properly, it can help us toward a deeper understanding of the events that create supernovae. And as supernovae in turn are the events that create the elements out of which we are made, it seems worthwhile to get the facts straight. Nomoto et al. have taken a step in the direction of understanding SN1994I, and we have a rich observing season ahead in which the

debris of the supernova will become transparent, to provide another observational chance to test this model for the origin of type Ic supernovae.

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**EVOLUTIONARY BIOLOGY -**

## Parents prefer pretty plumage

Mark Pagel

WOULD parents, if given the chance, choose among their offspring on the basis of a gaudy ornament? It would appear so. On page 240 of this issue<sup>1</sup>, Lyon et al. describe experiments with the American coot (Fulica americana) in which parents preferentially feed those chicks with colourful plumage over those lacking such plumage. This is reputedly the first experimental evidence that parents develop preferences among their offspring on the basis of an ornament, and provides a new impetus for the study of natal colouring.

Adult American coots are greyish-black birds with a spot of white on their bills. Coot chicks, however, sport bright orange plumes (see cover) that contrast sharply against their dark natal down. They also have a bald pate (hence the expression 'bald as a coot') that can turn bright red. Coot chicks do not beg vocally for food, but rather beg by displaying, in competition with other chicks in the clutch, their orange plumage to their parents.

Lyon et al. compared the feeding rates, and the growth and survival rates, of chicks whose orange plumes had either been trimmed or left intact. In black and orange groups, respectively, either all or none of the chicks in a clutch had their orange plumage removed. Surprisingly, chicks in these two groups did not differ on any of the three outcome measures. In experimental groups, half of the chicks were trimmed and half left untrimmed. In these mixed broods, orange chicks were fed at a higher rate, grew more rapidly, and had higher rates of survival than their trimmed clutch-mates, but were broadly similar to chicks in the two control broods. So coot parents fancy their young ornamented, but only when they have a choice between ornamented and nonornamented offspring. Why should this

Manipulating only the experimental factor of interest — here the chicks' colour — can be fiendishly difficult in behavioural ecological studies. Trimming the chicks may alter their behaviour, or their viability, or even make them appear smaller, as well as altering their colour. But the absence of differences between the black

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and orange groups suggests that, in itself, trimming did not affect viability, and the authors assert that trimmed chicks did not behave differently. Coot parents may also tend to feed smaller chicks more, not less. One might also quibble that parents treated orange versus black chicks differently because their experience with these two colours differs<sup>2</sup>. The authors may be on safe ground here because older chicks and adult coots are black.

The experiments of Lyon et al. do not explore the possibility that coot parents discriminate among degrees of ornamentation in their young. But, if parents do, at least three sorts of explanation might be offered for the authors' results. If the cost of the orange plumes (energetic costs of producing them plus increased risk of predation) mean that only the fittest of chicks can produce them, then parents should preferentially feed wellornamented chicks. Alternatively, the plumes and parents' preference for them may have co-evolved via a 'runaway' or Fisherian<sup>3</sup> process in which an initially advantageous plumage trait becomes exaggerated because the parents prefer it. A subset of this explanation has the plumage trait evolving to a fixed and pre-existing parental preference for it. However, whether the Fisherian process works for other traits than those that are sexually selected has not been investigated.

A third explanation rests on the coots' practice of brood reduction. Eggs hatch over a series of days, and, on average, later-hatched offspring suffer relative neglect and have higher mortality. Yet orange chicks in the experiments did not suffer higher mortality when they were late in the brood, whereas black chicks did. Coots' natal colouring normally disappears by three weeks after hatching. Parents may, therefore, use the degree of colouring to assess age; black chicks in the experiments were, perhaps, regarded as old enough to look after themselves.

If coot parents do use the natal plumes to assess age, coot chicks should use their plumes to try to convince their parents that they are young. Presumably, lying about one's age would be kept in check by the increased time-span over which a chick had to pay the costs of producing or having the ornament, and the possibly decreasing benefit of parental feeding to older chicks. Were this the case, parents should feed orange chicks more in the presence of black chicks, but they should not neglect their chicks as the whole brood turns black near the time of fledging a pattern consistent with the authors'

Coot chicks also use their bald pate to beg for food. Why should coot chicks employ (at least) two begging signals? Two signals may each provide a different piece of information, or two signals together may provide a more reliable estimate of the same quality. Alternatively, one signal may indicate something about the signaller's quality, whereas the other may have evolved via the Fisherian process. Theoretical studies4,5 suggest that adults can have more than one trait for attracting members of the opposite sex - for example, a male bird may have a long, colourful tail and a head plume. Coots are interesting in this regard because one of their two signals may provide information about an ephemeral condition (the colour of their bald pate may signal current nutritional or disease status, for example) whereas their plumes may signal something more immanent. If so, this would help to integrate a contrasting view of begging in chicks<sup>6</sup>, that the degree or strength of begging is an honest indicator of offspring need, with parents preferentially feeding the most needy, and not necessarily the most fit.

A tentative explanation, then, for why American coot parents choose among their young on the basis of a natal ornament is that, for brood-reducing species, the accurate assessment of which offspring to neglect may be under strong selection. Chicks, in turn, produce the ornament, and possibly other signals, to avoid being among the dispossessed. Whatever the eventual interpretation of the work by Lyon et al., the idea of parental preference for young on the basis of ornaments should stand astride the conventional views of natal colouring as attempts at crypsis, or as sign-stimuli or speciesrecognition signals. Evidence that parents prefer young with symmetrical ornaments<sup>7</sup> may be just around the corner.  $\Box$ 

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Lyon, B. E., Eadie, J. M. & Hamilton, L. D. Nature 371, 240-243 (1994).

<sup>2</sup> Dawkins M S Anim Behav 19 575–582 (1971)

Fisher, R. A. The Genetical Theory of Natural Selection (Clarendon, Oxford, 1930).

<sup>4.</sup> Pomiankowski, A. P. & Iwasa, Y. Proc. R. Soc. Lond. B253, 173-181 (1993).

<sup>5.</sup> Iwasa, Y. & Pomiankowski, A. Evolution (in the press) Godfrav, H. C. J. Nature 352, 328–330 (1991)

<sup>7.</sup> Møller, A. P. Nature 357, 238-240 (1992).