

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. ■

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Astronomy

Wrestling monsters in deep space

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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