

well understood as is the basis for the differential. Most temperate-zone agriculture crops are of the  $C_3$  type and possess a  $\delta^{13}C$  near  $-27\%$ . Many tropical grasses (including maize, sorghum and millets) and relatively few dicots are  $C_4$  and possess a  $\delta^{13}C$  near  $-13\%$ . The mean human tissue values of around  $-23\%$  reported by Lyon and Baxter may simply reflect a dietary carbon source which consists mainly of  $C_3$  plants. Thus, the human samples in the above study were probably of Northern European derivation. Also, I would expect subject variability to be high, as the ratio will vary in a manner related to the dietary carbon. Presumably, this would range from near  $-13\%$  for diets derived from  $C_4$  plants to near  $-27\%$  for food from  $C_3$  plants.

The real question is whether there is secondary fractionation following the initial carboxylation of  $CO_2$ . There is some direct evidence for this in plant tissues and biochemical fractions<sup>3,4</sup> and indirect evidence in animals<sup>3</sup>. This additional discrimination, however, is small and seems most important in lipid synthesis where further discrimination against  $^{13}C$  occurs<sup>3</sup>. Recent experimental data suggest that derived organic matter reflects dietary  $\delta^{13}C$  but tissues and biochemical fractions differ in  $\delta^{13}C$  values<sup>7</sup>.

As the organic matter of secondary production will reflect the dietary values, a further complication is introduced. Each tissue and biochemical fraction may also have an isotopic 'memory'. This will be a function of the  $\delta^{13}C$  of the carbon at the time of synthesis, the  $\delta^{13}C$  values of subsequent foodstuffs, and the biochemical turnover rate of the tissue or fraction. The persistence of this memory as well as the magnitude of secondary discrimination for various biochemical fractions must be established before results of certain ecological<sup>6</sup> and perhaps metabolic studies can be considered reliable.

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## Prevalence of male brood care in teleosts

DAWKINS AND CARLISLE<sup>1</sup> have suggested that male brood care among teleosts arises from the female's ability to spawn first and then desert her consort, placing him in Trivers' 'cruel bind'<sup>2</sup>. The vulnerability of sperm to diffusion ostensibly bars this option to males. A comparative analysis of teleost reproductive biology lends little support to this argument, however. Of the 38 teleost

families with at least one parental species for which the spawning behaviour is known, 23 (60.5%) are characterised by simultaneous expulsion of gametes<sup>3-5</sup>. As neither sex enjoys a temporal advantage in these cases, the desertion argument should predict a random distribution of paternal, maternal and biparental care. On the contrary, paternal care characterises 16 of these families<sup>6,7</sup>, a significantly nonrandom proportion ( $\chi^2 = 19.00$ , d.f. = 2,  $P < 0.005$ ).

The desertion argument predicts paternal care in species in which oviposition and ejaculation are well separated in time. In the cave-spawning cichlids, the best known group of fish of this type, brood care ranges from biparental to fully maternal, however<sup>4,8-11</sup>. Maternal mouthbrooding cichlids have the most clearly sequential spawning pattern known<sup>12</sup>. Yet the female commits herself irrevocably to a parental role before the eggs are even fertilised<sup>8,12</sup>.

Finally, maternal care is predicted where the male spawns first. This pattern occurs in the maternal mouthbrooding cichlid *Sarotherodon macrochir*<sup>13</sup> and the paternal custodial goby *Bathygobius soporator*<sup>14</sup>. In neither case has this behaviour led to a departure from the genus-typical pattern of brood care.

The data suggest that factors other than the sequence of gamete deposition may account for the prevalence of paternal care in fishes. I propose an alternative model, based on (1) the limited availability of suitable spawning sites<sup>15-19</sup>, which makes sequestration of a breeding territory selectively advantageous for many teleosts with demersal eggs<sup>5-7</sup>, and (2) the differential energetic unit-cost of producing ova and spermatozoa<sup>2,20,21</sup>, which makes sequestration less profitable for females than males as a means of maximising reproductive output. Extending the reasoning of Maynard-Smith<sup>22</sup> and of Dawkins and Carlisle<sup>1</sup> to include access to any resource necessary for reproductive success, male desertion after spawning would be selectively advantageous only where there is high probability of securing another breeding site. Where these are limiting, this eventuality is unlikely. Persistence is thus favoured because an immediate payoff to a territorial male is the continued opportunity to spawn.

Defending an area against intrusion incidentally affords some protection to eggs within its boundaries<sup>23,24</sup>. Thus in any system characterised by nest disturbance or egg predation, a difference in fry production between guarded and unguarded sites would strongly favour post-spawning territorial behaviour even if other factors reduce the likelihood of sequential polygyny. Its evolution would be facilitated because it would not require incorporation of new motor patterns or endocrine control systems into the reproductive repertoire. Only prolongation of elements already involved in prior

site sequestration would be necessary. Given a commitment to spawn defence, selection could then operate to produce complex brood care, following the schema outlined by Barlow<sup>25</sup>.

Within the framework of this model, biparental brood care is a derived state, its evolution favoured by environmental factors such as extreme scarcity of spawning sites<sup>8,18,26</sup> or severe spawn predation<sup>10,18,27</sup>, which make switching available energy from egg production to behavioural activities advantageous for females<sup>25</sup>. Maternal care could be derived from a biparental precursor, with male desertion explicable in terms of the modified parental investment model proposed by Dawkins and Carlisle<sup>1</sup>.

To conclude, the limiting nature of spawning sites and the differential bioenergetics of maturing eggs and sperm, rather than the mechanics of spawning with internal fertilisation, seem to account for the prevalence of male brood care among teleosts.

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DAWKINS REPLIES—I agree with Loiselle that the comparative data do not support the small part of our paper which was concerned with male brood care among teleosts. A similar conclusion is reached in a recent exhaustive review of the literature on paternal care<sup>1</sup>. The primary purpose of our paper, to expose the 'Concorde fallacy', remains valid.

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