matters arising

Superfoetation in fishes and the cost of reproduction

THIBAULT[1] has examined the effects of juvenile mortality on reproduction of normal and superfoetatious females of the family Poeciliidae and concluded that superfoetation conferred no selective advantage in an unpredictable environment in which mortality was catastrophic. A life-table model for the evolution of superfoetation shows this to be wrong.

The net reproductive rate of a population (R_0) summarises the interaction between survivorship and fecundity. In general,

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (1)$$

where l_x is age-specific survivorship and m_x is age specific fecundity. A consequence of superfoetation is that females produce fewer young more often than usual. For example, *Poecilia reticulata* females 30–35 mm long produce about 24 young every 21 d (ref. 1). They are not superfoetatious. By contrast, *Poeciliopsis lucida* and *P. monacha* are superfoetatious and females 30–35 mm long produce about 11 young every 11 d (ref. 1). A more general comparison of superfoetatious and normal life histories is given in Table 1.

The net reproductive rate of a superfoetatious female producing young twice as often as a normal female is:

$$R_0 = m_x B_s (1 + p_s + p_s^2 + \ldots) \quad (2)$$

Here, m_x is the number of young produced in interval x, B_s is survivorship to the age of first reproduction for superfoetatious females, and p_s is survivorship to subsequent reproductive intervals. Equation (2) can be simplified[2,3]

$$R_0 = m_x B_s / (1 - p_s) \quad (3)$$

Similarly, the net reproductive rate of a normal female is:

$$R_0 = n_y B (1 + p^2 + p^4 + \ldots) \quad (4)$$

Where n_y is brood size, B is survivorship of a normal female to reproductive age, and p is survivorship to subsequent (x) intervals (Table 1). Equation (4) can be rewritten

$$R_0 = \frac{n_y B}{(1 - p^2)} \quad (5)$$

We can define the circumstances in which superfoetation and normal patterns of reproduction have equal net reproductive rates, that is, when

$$m_x B_s / (1 - p_s) = n_y B / (1 - p^2) \quad (6)$$

or when

$$p = \sqrt{\{1 - [(n_y B / m_x B_s)(1 - p_s)]\}} \quad (7)$$

Whether or not superfoetation is advantageous depends on survivorship to age at first reproduction, subsequent survivorship, and the degree to which brood size is depressed in superfoetatious females. Our example comparing *P. reticulata* with *P. lucida* and *P. monacha* is illustrative. The species are of similar size when they first reproduce. Therefore, we assume equal survival to age at first reproduction. Brood size for the superfoetatious species is half that of the normal female[1], so $m_x = 1$ and $n_y = 2$. Thus equation (7) becomes

$$p = \sqrt{(2p_s - 1)} \quad (8)$$

The difference in adult survivorship (D) when net reproductive rates are identical for both strategies is defined as

$$D = \sqrt{(2p_s - 1)} - p \quad (9)$$

D increases as adult survivorship declines (Fig. 1). When the probability of a normal female surviving to produce another brood (11 d in our example[1]) is less than 50%, superfoetation cannot evolve. When survivorship is in excess of 80%, superfoetation results in a higher net reproductive rate if it increases adult survival as little as 2.5%. *P. lucida* and *P. monacha* occur in unstable environments and invade flood expanded habitats[1] possibly characterised by low competition and predation and, consequently, by high adult survival. As superfoetation will reduce the peak cost of reproduction and further increase adult survival, we interpret it as an adaptation that increases reproduction in transient environments.

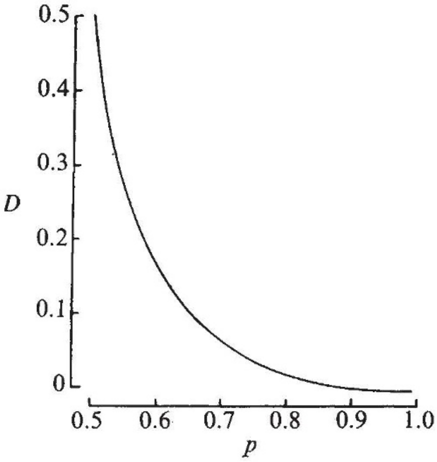

Fig. 1 Relationship between adult survivorship (p) of normal females and the minimum increase in survivorship (D) for superfoetation to be a more advantageous reproductive strategy.

JERRY F. DOWNHOWER
LUTHER BROWN

Department of Zoology, Ohio State University, Columbus, Ohio 43210

1 Thibault, R., *Nature*, **251**, 138–140 (1974).
2 Mertz, D., *Am. Nat.*, **105**, 437–454 (1971).
3 Goodman, D., *Am. Nat.*, **180**, 247–268 (1974).

Table 1 Basic life table for superfoetatious and normal species

Reproductive event	Superfoetatious m_x	Superfoetatious l_x	Normal n_y	Normal l_x
Birth	0	1.00	0	1.00
↓	↓	↓	↓	↓
First reproduction	m_1	B_s	n_1	B
2	m_2	$B_s p_s^1$	0	Bp^1
3	m_3	$B_s p_s^2$	n_2	Bp^2
↓	↓	↓	↓	↓
i	m_i	$B_s p_s^{i-1}$	n_i	Bp^{i-1}

THIBAULT REPLIES — Downhower and Brown[1] contend that natural selection will favour fishes with superfoetation over