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ORIGINAL ARTICLE

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Nestling recognition via direct cues by parental male bluegill sunfish (*Lepomis macrochirus*)

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Abstract Parental care can be costly to a parent in terms of both time and energy invested in the young. In species with cuckoldry or brood parasitism not all of the young under a parent's care are necessarily offspring. In such cases, distinguishing between kin and non-kin, and investing only in the former (nepotism), can be advantageous. Bluegill sunfish (*Lepomis macrochirus*) are characterized by paternal care and cuckoldry, and care-providing males appear to show nepotistic behaviours. Here, we investigated nestling recognition in bluegill, determining whether parental males can differentiate between young from their own nest (familiar and related) and young from non-neighbouring nests (unfamiliar and unrelated) using (1) visual and chemical cues, and (2) chemical cues only. In the first experiment, wild-caught parental males were presented with samples of eggs or fry (newly hatched eggs) collected from their own nest or a foreign nest and placed on opposite sides of an aquarium. The time these parental males spent associating with each sample, and their "pecking" behaviours (indicating cannibalism), were recorded. Parental males showed no preference between eggs from their own nest and eggs from a non-neighbouring nest, but they preferred to associate with fry from their own nest over foreign fry. There also was a positive relationship between male body size and the time spent associated with fry from their own nest. Parental males pecked at foreign fry more than 5 times as often as fry from their own nest, though this difference was not statistically significant. In the second experiment, fry that were collected from the nest of a wild-caught parental male or a non-neighbouring nest were placed in different containers and the water from each was dripped into opposite ends of an aquarium. The time the male spent on each side was recorded. In this case, parental males spent more time near the source of water conditioned by unrelated fry, but there was a positive relationship between male condition (fat reserves) and the time he spent near the source of water conditioned by fry from his own nest. Results confirm that chemicals cue nestling recognition by parental male bluegill.

Keywords Kin recognition · Olfaction · Paternity · Parental care · Bluegill

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Introduction

Many animals can distinguish kin from non-kin based on assessments of phenotypic attributes, such as odours, facial features, or vocalizations (Fletcher and Michener 1987; Brown et al. 1993; Sherman et al. 1997; Mateo 2002; Tibbetts 2002). Such "direct" recognition (Waldman et al. 1988) involves use of templates, which are internal representations of the characteristics expected in various relatives. Recognition occurs when phenotypes of recipients match templates closely enough (Lacy and Sherman 1983; Reeve 1989). Although templates can be genetically determined (e.g., Grosberg and Quinn 1986; Keller and Ross 1998), typically they are learned. Kin recognition based on social learning is well documented (Fletcher and Michener 1987; Alexander 1990; Sherman et al. 1997).

Kin recognition is especially important during parental care when broods are of mixed parentage, as occurs when there is cuckoldry or parasitism. In such instances, nepotism can be adaptive and parents are expected to distinguish between their offspring and unrelated young that are under their care, or between broods that contain many versus fewer offspring (Trivers 1972; Westneat and Sherman 1993). In many birds there is evidence that parents distinguish between broods based on the number of young that are related, but there is no evidence that parents use direct cues to recognize individual chicks within a brood

that are their offspring (Westneat et al. 1995; Whittingham and Lifjeld 1995; Kempenaers and Sheldon 1996; Neff and Sherman 2002).

In contrast, among the fishes that provide parental care, adults do use direct (chemical) cues to distinguish offspring from non-kin. For example, chemical cues enable male *Cyprinodon macularius californiensis* to distinguish between eggs they fertilized and eggs fertilized by another male (Loiselle 1983). Discrimination of offspring and siblings from non-kin is accomplished via waterborne chemosensory cues in various species in the families Salmonidae (Brown and Brown 1996; Olsén et al. 2002) and Cichlidae (Myrberg 1975). In *Cichlasoma citrinellum* (McKaye and Barlow 1976) and *C. nigrofasciatum* (Lutnesky 1989) maternal females can distinguish offspring from unrelated young at different stages of their development (prolarvae versus postlarvae).

In the bluegill sunfish (*Lepomis macrochirus*) some males behave parentally, by guarding, cleaning, and aerating eggs and young, and these males are commonly cuckolded (Neff 2001). Presumably a male that could detect he had been cuckolded and reduce his investment in that brood accordingly would gain an advantage. Interestingly, during the egg phase the amount males invest in entire broods depends on an indirect cue of relatedness, namely, their effectiveness at excluding conspicuous cuckolders (Neff and Gross 2001). Males do not vary their egg-stage investments depending on the degree of cuckoldry by female-mimicking males. However, after the eggs hatch parental males begin making dynamic, adaptive adjustments in their investments based on their paternity (Neff and Gross 2001). Sometimes parental males even abandon their brood shortly after the eggs hatch, and these males re-nest sooner and with greater energy reserves than males that continue to behave parentally (Gross 1982; Coleman and Fischer 1991). The shift in the precision of discrimination behaviour that accompanies hatching implies that a direct cue becomes available at that time.

This study follows up on these observations by investigating abilities of parental male bluegill sunfish to recognize eggs and fry (newly hatched eggs) based on direct cues. Using a two-choice apparatus, we tested whether parental males can distinguish (1) eggs or fry from their own nest (most of which are offspring) from eggs or fry from a non-neighbouring nest (all unrelated), and (2) fry from their own nest from fry from a non-neighbouring nest based solely on waterborne chemical cues.

Methods

Study animal

L. macrochirus is native to lakes and rivers of North America (Lee et al. 1980). Males exhibit a polymorphism in life histories termed "parental" and "cuckolder" (Gross 1982). In Lake Opinicon, Ontario (44°16′N, 76°30′W) parental males delay maturation for 7 years and then compete for preferred territories in nesting aggregations. Nesting males court and spawn with multiple females and subsequently behave parentally towards eggs and fry in their nests for up to 10 days: eggs hatch 2–3 days after fertilization and fry remain in the nest for up to 7 more days. Parental males do not leave their nest to forage and they lose up to 15% of their body mass (Coleman and Fischer 1991). Parental males do, however, consume some of the eggs and fry within their nest, which partially compensates for their energetic investment in guarding (Gross 1982). In contrast, cuckolder males mature precociously at 2 years of age and do not compete for territories, build nests, or associate with young. Rather, cuckolders steal fertilizations at the nests of parental males by behaving as "sneakers" or "satellites." Sneakers are small cuckolders that hide in refugia around nests (plants, rocks, debris) until a female arrives, then dart out and ejaculate simultaneously with the territory holder. Satellites are large cuckolders that behave like females to gain access to nests when real females are present. As a result, eggs within a nest usually are sired by more than one male (Philipp and Gross 1994; Neff 2001).

Experimental individuals

Our experiments were conducted during May–July 2001 at the Queen's University Biological Station on Lake Opinicon. Breeding colonies of male bluegill were located along the lake's shore and surveyed by snorkeling (see Gross 1982). The developmental stage of the young in each nest was recorded daily: for eggs, the number of days post spawning, and for fry, the number of days post hatching. In preparation for a recognition trial, a focal parental male was randomly selected from within a field colony and he and about 50% of the eggs or fry in his nest were collected (2,000–3,000 individuals). Soon thereafter, a similar number of eggs or fry were collected from a non-neighbouring male's nest in the same colony. Nests of non-neighbouring males were not adjacent to the focal male's nest and always were located at least 1 m away (e.g., see Fig. 1 in Neff 2001). Eggs or fry were immediately placed in 1 l of fresh lake water and returned to the field station.

Samples of eggs and parental males (n=10) were collected the day after spawning; samples of fry and parental males (n=14) were collected on post-hatching days 1 (5), 2 (4), 3 (3), or 4 (2). At capture, each parental male's length and mass were measured. Fulton's condition factor (mass divided by total length cubed) was used to estimate energy reserves (Sutton et al. 2000; Cargnelli and Neff, unpublished data). A high proportion of the eggs and fry collected from nests of parental males undoubtedly were related to those males, whereas the eggs and fry we collected from nests of non-neighbouring males were completely unrelated. This is because within spawning colonies male bluegill sire an average of 79% (range: 26–100%) of the eggs in their nest and 2% in neighbouring nests but never fertilize eggs in nests of non-neighbouring males (Neff 2000, 2001; Gross 1982). Experiments always began within 2 h after the fish were collected.

Discriminations using visual and olfactory cues

A parental male was introduced into a large aquarium (120×60×60 cm) containing 250 l of fresh lake water (17–19°C). Two glass pie plates (30 cm in diameter) were placed 20 cm on either side of the tank's centre line. The male was left undisturbed for 1 h to acclimatize.

In the meantime, samples of eggs or fry from the male's own nest and from a non-neighbour's nest were gently placed on equal-sized grid trays using a turkey baster, so that a monolayer covered the bottom. This enabled us to obtain roughly equal numbers (around 2,000) of eggs or fry (exact counts were not made to minimize handling and avoid stressing or injuring the young). Any potential difference in signal strength between the paired samples (i.e., due to small differences in numbers) was unbiased with regard to relatedness.

The sample of eggs or fry from the test male's own nest and from the non-neighbour's nest were placed into the pie plates, and the male and young were left undisturbed for 1 h. This was done to allow potential chemical cues to develop in the pie plates, because

the eggs and fry had been "washed" twice (i.e., when they were transferred to fresh lake water upon collection and again when introduced to the aquarium).

A video camera was positioned directly above the aquarium so that its field of view included the entire tank. The camera was switched on, and for the next 2 h the male's behaviour was recorded. Tapes were analysed later to quantify (1) the difference in time each male spent on either side of the centreline, and (2) the number of "pecking" behaviours towards young (usually indicative of cannibalism: Gross 1982). Each male was tested only once, and the sides of the test tank with related versus unrelated young were alternated in each successive trial. At the end of each trial all the fish were released at their sites of origin in Lake Opinicon.

Discriminations using olfactory cues

Experiments always began within 2 h after fish were collected. To begin a trial a parental male was introduced into a large aquarium filled with 250 l of fresh lake water (as above). Simultaneously, samples of fry, roughly equal in numbers (around 2,000), were placed into 1 l of fresh lake water inside 5-l plastic carboys. One set of fry was from the male's own nest and the other was from a non-neighbour's nest. All the fish were left undisturbed for 1 h to acclimatize.

Then, water from each jug was dripped into opposite sides of the aquarium at a rate of 10 ml per minute. A video camera whose field of view included the entire tank was switched on and behaviours of the test male were recorded for 1 h. Tapes were analysed later and the time the male spent on each side of the centreline was recorded. Each male was tested only once, and the sides of the test tank with related versus unrelated young were alternated in each successive trial. At the end of each trial all the fish were released at their sites of origin in Lake Opinicon.

Statistics

When data are expressed as means they include plus or minus one standard error. We performed two-tailed statistical tests using SPSS (version 10.0). We used Wilcoxon signed rank tests for two related samples (Zar 1999) to determine if parental males spent more time on the side of the aquarium with, or pecked at, young from their own nest or a non-neighbour's nest, and to determine if parental males spent more time on the left versus right side of the aquarium. Although our data did not deviate from normality (Shapiro–Wilk test: $P>0.05$) we relied on non-parametric statistics for these tests because they are more conservative than parametric tests. Linear regressions were used to examine the relationships between male body length or condition and times spent with eggs or fry collected from their own nest. We used Spearman's correlation to explore relationships between these times, male body length or condition and the number of times parental males pecked at their own eggs or fry, or those collected from non-neighbouring nests. Spearman's correlation was selected because pecking behaviour had large variation, sometimes deviating from normality, and non-parametric correlations are minimally affected by outliers (Zar 1999). Finally, Pearson's correlation was used to examine the relationships between the developmental stages of the eggs or fry and the association times.

Results

Visual and olfactory cues

The ten parental males we tested with eggs spent 54.7±6.3 (SE) min on the side of the test tank with eggs collected from their own nest and 65.3±6.3 min on the side with eggs from a non-neighbour's nest (z=–0.255, n=10, P=0.80). Parental males pecked at eggs from their own nest 14.2±5.1 times/trial and at non-neighbour's eggs 18.8±7.8 times/trial (z=–0.816, n=10, P=0.41). Males in poorer condition pecked more at the egg samples (r_S=–0.64, n=10, P=0.048), but there was no significant relationship between body length and the total number of pecks (r_S=–0.34, n=10, P=0.33). Males showed no consistent preference for the left or right side of the test tank during the trial (z=–0.153, n=10, P=0.88).

The 14 parental males we tested with fry spent 69.1±3.1 min on the side of the test tank with fry collected from their own nest and 50.9±3.1 min on the side with fry from a non-neighbour's nest (z=2.54, n=14, P=0.011). Parental males pecked at fry from their own nest 3.0±1.0 times/trial and at non-neighbour's fry 16.0±7.2 times/trial (z=–1.86, n=14, P=0.063). To do so parental males darted to

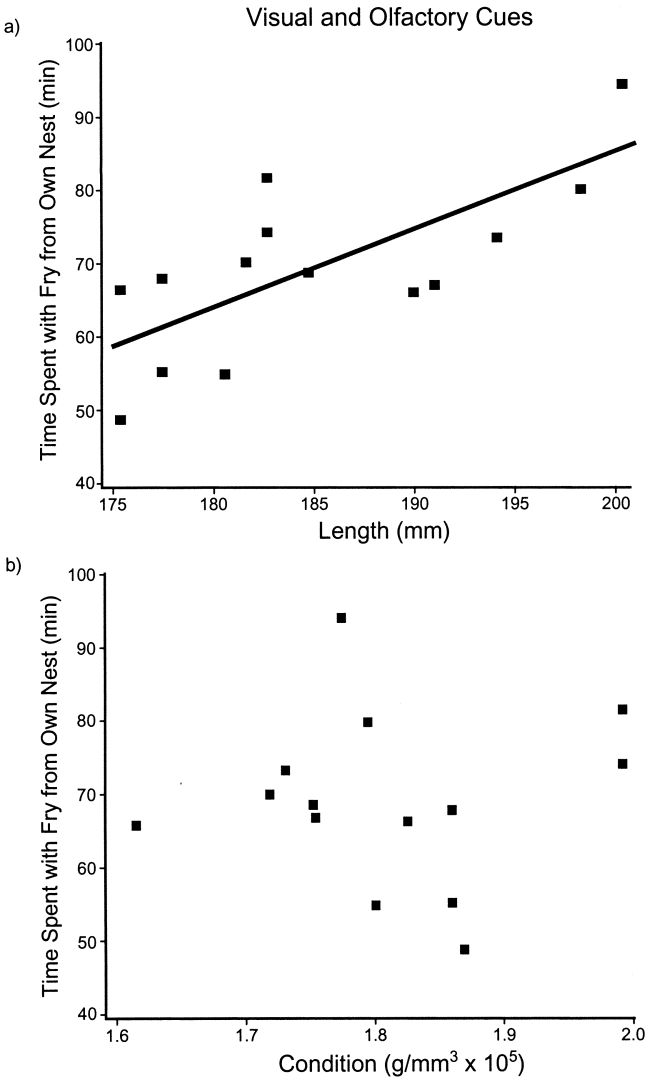

Fig. 1a, b Relationship between the time parental males spent associated with fry collected in the field from their own nest (familiar, related) and their length (**a**) or condition (**b**) when both visual and olfactory cues were available

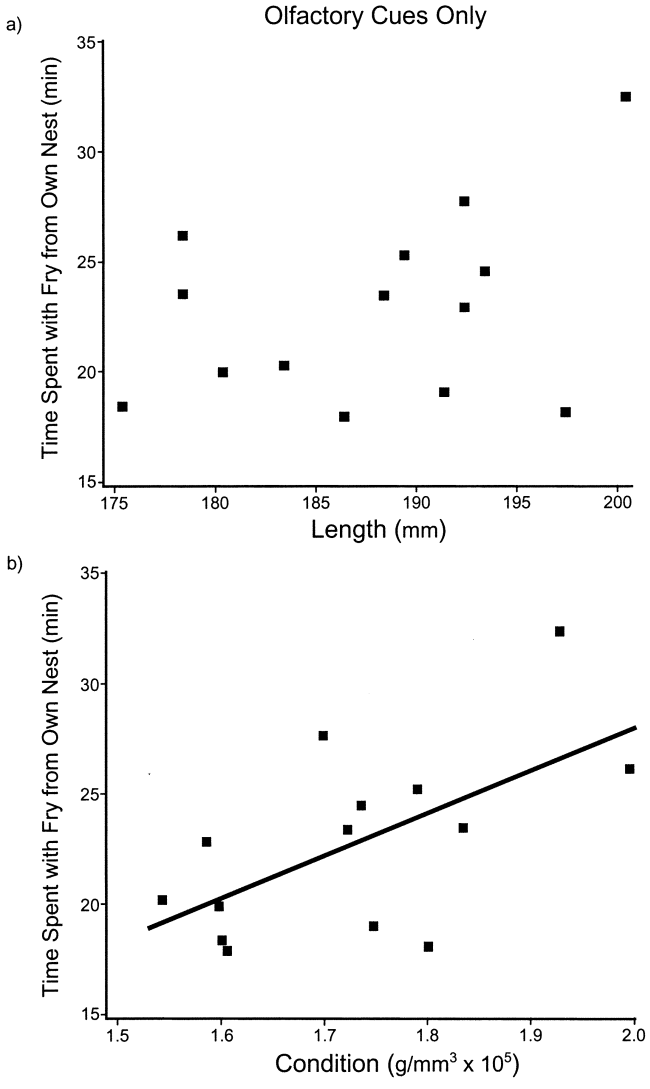

Fig. 2a, b Relationship between the time parental males spent associated with fry collected in the field from their own nest (familiar, related) and their length (**a**) or condition (**b**) when only olfactory cues were available

the opposite side of the tank, pecked at the non-neighbour's fry, and then returned to hover over fry from their own nest. Similar behaviour by nest-tending males has been observed in field colonies (Gross 1982).

There was a positive relationship between the time parental males spent on the side of the tank with fry from their own nest and body length (r^2=0.49, n=14, P=0.005; Fig. 1a), but not condition (r^2=0.001, n=14, P=0.90; Fig. 1b). There was a negative correlation between the time parental males spent on the side of the tank with fry from their own nest and the number of pecking behaviours at non-neighbour's fry (r_S=–0.54, n=14, P=0.045), but not the number of pecking behaviours at their own fry (r_S=–0.15, n=14, P=0.62). There was no relationship between the number of pecks at either fry sample or collectively and male length or condition (P>0.25 for all). There also was no relationship between the time males spent on the side of the tank with fry from their own nest and the developmental stage of the fry (1–4 days post hatch; r_P=0.261, n=14, P=0.37), nor was there a consistent preference for the left or right side of the test tank (z=–0.534, n=14, P=0.59).

Olfactory cues only

The 14 parental males we tested spent considerably more time (37.1±1.1 min) on the side of the test tank with dripping water that had been conditioned by fry collected from a non-neighbour's nest than they spent (22.9±1.1 min) on the side of the tank with dripping water conditioned by fry from their own nest (z=–3.17, n=14, P=0.002). There was no relationship between this latter time and body length (r^2=0.14, n=14, P=0.19; Fig. 2a), but there was a positive relationship with condition (r^2=0.37, n=14, P=0.021; Fig. 2b). There also was no relationship between these times and the developmental stage of the fry (1–5 days post hatch; r_P=–0.362, n=14, P=0.20), and males showed no consistent preference for the left or right side of the test tank (z=–0.220, n=14, P=0.83).

Discussion

Results of our experiments indicate that parental male bluegill sunfish distinguished between fry from their own nest (familiar, related) and fry from a non-neighbouring male's nest (unfamiliar, unrelated). This discrimination occurred both when fry were physically present, so that both visual and chemical cues were available, and when fry were not present but water conditioned by fry was provided (i.e., only chemical cues were available). When fry were present, males spent more time with the ones collected from their own nest than with those collected from non-neighbours' nests, but when fry were not present males spent more time near the source of water conditioned by non-neighbouring fry than the source of water conditioned by fry from their own nest. These discriminations occurred in an artificial setting (a test tank), indicating that nestling recognition was based on direct cues (i.e., attributes of the individuals themselves: Waldman et al. 1988) and did not require habitat features in Lake Opinicon. The cues used were chemical and may have emanated from the parental male while on his nest (a "label"), or more likely, from bile acids, amino acids, or urine of the newly hatched fry (e.g., McKaye and Barlow 1976; Quinn and Busack 1985; Brown and Colgan 1986; Moore et al. 1994; Brown and Brown 1996).

The parental males readily associated with fry from their own nest, but when fry were not physically present they associated with water conditioned by fry from non-neighbouring nests. Possibly the visual stimulus of fry in a nest-like structure (the pie plate in our experiments) triggers paternal behaviours, as it does in some cichlids (e.g., Myrberg 1975; McKaye and Barlow 1976; Nelson and Elwood 1997). Visual stimuli also are required to trigger ag-

gregation behaviour of rainbowfish (Arnold 2000). In the absence of the visual stimulus of fry, parental males may have been looking for food. Indeed males in poorer condition (the "skinny" males) spent more time associating with water conditioned by fry from nests of non-neighbouring males (Fig. 2). This did not occur when fry were physically present. It is also possible that there were differences in the concentration of the chemical cue between the two types of experiments. Although similar numbers of fry were used in both, the "olfactory cues only" tests involved dripping water into the tank, whereas the "visual and olfactory cues" experiment involved subjecting the parental male to the entire fry sample in the pie plate. Parental males exposed to a low concentration of the chemical cue (the dripping water) might adopt a different behaviour (e.g., aggressive), whereas males exposed to a high concentration (the pie plate of fry) might adopt a parental behaviour. Such plasticity in behaviour in response to differences in cue concentration and hunger state is common among fishes (reviewed by Chivers and Smith 1998).

Larger parental males spent more time associated with fry collected from their own nest than did smaller males (Fig. 1). It is unlikely that smaller males were simply hungrier and so spent more time attempting to consume foreign fry because we found no relationship between pecking behaviour and male length or condition on either fry sample. Instead, because larger males are older and generally more experienced breeders they may have already learned chemical cues expected in their nestlings prior to being tested – that is, they imprinted on a former brood to form their template. This mechanism has been observed in female great reed warblers, *Acrocephalus arundinaceus*, who imprint on the colour patterns of their first clutch, presumably enabling them to reject parasitic eggs laid by European cuckoos, *Cuculus canorus*, in later clutches (Lotem et al. 1992; Lotem 1995). We can, however, rule out that the larger parental males in our study were more familiar with their current nestlings because their was no relationship between male length and the developmental stage of the brood when tested.

Although our study was not designed to address the mechanism of bluegill recognition, it yielded some clues. For example, the onset of behavioural discrimination clearly coincided with hatching because males did not distinguish between eggs from their own nest and eggs from a non-neighbouring male's nest. This also seems to occur in the field because when parental males abandoned broods, they typically did so right after the eggs hatched (Gross 1982). Similar time-dependent recognition of young has been documented in other fishes (Myrberg 1975; Brown and Brown 1996). The absence of egg recognition undoubtedly has mechanistic and functional correlates. Mechanistically, hardening of the egg membrane, which occurs shortly after fertilization in most species, may impede the passage of recognition chemicals. Functionally, eggs are small (containing minimal nutrients), the egg stage is short (2–3 days), and there are many chances of making errors in egg recognition with thousands of eggs per nest. As a result egg discrimination may not be strongly favoured because the costs are high relative to the payoffs.

Once eggs hatch, parental males may learn the chemical characteristics of the entire brood in their nest. This "gestalt learning" mechanism (Crozier and Dix 1979) could enable males to distinguish between fry from their own nest and fry from other nests. This mechanism, however, would not enable parental males to distinguish offspring from unrelated young *within* their nest. The discovery by Neff and Gross (2001) that nepotism varies directly with parentage during the fry stage of care, but not during the egg stage, implies that males can directly assess the proportion of young in their nest that they actually sired. Investigating the possibility that parental males discriminate between offspring and unrelated young within broods offers exciting possibilities for future research on bluegill recognition.

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