

of colonists, are especially vulnerable to environmental change. Marine and estuarine assemblages are already affected by climate change; this data set tracks the recent expansion of range and population size in fish that are close to the northern limit of their range in British waters such as sole (*Solea solea*¹⁸), seabass¹⁹ and trigger fish (*Balistes carolinensis*). Conversely, it also shows the decline in species that reach the southern limit of their range in British waters, for example sea snail (*Liparis liparis*²⁰) and dab (*Limanda limanda*²¹). If conditions alter sufficiently we predict that new core species, drawn from the pool of occasional species, will replace the existing ones. Temporal components of species abundance also have important implications for conservation planning, as recognized by the latest generation of reserve selection algorithms, which incorporate information on species permanence²². □

Methods

Fish samples were collected from the cooling-water filter screens at Hinkley Point B Nuclear Power Station, situated on the southern bank of the Bristol Channel in Somerset, England. The power station intakes are placed in front of a rocky promontory within Bridgwater Bay; to the east are the extensive Stert mud flats with an intertidal area of ~40 km². The water intakes are placed between -1 and -5 m MLWS (mean low water springs), so the fish are sampled from water of between 8 and 18 m depth. Full descriptions of the intake configuration and sampling methodology are given in refs 18 and 23. Quantitative sampling began in 1980 when 24-h surveys of the diurnal pattern of capture were undertaken in October and November. From these surveys it was concluded that samples collected during daylight were representative of the 24-h catch²⁴, and monthly quantitative sampling began in January 1981. The total volume of water sampled per month, which has not varied over the entire 21-year period, is 3.24 × 10⁵ m³. To standardize for tidal influence, all sampling dates are chosen for tides halfway between springs and neaps, with sampling starting at high water (normally about 12:00). Fish are collected hourly from two filter screens for a 6-h period, identified to species, measured and the number of individuals recorded. Since 1987 the standard lengths (SLs) of all captured fish have been recorded to the nearest millimetre. The filter screens have a solid square mesh of 10 mm and start to retain fish >25 mm SL. A 100% retention for many species occurs at SLs > 40 mm. For fish such as sprat, whiting and pout the screens retain all fish captured with a SL greater than ~60 mm (ref. 25). The sampling method therefore catches adults and juveniles older than 6 months for all known British marine fish.

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Correspondence and requests for materials should be addressed to A.E.M. (e-mail: aem1@st-andrews.ac.uk). The full data set can be downloaded from the Pisces Conservation Ltd website (<http://www.irchouse.demon.co.uk/latestreports.html>).

Decisions about parental care in response to perceived paternity

Bryan D. Neff

Department of Biology, University of Western Ontario, London, Ontario N6A 5B7, Canada

Evolutionary ecologists are attempting to explain how parents make behavioural decisions about how much care to provide to their young^{1–4}. Theory predicts that when genetic relatedness to young is decreased by cuckoldry, for example, parents should reduce their care in favour of alternative broods that provide greater reproductive success^{5–7}. Experimental manipulation of perceived paternity has been used to test the theory^{8,9}, but such studies have generated mixed results^{10–13}. Some manipulations can fail to alter a parent's perceived paternity¹⁴, whereas others may directly affect parental behaviour when, for instance, the manipulation involves capturing the parent^{15–18}. No study has demonstrated parental care adjustment in a manner uncomplicated by experimental design or life history correlates. Here I test the theory using the fact that nest-tending parental male bluegill sunfish (*Lepomis macrochirus*) can assess their paternity using both the visual presence of parasitic cuckolder males during spawning¹⁹, and olfactory cues released by newly hatched eggs^{20,21}. By manipulating both types of cues I show that parental males dynamically adjust their parental care, favouring broods that are apparently most closely related. These results confirm the importance of genetic relatedness in parental care decision-making.

Bluegill are native to lakes and rivers of North America. Males are characterized by a discrete polymorphism in life histories termed 'parental' and 'cuckolder'^{22,23}. In Lake Opinicon (Ontario, Canada), parentals mature at age 7 years and construct nests in a colony during the breeding season²³. Nesting parentals court and spawn with multiple females over the course of a single day and then provide sole care for the developing young in their nests. Parental care involves fanning and defending eggs (which can number in the tens of thousands) until they hatch (2–3 days), and then defending developing fry from predators until the young leave the nest (5–7 days). If a parental abandons his nest before this time, the young do not survive. Parentals do not forage while they are tending their brood and so they lose about ten per cent of their body weight, although they do occasionally cannibalize some of the eggs or fry in their nest²⁴. After the fry have dispersed, parentals return to deeper waters to feed and replenish their energy reserves before re-nesting in a subsequent spawning bout²⁵.

In contrast, cuckolders do not build nests or care for young but instead mature precociously and steal fertilizations in the nests of

parentals using two age-dependent tactics. ‘Sneakers’ (age 2–3 yr) hide behind plants and debris near the nest edge but are visible as they dart into the nest to release sperm when a female deposits her eggs. ‘Satellites’ (age 4–5 yr) are about the size of mature females (age 4–8 yr) and they exhibit female colouration and behaviour, leading parentals to misidentify them as a second female in the nest^{19,22}. Thus, parentals can use the presence of sneakers during spawning as an indirect cue of reduced paternity^{19,26}. In addition, once the eggs hatch the developing fry release a direct (chemical) cue, possibly in their urine²⁷, that parentals can use to distinguish their offspring from those of both sneakers and satellites^{19–21}.

I manipulated the perceived paternity of nesting parental males to see how it affected their guarding and cannibalistic behaviours using two experiments (see Methods). In both, the parental’s actual paternity was revealed by olfactory cues released by the fry^{20,21}. These cues were not present during the egg phase of care²⁰. The strength of the two experiments lies in their opposite predictions with respect to the change in parental care from the egg phase to the fry phase. In the first, treatment parentals (fish whose nests were manipulated) had a lower perceived paternity during the egg phase of care, but a higher perceived paternity during the fry phase, whereas in the second, treatment parentals had a higher perceived paternity during the egg phase of care than during the fry phase.

In the first experiment, four sneakers (young cuckolders) were placed inside small transparent plastic containers near the nests of 34 randomly selected parentals within a colony for the duration of spawning. This manipulation should have reduced parentals’ perceived paternity because proximity of sneakers to the nest during spawning is a reliable threat to paternity²⁶. Six of these males abandoned their nests shortly after spawning, while an additional two abandoned nests shortly after the eggs hatched. Empty containers were similarly placed around 20 other ‘control’ nests. In this case, two males abandoned their nests shortly after spawning and three abandoned nests after the eggs hatched. The day after spawning, male behaviour was quantified by evaluating each parental’s willingness to defend his brood from a potential egg predator (a pumpkinseed sunfish in a clear plastic container: see Methods). The results showed that egg defence was significantly lower by the treatment males than the control males (excluding males that abandoned nests: $t_{39} = 2.7$, $P = 0.011$; Fig. 1a).

Sneakers in the plastic containers were prevented from siring any eggs, so after the eggs of experiment 1 males hatched, the parental males should have been able to use the olfactory cues released by the fry to reassess their actual paternity (and discover that they had been cuckolded less than anticipated). As predicted, after the eggs

hatched there was no difference in the parental care of the treatment and control groups of males ($t_{39} = 0.64$, $P = 0.52$; Fig. 1a). This test assumes that ‘natural’ cuckoldry rates were not significantly higher in control nests. Examining the change in parental care between the egg and fry phases, treatment males increased their level of care significantly more than control males ($t_{39} = 2.79$, $P = 0.008$; Fig. 2).

In the second experiment, the day after spawning, approximately one-third of the eggs were removed from nests of 20 parentals and replaced with unrelated eggs from one of the other males’ nests. Four of these males abandoned their nests shortly after the eggs hatched. Sham-swaps were performed on eggs of 15 control parentals, but one of these males abandoned the nest shortly after the swap, and another abandoned his shortly after the eggs hatched. The parental behaviour of each male was quantified three times: before the egg swap (to provide a baseline), the day after the swap, and the day after the eggs hatched. There was no difference in the willingness of treatment or control parental males to defend their nests prior to ($t_{27} = 0.97$, $P = 0.34$) or the day after the manipulation ($t_{27} = 1.22$, $P = 0.23$) (Fig. 1b). Both groups did increase their level of care between these two periods (paired t -test for control: $t_{12} = 5.60$, $P < 0.001$; for treatment: $t_{15} = 5.22$, $P < 0.001$), but the change was similar ($t_{27} = 0.37$, $P = 0.71$; Fig. 2). Thus, if the manipulation affected the parental males, it did so equivalently.

However, after the eggs hatched, there was a significant difference between the two groups—treatment parental males provided less care than controls ($t_{27} = 2.08$, $P = 0.047$; Fig. 1b). This occurred because treatment males decreased their level of care significantly more than control males ($t_{27} = 4.58$, $P < 0.001$; Fig. 2). This test is powerful because it controls for natural variation in the level of care among parentals within the treatment and control groups. Within-group variation may be attributed to, for example, differences in condition¹⁹. Furthermore, relative to the baseline measure, control males increased their level of care (paired t -test: $t_{12} = 2.65$, $P = 0.021$), but treatment males decreased their level of care (paired t -test: $t_{15} = -3.30$, $P = 0.005$), and these adjustments in parental behaviour were significantly different between

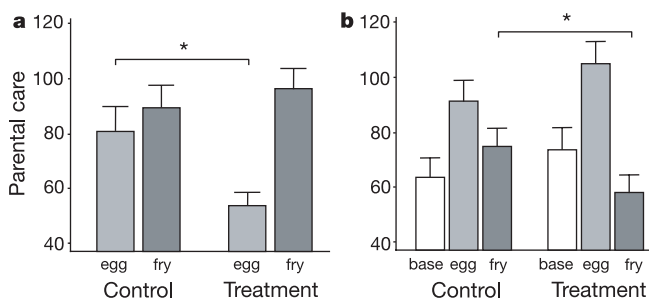


Figure 1 Parental care by control and treatment parental male bluegill. **a**, Results from the sneaker manipulation (experiment 1) showed that the parental care of treatment males was significantly lower than control males during the egg phase but not during the fry phase of care. **b**, Results from the egg manipulation (experiment 2) showed that the parental care of treatment males was similar before the manipulation (baseline) and the day following the manipulation (egg phase), but was significantly lower than control males during the fry phase of care. Error bars represent 1 s.e. and horizontal lines with asterisks denote significant differences.

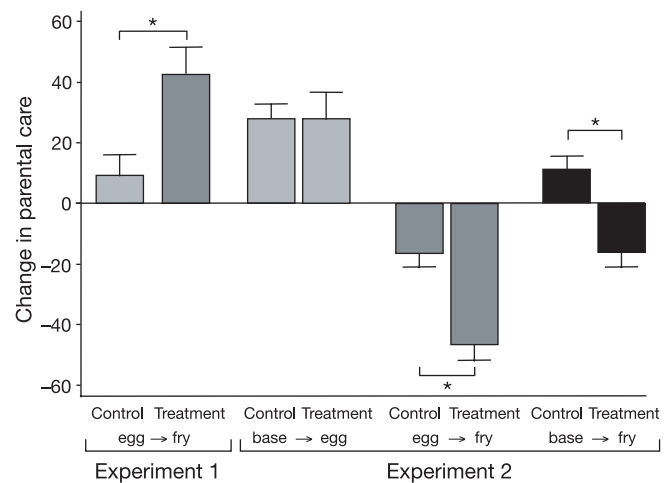


Figure 2 Changes in parental care by control and treatment parental male bluegill. In experiment 1, treatment males increased parental care more than did control males between the egg and fry phases of care (egg → fry). In experiment 2, both treatment and control males increased parental care similarly between the baseline and the day after the manipulation (base → egg). However, after the eggs hatched (egg → fry) treatment males decreased parental care more so than did control males and relative to the baseline (base → fry) these latter levels reflect a decrease for treatment males and an increase for control males. Error bars represent 1 s.e. and horizontal lines with asterisks denote significant differences.

the two groups ($t_{27} = 4.41$, $P < 0.001$; Fig. 2).

Further support comes from three additional analyses. First, in experiment 1, the manipulation should have led to greater abandonment shortly after spawning in the treatment than control group, whereas in experiment 2 abandonment should have been greater in the treatment than control group shortly after the eggs hatched. Combining data from both experiments, 10 treatment males (6 in experiment 1 and 4 in experiment 2) and 3 control males (2 in experiment 1 and 1 in experiment 2) abandoned nests during these predicted times. The probability that 10 or more males would abandon from the treatment group yet 3 or fewer from the control group is unlikely to occur by chance (cumulative binomial probability: $P = 0.065$).

Second, as expected in experiment 1, there was no difference in the pecking behaviour (indicative of partial brood cannibalism) of treatment and control males during the fry phase of care (treatment: 5.7 ± 0.6 (s.e.); control: 7.5 ± 1.5 ; $t_{39} = 1.34$, $P = 0.19$). However, in experiment 2 treatment males did peck at their fry more often, although the difference was not significant (treatment: 15.3 ± 1.8 ; control: 10.8 ± 1.6 ; $t_{27} = 1.81$, $P = 0.081$).

Third, I compared the changes in parental care between the baseline and fry phase in experiment 2 to those made by parentals in response to natural variation in perceived paternity observed in a previous correlative study¹⁹. On the basis of those data¹⁹, the relative level of parental care C_{rel} between the egg and fry phases ($C_{rel} = C_{fry}/C_{egg}$) was related to the change in an individual's perceived paternity ($\Delta P_{per} = P_{fry} - P_{egg}$) (see Fig. 1 in ref. 19) according to the following equation: $C_{rel} = 10^{(0.078 + 0.873 \times \Delta P_{per})}$. Thus, my control males should have had a C_{rel} of 1.20 ($\Delta P_{per} = 0$). They in fact had a very similar C_{rel} of 1.18 ($=75.6/63.9$). For the treatment males, ΔP_{per} should have averaged -26% ($= -\frac{1}{3} \times 79\%$, where the proportion of eggs that were swapped was one-third and 79% is the average paternity of parentals in their nests²⁸) and therefore they should have had a C_{rel} of 0.71. Although the observed C_{rel} of 0.78 ($=57.8/74.3$) is higher than this expected value, the observed value suggests that I swapped an average of 27% of the eggs, which is only marginally fewer than the estimated 33.3%.

My results cannot be due to natural variations in life history (for example, male quality, condition, age) or ecology (for example, nest location, vegetation, refugia) because parental males were randomly assigned to treatment and control groups, and only perceived paternity was experimentally manipulated. Indeed, there were no differences in the size, condition, number of eggs, or nest location of treatment and control males ($P > 0.16$ for each). It is possible that in the first experiment, treatment males expended more energy during spawning by attempting to chase away the sneakers in the containers and had less energy to invest in brood defence, or perhaps thought that these sneakers were brood predators (although sneakers are much smaller than typical brood predators²³). However, these explanations would not predict the observed change in parental care made by the treatment males between the egg and fry phases relative to the control males. Furthermore, the second experiment employed analogous, simultaneous manipulations in both treatment and control nests. Collectively, these results provide compelling support for a fundamental prediction of parental care theory: parents invest care according to the evolutionary value (genetic relatedness) of their young. □

Methods

Study site

Bluegill spawning activity was monitored at Lake Opinicon (44° 34' N, 76° 19' W) during the May–July breeding season in 2000. Lake Opinicon is an 890-hectare, mesotrophic, warm-water lake, which sustains a large natural population of bluegill whose reproductive biology has been studied since the mid-1970s²³. For this study, reproductive activity was examined by swimmers equipped with snorkelling gear in an area bounding 2 km of littoral zone along the northern shore of the lake. Surveys were made daily beginning before the onset of breeding in May and ending after breeding ceased in July. During this time, two breeding colonies were selected for the manipulations and each nest was tagged

with a small numbered tile. Each colony was mapped and the position of each nest was recorded. Control and treatment nests were then randomly assigned. At the conclusion of the experiment, each parental was briefly captured to measure total body length (to the nearest mm) and weight (to the nearest 0.1 g). Fulton's condition was then calculated from weight divided by cubic length.

Experiment 1

On the morning of spawning (identified by the presence of a large school of females near the colony at about 08:00 Eastern Standard Time, EST), two sneakers were placed inside each plastic container (20 × 15 × 10 cm), and two containers were then placed on either side of each treatment nest within the colony for the duration of spawning (09:00–17:00). Thus, there were a total of four sneakers in proximity to treatment nests at all times. Sneakers ranged in size from 71–101 mm and averaged 80 mm. Control nests had two empty containers placed around the nest edge. The empty containers appeared not to interfere with spawning, while the containers with sneakers occasionally solicited an aggressive approach by the nest-tending parental. Sneakers reacted to the approach by manoeuvring to the bottom of the container where they were less conspicuous. When spawning concluded all containers were removed from the colony. The following day (09:00–11:00), the parental care of each male was quantified using established methods (see below) and an egg number score was recorded for each nest as a rank between 1 (few eggs) and 5 (many eggs)²⁵. Parental care was again recorded the day after the eggs hatched, and the following day the pecking behaviour was quantified (see below).

Experiment 2

The day after spawning (09:00–11:00), egg number scores were recorded and a baseline level of parental care was calculated for each male. Approximately one-third of the eggs from the nests of experimental parental males were then swapped. Swaps were performed between nests that had equivalent egg scores, and were always between non-neighbouring parentals to ensure the foreign eggs introduced were unrelated to the focal parental²⁸. Sham-swaps were performed in each of the control nests by removing a third of the eggs, swimming away from the nest and then returning to the nest and replacing the same eggs. Parental care was retested the day following the manipulations, and a third time the day after the eggs hatched. Two days after egg hatching, the pecking behaviour was quantified.

Parental care

Parental care was quantified using brood defence by presenting a live brood predator (pumpkinseed sunfish, *Lepomis gibbosus*) in a clear bag at the edge of each parental male's nest¹⁹. A trial consisted of presenting the predator for 30 s, removing it for 30 s, and then presenting the predator for another 30 s. Control and experimental males were tested alternately. The experimental status of each nest was unknown to the observer. An index of the parental's willingness to defend his brood was later calculated from the equation: Brood defence = $1 \times L + 2 \times F + 3 \times B$; where L , F and B are the total number of lateral displays, opercular flares and bites performed by the parental male during the trial. The coefficients were selected to reflect the relative intensity of the parental's reaction and the potential for personal injury^{19,24}. Brood defence should be a good estimate of actual parental investment.

Pecking behaviour

Parentals will occasionally 'peck' at their nest and presumably consume some of their brood (partial cannibalism)^{20,23}. A peck is an obvious behaviour whereby a male angles downward towards his nest, followed by forward movement towards the base of the nest, where the eggs or fry reside. The total number of pecks on a brood was counted for each parental based on two 30-min observation periods: one in the morning and one in the afternoon. Typically, four nests were simultaneously observed. It was not possible to record pecking behaviours during the egg phase of care owing to time constraints with the defence measurements. However, during the fry phase there was consistency between the number of pecks and each male's fry defence score ($r = -0.35$, $P = 0.003$, $n = 70$).

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Correspondence and requests for materials should be addressed to B.D.N. (e-mail: bneff@uwo.ca).

Adaptation of photoperiodic control pathways produces short-day flowering in rice

Ryosuke Hayama*†, Shuji Yokoi*, Shojiro Tamaki*, Masahiro Yano‡ & Ko Shimamoto*

* Laboratory of Plant Molecular Genetics, Nara Institute of Science and Technology, 8916-5 Takayama, Ikoma 630-0101, Japan

‡ National Institute of Agrobiological Sciences, Kannondai 2-1-2, Tsukuba, Ibaraki 305-8602, Japan

The photoperiodic control of flowering is one of the important developmental processes of plants because it is directly related to successful reproduction¹. Although the molecular genetic analysis of *Arabidopsis thaliana*, a long-day (LD) plant, has provided models to explain the control of flowering time in this species^{2–4}, very little is known about its molecular mechanisms for short-day (SD) plants. Here we show how the photoperiodic control of flowering is regulated in rice, a SD plant. Overexpression of *OsGF*, an orthologue of the *Arabidopsis GIGANTEA (GI)* gene^{6,7} in transgenic rice, caused late flowering under both SD and LD

conditions. Expression of the rice orthologue⁸ of the *Arabidopsis CONSTANS (CO)* gene⁹ was increased in the transgenic rice, whereas expression of the rice orthologue¹⁰ of *FLOWERING LOCUS T (FT)*^{11,12} was suppressed. Our results indicate that three key regulatory genes for the photoperiodic control of flowering are conserved between *Arabidopsis*, a LD plant, and rice, a SD plant, but regulation of the *FT* gene by *CO* was reversed, resulting in the suppression of flowering in rice under LD conditions.

We previously isolated *OsGI*, a rice orthologue of the *Arabidopsis GI*, by a differential display method⁵. We found that *OsGI* expression was suppressed in the photoperiod-insensitive *se5* mutant¹³, indicating that it might have a role in inhibiting the flowering of rice under LD⁵. We also found that expression of the *OsGI* messenger RNA was circadian-controlled and that its temporal expression pattern was very similar to that of *GI* under both SD and LD conditions⁵. To further understand the role of *OsGI* in the photoperiodic control of flowering in rice, we fused this gene with a gene promoter that gives constitutively high expression in rice and introduced it into rice by *Agrobacterium*-mediated transformation. The analysis of flowering time for three independent transgenic lines clearly indicated that the flowering times of these lines were later than those of the wild type both under SD and LD conditions (Fig. 1). Particularly under SD conditions, line 18 showed a markedly late phenotype, about 90 days later than that of the wild type. Even under LD conditions, which are suppressive conditions for the flowering of rice, a significant delay of flowering was observed. These results suggested that *OsGI* acts as a suppressor of flowering in rice, which is a reversal of the role of *GI* in the photoperiodic control of flowering in *Arabidopsis*^{6,14}.

The rice orthologues of the two key regulators of flowering time in *Arabidopsis*, *CO* and *FT*, were recently shown to be important in the photoperiodic control of flowering in rice^{8,10}. The rice *Hd1(Se1)* gene, which is an orthologue of the *Arabidopsis CO* gene, was required for the suppression of flowering under LD conditions and for the promotion of flowering under SD conditions⁸. Furthermore, the rice *Hd3a* gene, an orthologue of the *Arabidopsis FT* gene, was shown to be an activator of flowering in rice¹⁰. It was previously demonstrated that *CO* controls the flowering time by integrating signals from the circadian clock and light to regulate *FT* expression in *Arabidopsis*^{15–17}. Because *GI* was shown to function as an activator of *CO*¹³, we measured the mRNA levels of *Hd1(Se1)* (rice *CO* orthologue) and *Hd3a* (rice *FT* orthologue) in transgenic rice overexpressing *OsGI* (Fig. 2; Supplementary Fig. 1). The results of

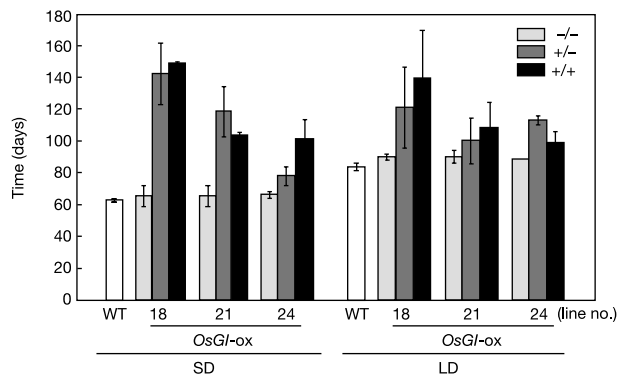


Figure 1 Flowering times of transgenic rice plants overexpressing *OsGI*. Segregating T₁ generation and wild-type (WT) plants were grown under LD and SD conditions, and the number of days to heading (flowering) was measured. In each transgenic line, 10–15 plants were used. Southern blot analysis was performed to determine the genotype of each plant and classify them into groups (+/+, homozygous for transgene; +/-, heterozygous for transgene; -/-, no transgene).

† Present address: Max Planck Institute for Plant Breeding Research, Carl-von-Linné-Weg 10, D-50829 Köln, Germany.

Wise fathers

John D. Reynolds and Ben C. Sheldon

As Shakespeare put it, "It is a wise father that knows his own child". Male bluegill sunfish do: they adjust their behaviour towards their young according to how sure they are of being the real father.

Studies of humans suggest that maternal relatives are more likely to comment on a newborn baby's resemblance to its putative father than to its mother¹. Perhaps these comments provide reassurance about a father's likelihood of being the true father of the child. This interpretation makes evolutionary sense if, as theory predicts, males adjust their level of parental care to their certainty of paternity. Although this expectation fits with the widespread use of DNA tests in messy divorce cases, it has proved extremely difficult to determine whether males in other species play by similar rules.

An elegant new study by Bryan Neff², on page 716 of this issue², breaks through the usual practical difficulties and shows that male bluegill sunfish (*Lepomis macrochirus*; Fig. 1) do indeed adjust their parental behaviour in response to their certainty of paternity. These findings advance our understanding of the evolution of parental care and raise new questions about the conditions under which offspring should reveal their identity to parents, or conceal it.

The study of bluegill sunfish overcomes a stumbling-block that has hampered many previous attempts to test the theory of parental investment in relation to paternity^{3,4}: how to manipulate certainty of paternity. 'Certainty' is not something that can be measured directly. Many researchers have substituted actual measures of paternity using genetic markers³. The hope is that, although the study species won't be able to read DNA bands on gels, it will have picked up some correlate of its paternity, such as the behaviour of its mate towards other suitors. A much more satisfactory approach would be to manipulate the actual cues that males are known to use when assessing their paternity. This is where Neff's study of bluegill sunfish comes in.

Bluegill sunfish are native to most of the United States and adjacent Canada and Mexico, where they nest in colonies in lakes (Fig. 1). Intense competition among males during the breeding season has led to the evolution of two distinct life-history pathways. Males termed 'parentals' defend nest sites, attract females, and then care for the eggs and newly hatched offspring. The others mature at an earlier age as 'cuckolders' and steal fertilizations from parentals either by darting into nests at the critical moment of spawning ('sneakers') or by mimicking



Figure 1 A colony of breeding bluegill sunfish in Lake Opinicon, Ontario, Canada. Parental males are tending their nests, while females ready to spawn are swimming higher up in the water. Neff² has shown that male bluegills use two cues to assess how likely it is that they are the father of the offspring: the more certain they are of their paternity, the more attentive they are as parents.

females, apparently fooling the parental male into thinking he has attracted two females at once⁵. Sneakers are particularly effective, fertilizing 89% of the eggs released by a female during the 8% of spawnings in which they participate⁶.

The occurrence of sneaking thus provides a cue that parental males could use as a guide to their paternity. The second cue is more surprising, but has been confirmed by controlled experiments⁷. Parental male sunfish can apparently assess their relatedness to newly hatched fry using water-borne odour cues; the mechanism is unknown, but other studies of fish suggest a role for genes in the major histocompatibility complex (MHC) in olfactory discrimination of kin⁸ and potential mates⁹.

Neff exploited these mechanisms of assessing paternity in two experiments that examined the males' willingness to defend the nests against an egg predator. In the first, parental males in the midst of spawning were exposed visually to four sneaker males, enclosed in transparent plastic containers so that they could not fertilize any eggs. Control males were exposed to empty containers. As predicted, males reduced their level of care

during the egg phase when they were tricked into expecting lower paternity. Then, male care was tested a second time after the eggs hatched, when the second mechanism for assessing paternity — olfaction — was predicted to restore the certainty of paternity of the experimental males. This is exactly what happened: these males increased their care when the new information suggested that their paternity was not lower than in the control group. These reductions and increases in care fit perfectly with predictions based on the two mechanisms of assessing parentage.

In a second experiment, Neff transferred one-third of a clutch of eggs between nests of parental males, and, as before, assessed the nest defence of parental males before and after hatching. This experiment could therefore only influence male behaviour through the second mechanism for paternity assessment (olfaction), as males seem to be unable to distinguish their relatedness to offspring before hatching occurs⁷. As expected, there was no difference in the behaviour of experimental and control males before egg hatching, but the experimental males decreased their intensity of defence after the eggs hatched.

Two aspects of these experiments are

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particularly notable. First, the changes in behaviour were measured for individual males, which is likely to have reduced the influence of other sources of variation between individuals. Second, the responses to the two experiments are in different directions, showing that males adjust their level of care both up and down in response to changes in certainty of paternity. Taken as a whole, these experiments provide convincing evidence that male bluegills adjust their behaviour in response to their certainty of paternity.

This research suggests some fascinating areas for future work. It would be interesting to follow the fortunes of males through successive spawning bouts to see whether their decisions to adjust care in relation to paternity enhance their lifetime reproductive output, as predicted by life-history theory. The male's ability to determine his relatedness to offspring on the basis of odour cues raises the question of why offspring sired by cuckolders have not evolved an ability to conceal their identity, and whether they might use any tricks to exploit the males that guard them, in the same way that nestling cuckoos manipulate their foster parents¹⁰. Theory

to address the concealment of identity is already partly in place^{11,12}: bluegill sunfish might provide just the system to add empirical flesh to this framework. ■

John D. Reynolds is at the Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK.

e-mail: reynolds@uea.ac.uk

Ben C. Sheldon is at the Edward Grey Institute, Department of Zoology, South Parks Road, University of Oxford, Oxford OX1 3PS, UK.

e-mail: ben.sheldon@zoo.ox.ac.uk

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Astronomy

Wrestling monsters in deep space

Lennox Cowie

Observing distant galaxies is always problematic. But when it comes to the biggest star-forming galaxies, far across the Universe, only indirect approaches can give astronomers any handle at all.

One of the big questions in observational cosmology is when and where the stars in galaxies formed. Giant optical telescopes can now pick out galaxies at huge distances across the Universe, but curiously they miss the galaxies in which the greatest number of stars are forming. Much of the star formation in the Universe occurs in bursts, and the processes that fire up these monster galaxies also produce huge amounts of dust that blot out starlight at most wavelengths, including optical ones. The energy that is absorbed by the dust is re-radiated at much longer wavelengths (in the submillimetre range), and observations at these wavelengths have only recently revealed the presence of these hidden systems.

The fact that so little optical light escapes from the giant star-formers also makes it very difficult to determine how far away they are — distance is usually derived from the spectra of optical emission from galaxies. Two new approaches to finding the distances, or redshifts, of monster galaxies are now reported: by Chapman *et al.*¹ on page 695 of this issue, and by Wiklind² in the *Astrophysical Journal*. Wiklind uses the spectral shape of the galaxies at long wavelengths

to estimate their redshifts. Chapman *et al.* use radio data to locate the galaxies accurately and then obtain the best possible optical spectra.

In 1996, the COBE satellite measured the energy density of the Universe at submillimetre wavelengths and made the remarkable discovery that, over the lifetime of the Universe, galaxies have radiated as much energy at submillimetre as at optical wavelengths³. Clearly there had to be an as-yet undetected population of galaxies that has produced this energy — which is remarkable because such a population would have to have formed as many stars as all the galaxies seen in optical observations. But this population does exist: the Submillimetre Common-User Bolometer Array, or SCUBA, on the 15-m James Clerk Maxwell Telescope on Mauna Kea, Hawaii⁴, has found a huge number of luminous galaxies^{5,6} radiating at submillimetre wavelengths — enough to produce nearly all of the submillimetre light seen by COBE⁷.

Simply imaging the galaxies, however, is not sufficient. To measure how they evolved with time, and to map the history of star formation, we also need to know the distances

to these galaxies. This has proved to be a hard problem. Identifying the optical counterparts to the submillimetre sources is difficult because observations at long wavelengths are limited in their positional accuracy, even when very large telescopes are used. Ultimately, this problem will be resolved with a new generation of submillimetre-telescope arrays, the first of which is now coming online on Mauna Kea⁸. But for the moment it is still difficult to match up the images of the same object seen at optical and at submillimetre wavelengths.

The first attempts to measure redshifts for the submillimetre sources involved identifying every one of the handful or so optical galaxies near the position of each detection. The method was tedious, but distances could be measured for about a quarter of the submillimetre sources and were typically about two-thirds of the way across the Universe⁹. A more promising alternative, however, is to locate the submillimetre counterparts through radio observations. This works because there is a relatively tight empirical correlation in local star-forming galaxies between radio emission and thermal emission from dust¹⁰. The locations of about 60% of the bright submillimetre sources can be pinpointed in this way¹¹.

Chapman *et al.*¹ have drawn on this result and used radio observations to locate the optical counterparts to the submillimetre sources. They then obtained optical spectra over very long exposure times to identify emission lines in the small amount of optical light that emerges from the galaxies. Chapman *et al.* have measured redshifts for ten submillimetre sources, which is a substantial increase in the number of such sources with known redshifts. Even so, this approach unfortunately only samples sources from the same bright submillimetre population that had previously been identified. Although these redshifts are obtained with much less effort, distances to most of the sources still cannot be measured.

In the not so distant future, it should be possible to measure redshifts directly using the Atacama Large Millimetre Array — an ensemble of 64 dishes, each 12 m in diameter, to be built in Chile. Until then, the distances to most submillimetre sources can only be measured using crude redshift estimators. The most widely used estimator is based on the ratio of the amount of emission, or flux, at submillimetre wavelengths to the flux at radio wavelengths¹². Unfortunately, this method fails when the submillimetre sources become too faint — too distant — to detect in the radio. Wiklind² shows that redshifts for these distant sources can be estimated using an alternative method that is based on the shape of the submillimetre region of their spectra. But even this method requires more sensitive submillimetre imaging observations than have yet been made