assessed paternity in another study of our bluegill population (Fu *et al.* 2001). This suggests that low perceived paternity early in brood development may result in desertion of the young. It also suggests that sneakers but not satellites are detected and influence parental investment decisions.

The genetic analyses revealed that those parental males providing care through to fry maturity had, on average, fertilized 79% of the young in their nests (range = 26–100% and $n = 38$). Sneakers fertilized 10% (range = 0–31% and $n = 32$) and satellites fertilized 11% (range = 0–45% and $n = 26$). Parental investment among these males was significantly related to paternity (figure 2). Care-providing males that were heavily cuckolded by sneakers (but not so much as to cause abandonment) were less willing to defend their broods from predators, as demonstrated by a negative correlation between parental male defence effort and the proportion of eggs fertilized by sneakers ($r^2 = 0.12$, $\beta = -0.35$, $F_{1,37} = 5.1$ and $p = 0.03$) (figure 2*a*). As expected from the apparent inability of parental males to detect cuckoldry by satellites, there was no relationship between the level of egg defence and the paternity of satellites ($r^2 = 0.03$, $F_{1,37} = 0.3$ and $p = 0.86$) (figure 2*b*). Multiple linear regression of sneaker and satellite paternity at the level of parental male defence during the egg stage ($r^2 = 0.24$, $F_{2,37} = 5.6$ and $p = 0.008$) revealed that sneaker paternity had a strong negative effect (standardized slope $\beta = -0.65$ and $p = 0.002$), while satellite paternity had a positive effect (standardized slope $\beta = 0.45$ and $p = 0.026$). This positive effect suggests that a parental male does not perceive a satellite as a threat to his paternity, but rather as a second female releasing eggs and thereby increasing his reproductive success. It may also contribute to the observed lack of relationship between the level of egg defence and satellite paternity (i.e. figure 2*b*). For example, since satellite paternity was positively correlated with sneaker paternity ($r = 0.66$, $p < 0.01$ and $n = 38$), which is negatively correlated with a parental male's level of egg defence, it might be expected that egg defence would also be negatively correlated with satellite paternity, even if only spuriously. However, since a parental male perceives a satellite as a second female (and, hence, as increasing his reproductive success), this positive association will oppose the potentially spurious negative effect (figure 3). Additional support is provided by the fanning data. While there was

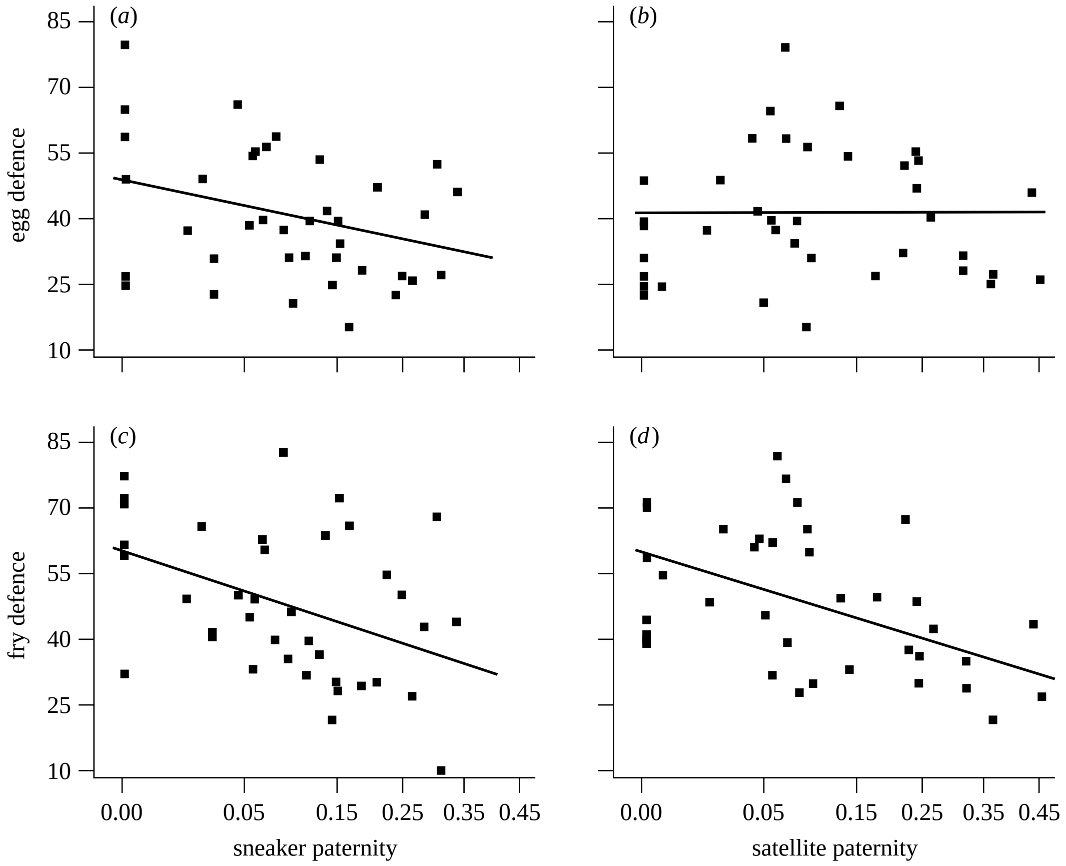

Figure 2. The parental investment of individual parental males is related to their perceived loss of paternity to cuckolder males. (*a*,*b*) Egg stage and (*c*,*d*) fry stage. (*a*) The willingness of parental males to defend the eggs in their nest was negatively correlated with the proportion of the eggs fertilized by sneakers. (*c*) The same holds true for the defence of fry in the nest. (*b*) There was no such relationship between the willingness of parental males to defend the eggs in their nest and the proportion of the eggs fertilized by satellites, but (*d*) after the eggs hatched there was a negative relationship. The slope in (*b*) was significantly different from the slopes in the other three graphs ($t > 6.2$, $p < 0.001$ and d.f. $= 36$ for each). All other comparisons were not significantly different ($p > 0.20$). Sneaker and satellite paternities were arcsine square-root transformed prior to analysis (Zar 1999). The axes are back adjusted to the actual paternity values and, therefore, have uneven intervals.

a negative effect of sneaker paternity on the amount of fanning by parental males ($r^2 = 0.13$, $F_{1,37} = 5.3$ and $p = 0.03$), there was no independent effect of satellite paternity on fanning ($p > 0.05$).

Parental males adjusted their parental investment after the eggs hatched. Defence of the brood was now negatively correlated with the paternity of both sneakers (figure 2*c*) and satellites (figure 2*d*) (sneaker, $r^2 = 0.16$, $\beta = -0.39$, $F_{1,37} = 6.6$ and $p = 0.01$ and satellite, $r^2 = 0.24$, $\beta = -0.49$, $F_{1,37} = 11.1$ and $p = 0.002$). It was also negatively correlated with the overall paternity of cuckolders ($r^2 = 0.26$, $\beta = -0.51$, $F_{1,37} = 12.9$ and $p = 0.001$), which was not the case during the egg stage ($r^2 = 0.03$, $F_{1,37} = 1.0$ and $p = 0.33$). There was no effect of brood size on parental investment during either the egg or fry stages ($p > 0.29$ for both) and brood size was not correlated with the paternity of sneakers, satellites or parental males ($p > 0.18$ for all). Thus, parental males appear to reassess their paternity after the eggs hatch and adjust their investment accordingly.

Figure 4 provides a direct test of how each parental male in the colony responded to information on his paternity between the egg and fry stages. There was a positive relationship between the change in parental investment and the change in perceived paternity ($r^2 = 0.18$, $\beta = 0.43$, $F_{1,37} = 8.1$ and $p = 0.007$). Thus, assuming that parental males can detect the loss of paternity to satellites only after the eggs have hatched, parental males are adaptively adjusting their investment based on changes in their perceived paternity during brood development.

Overall, parental investment was higher during the fry stage of care than during the egg stage ($\text{defence}_{\text{egg}} = 41 \pm 2$ (s.e.) and $\text{defence}_{\text{fry}} = 49 \pm 3$) (paired *t*-test, $t = 2.7$, $p = 0.01$ and d.f. $= 37$). Thus, β was positive, indicating that, as the value of parental investment (brood defence) increased relative to the parent's own future reproduction, so too did their investment. The value of a brood may increase in response to several factors such as the increased likelihood that an offspring will survive to maturity (see Coleman *et al.* 1985; Sargent & Gross 1993).

4. DISCUSSION

In order to allocate parental investment adaptively, males must first be able to assess their paternity (Westneat & Sherman 1993; Kokko 1999). The visible intrusions of sneakers into the nest provide the parental male with an opportunity for estimating his genetic relatedness to the young, since intrusion rates are inversely correlated with

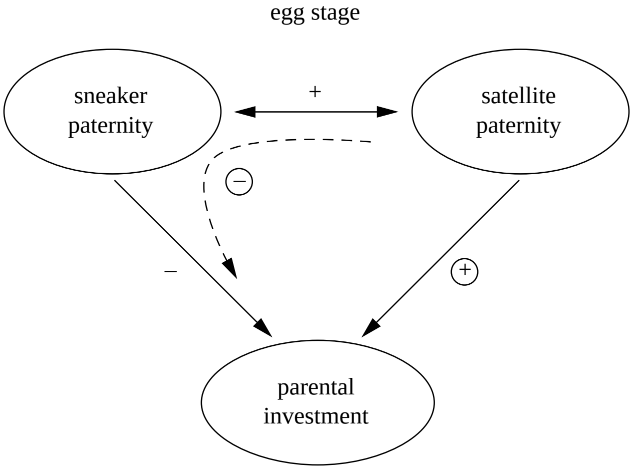

Figure 3. The relationship between sneaker paternity, satellite paternity and parental investment during the egg stage of care. Since satellite paternity is positively correlated with sneaker paternity, which in turn is negatively correlated with parental investment, there is the potential for a spurious negative correlation between satellite paternity and parental investment (dashed line). However, satellite paternity appears to have a direct positive effect on parental investment during the egg stage of care. This counteracts the negative spurious correlation and may explain why there was no direct correlation between satellite paternity and parental investment. The circles around the positive and negative symbols indicate the counteracting effects.

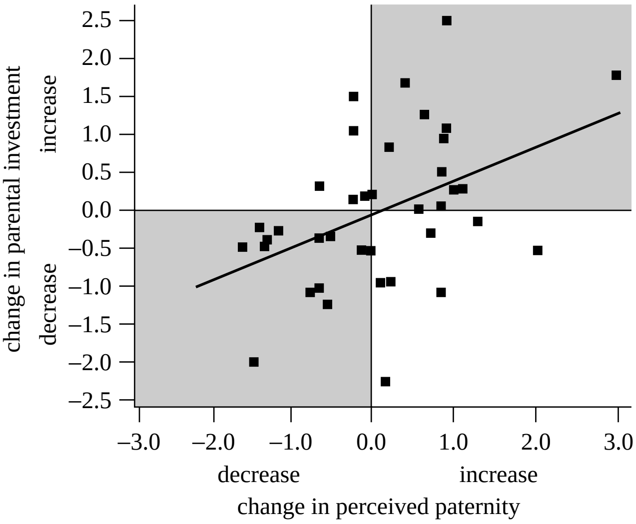

Figure 4. Change in parental investment in response to change in perceived paternity between the egg and fry stages. There was a positive relationship between the change in parental investment that individual parental males make between the egg and fry stages and the change in their perceived paternity. As an example, individuals with a large negative change in perceived paternity had more cuckoldry by satellites than was expected given the amount of cuckoldry by sneakers. These individuals may detect this additional loss in paternity to satellites only after the eggs hatch and, subsequently, they lowered their parental investment. Shaded areas represent evolutionarily adaptive changes in parental investment in response to the information available on the change in perceived paternity.

a parental male's paternity (Phillip & Gross 1994; Fu *et al.* 2001). In contrast, parental males court satellites mimicking females and only rarely recognize them as cuckolders and chase them from the nest (Gross 1982). However, since cuckoldry by sneakers is correlated with cuckoldry by satellites, parental males could also use the visible intrusions of sneakers in order to provide an estimate of the rate of cuckoldry by satellites and, thus, their overall paternity and brood value. After the eggs hatch, parental males may be able to use a cue present in the fry that was not present in the eggs for reassessing and calculating their paternity more accurately. A new cue detectable only in the fry could also explain the observed second wave of abandonment that occurs shortly after the eggs hatch (the first wave occurs shortly after spawning in response to egg number and sneaker intrusion rates) (e.g. Gross 1980, 1982). Recent evidence from kin recognition studies in other fish and behavioural observations in bluegill sunfish has suggested that this cue may be olfactory based.

The olfactory systems of many fish allow the detection of kin through cues present in secreted bile acids, amino acids and urine (e.g. McKaye & Barlow 1976; Loiselle 1983; Quinn & Busack 1985; Brown & Brown 1996). Thus, a parental male bluegill sunfish may be able to assess his paternity from the odour in the secretions of the newly hatched fry (e.g. self-referent phenotype matching) (Sherman *et al.* 1997; Mateo & Johnston 2000). This new information, which is potentially available through olfaction, provides an opportunity for dynamic adjustment of investment decisions (figure 4). Parental males that are cuckolded by satellites more than is predicted based on the level of cuckoldry by sneakers (see figure 1) should decrease their level of investment in response to a lower perceived paternity at the fry stage relative to the egg stage (lower-left quadrant in figure 4). Conversely, males that are cuckolded by satellites less than predicted should increase their level of investment in response to a higher perceived paternity at the fry stage relative to the egg stage (upper-right quadrant in figure 4). When perceived paternity does not change between the egg and fry stages (i.e. satellite paternity is equal to that predicted based on sneaker paternity), males should not change their level of investment (origin in figure 4). Nearly 70% (26 out of 38) of the parental males studied made decisions falling within the calculated adaptive regions. This was significantly different from chance (binomial test, $p = 0.02$). The remaining 12 individuals may have made adaptive decisions that were obscured by measurement errors in the estimation of their brood defence or paternity. Given that parental males can in fact assess their overall paternity better after the eggs hatch (e.g. by evaluating an odour cue present in the fry), our study provides compelling evidence that individual parental male bluegill sunfish make adaptive adjustments to their parental investment based on incoming information on their paternity during brood development.

We also examined several competing hypotheses for our results. For instance, nests on the periphery of the colony are more susceptible to brood predation by snails and other fish (bluegill sunfish, pumpkinseed sunfish and smallmouth bass, *Micropterus dolomieui*) as compared with central nests (Gross & MacMillan 1981), and satellites appear to avoid spawning in these nests (B. D. Neff and M. R. Gross, unpublished data). Conceivably, brood predation might explain the positive relationship in figure 4 if males on the periphery spent more time during the egg stage of care actively chasing predators and subsequently had less energy to invest in defence during the fry stage. However, nest location, as measured by the shortest distance to the periphery of the colony, had no independent effect on the change in parental investment ($p = 0.99$). We also found that the hatching success of the eggs increased with the parental male fanning rate ($r^2 = 0.17$, $\beta = 0.41$, $F_{1,37} = 7.6$ and $p = 0.009$), but neither the hatching success or fanning rate influenced the observed change in parental investment ($p > 0.39$ for both). Brood size, parental male quality or mean female quality (as assessed by body length, mass, age, fluctuating asymmetry and parasite load) also had no effect on the observed change in parental investment ($p > 0.29$ for all comparisons). Interestingly, we did find that males with overall higher paternity were more likely to increase their parental investment independent of the change in perceived paternity (paternity, $\beta = 0.26$ and $p = 0.08$, change in perceived paternity, $\beta = 0.42$ and $p = 0.007$ and overall, $r^2 = 0.25$, $F_{2,37} = 5.9$ and $p = 0.006$). Males with higher paternity may have more energy to invest in parental care, particularly after the eggs hatch, or may pay a lower opportunity cost to this care in terms of future reproduction (see Coleman *et al.* 1985; Sargent & Gross 1993).

We have shown that parental males adjust their investment across all young in their nest. Do they show differential investment in individual young? Given that the fry are tiny and there are several thousands within the nest, parental males may not be able to isolate odours specific to individual fry. Thus, in bluegill sunfish olfaction may provide a non-discriminating cue of paternity (see Westneat & Sherman 1993). A similar lack of paternity discernment on an individual scale has been observed in birds (e.g. Burke *et al.* 1989; Dixon *et al.* 1994; Johnsen *et al.* 2000). However, the adjustment of overall parental investment does have implications for the potential success of cuckolder males. First, the selective decrease in parental investment in nests with high cuckoldry will reduce the average fitness of the cuckolder life history. Second, even if cuckoldry provides better genes for a female (e.g. Gross 1996; Petrie & Kempenaers 1998; Jennions & Petrie 2000; Johnsen *et al.* 2000), paternity-based allocation of overall parental investment can reduce offspring survivorship, thereby negating some of the advantages of infidelity in females. Therefore, while cuckoldry may provide 'good genes', it can also be balanced by a trade-off in 'good care'. This trade-off presents an interesting avenue for future research (e.g. Kokko 1999; Shellman-Reeve & Reeve 2000).

In summary, parental male bluegill sunfish make dynamic adjustments in their parental investment between the egg and fry stages of care. These adjustments seem best predicted by changes in perceived paternity and, therefore, support a fundamental prediction of parental investment theory: parents invest according to the evolutionary value of their young. Although evidence suggests that olfaction may be the cue used by parental males in assessing their paternity after the eggs hatch, this remains to be confirmed and is an active area of our current research on recognition systems in bluegill sunfish.

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