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Commentary

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On Optimal Parental Care

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What should a parent do when it has an exceptionally small brood? WICKLER & SEIBT (1983) asked this question for species with repeated breeding and a mean brood size of > 1 (i.e. iteroparous and polytokous species). Would a mother benefit by rejecting rather than investing further in a small brood thereby postponing its next brood? Cost was measured in time.

WICKLER & SEIBT suggest two methods for calculating the optimal decision of a mother. I shall demonstrate that one technique is incorrect and that the other disregards information necessary for specific predictions. I shall also suggest an alternative method.

I. Symbols

N = size of an exceptionally small brood, the acceptance of which is in question,

$\overline{N}$ = average expected brood size,

M = mean nursing time,

t = time interval succeeding the decision point ("D" of WICKLER & SEIBT),

X_t = number of young expected at a time t (a function of "accepting" or "rejecting" the current brood),

$C_{N,O}$ = length of complete breeding cycle, when the current brood of size N is raised (C_N) or rejected (C_O). This equals gestation time in species with post partum oestrus. It also includes the time lag between completion of one brood (due to weaning, abandonment or abortion) and conception. $C_{\overline{N}}$ = interbirth interval when raising a brood of mean size.

A common time measurement must be used; in this paper it is days.

II. A Critique on Available Methods

The "Rule-of-thumb Approach" of WICKLER & SEIBT investigated how many young a mother would have at a time T either if it "accepted" a brood of size N and how many if it "rejected" this brood. T is the point of time when the young, if accepted, would be weaned (i.e. the end of nursing time). Although WICKLER & SEIBT only give numerical examples, their calculus for species with post partum oestrus would read:

$$X_T = N + \frac{M}{M + C_{N,0}} \cdot \bar{N} \qquad (1)$$

This is incorrect, as the nursing time (M), in effect, appears twice in the denominator of the second term. In species with post partum oestrus the prolongation of gestation (e.g. 5—11 d in gerbils, 19 d in tupaias) is a function of nursing.

The correct general expression for all time intervals exceeding the current breeding cycle (i.e. $\frac{t}{C_{N,0}} > 1$) is:

$$X_t = N + \sum_0^i \bar{N} + \frac{t - (C_{N,0} + \sum_0^i C_{\bar{N}})}{C_{\bar{N}}} \cdot \bar{N} \qquad (2)$$

where N reduces to zero if the brood in question is not accepted. $\sum_0^i \bar{N}$ is the number of young of average sized broods already born within t, and the third term evaluates the developing brood. This equation is applicable to animals with post partum or post weaning oestrus. For $\frac{t}{C_{N,0}} < 1$, i.e. time intervals within the breeding cycle in question, even a revised version of WICKLER & SEIBT's approach ($X_t = N + \frac{t}{C_{N,0}} \bar{N}$ for post partum oestrus mothers) would not be correct. The gain from the developing brood would change with time (t) relative to the potential gain of N.

WICKLER & SEIBT's second approach, an optimality model, is also incorrect. For example, the number of young produced by a tupaia mother would be 1.89 in 45 days if she "accepts" a brood of 1 and 1.70 in 41.4 days if she "rejects" it. Both values are calculated using the optimality approach (2nd paragraph, p. 204, WICKLER & SEIBT 1983). These figures are 2.9 and 2.55 respectively when the corrected "rule-of-thumb method" [equation (2); 2.7 would be the value for rejecting mothers after 45 d] is used. The error in the optimality approach is partly due to the fact that a current brood of size N is not included as a gain of an accepting mother, although the effect of her decision (accept or reject) is included as a cost. WICKLER & SEIBT (p. 204) found different optimal rejection levels for tupaia mothers when applying two versions of the same model to the same data. The levels depended on whether information on the frequencies of specific brood sizes was included.

III. A Simple Alternative

Let us assume that time is the only cost to a mother, i.e. the cost of raising a brood is simply the prolongation of interbirth intervals (this was also assumed by WICKLER & SEIBT). Let us further assume that it pays a mother to raise a brood of size $\overline{N}$. How much longer would the interbrood interval of a mother with post partum oestrus be if she raised a brood of size N? The number of days the subsequent brood is postponed ($C_N - C_0$) divided by the brood size (N) is the net cost of each of N young to the rearing mother. A mother's decision should be based on a comparison of the number of young gained at the cost of this time delay and the mean brood size (i.e. the expected size of the subsequent brood) over the time cost of raising the latter to independence. If

$$\frac{N}{C_N - C_0} > \frac{\overline{N}}{C_{\overline{N}}} \tag{3}$$

then a mother should raise a brood of size N. The critical brood size, N^*, is thus

$$N^* = \frac{(C_{N^*} - C_0)}{C_{\overline{N}}} \cdot \overline{N} \tag{4}$$

An unknown N^* may be first approached by taking C_N of the smallest N known. If the calculation reveals an N^* (calculated to the nearest integer) $> N$, one should substitute C_{N+1} until the equation is balanced. If we again consider the tupaia, an example given by WICKLER & SEIBT, the critical N^* would be

$$N^* = \frac{45 - 26}{45} \cdot 1.9 = 0.8$$

Therefore, tupaia mothers should accept any brood size. We can further examine this by applying equation (2): at the hypothetical N^* of 0.8 a tupaia mother should do equally well whether she accepts or rejects it. We may ask how many young do accepting or rejecting mothers gain after a time span of, say, 100 days?

$$\text{(accept)} \quad X_{100} = 0.8 + 1.9 \cdot 2 + \frac{100 - (45 + 45)}{45} \cdot 1.9 = 5.02$$

$$\text{(reject)} \quad X_{100} = 0 + 1.9 \cdot 2 + \frac{100 - (26 + 45)}{45} \cdot 1.9 = 5.02$$

If we are interested in the critical $\overline{N}^*$, up to which a brood of a given size N should be reared, we have from (3)

$$\overline{N}^* = \frac{C_{\overline{N}}}{C_N - C_0} \cdot N \tag{5}$$

This is almost the same as the derived version of the optimality approach used by WICKLER & SEIBT [p. 204, equation (3)]. However, $\overline{N}^*$ refers to the overall mean and does not exclude the probability of any specific brood size, unlike WICKLER & SEIBT's model. The latter disregards the information on N (the brood size in question) necessary for specific predictions ($\bar{N}^*$ is a function of N).

In post-weaning oestrus animals equation (3) simplifies to

$$\frac{N}{C_N} > \frac{\bar{N}}{C_{\bar{N}}} \tag{6}$$

i.e. developing the young is advantageous if the number of young gained per time is higher than that obtained by raising the average brood in a full cycle.

$$N^* = \frac{C_{N^*}}{C_{\bar{N}}} \cdot \bar{N} \tag{7}$$

is the critical brood size. A female domestic pig which absorbs a brood would only lose 22 days at time D (see WICKLER & SEIBT 1983). This is small compared to the 180 days of a complete cycle.

$$N^* = \frac{158}{180} \cdot 8 = 7.02$$

i.e. domestic pigs should absorb all broods of less than 7. They do not do this, perhaps because of other factors (see below).

Table 1 gives the values of N^* and $\bar{N}^*$ for all of WICKLER & SEIBT's examples.

Table 1: Data from examples given by WICKLER & SEIBT (1983).
+ the N questioned by WICKLER & SEIBT

Species	$\bar{N}$	M	N+	C_O	C_N	C_N	N^*	$\bar{N}^*$ (at N)
Mongolian gerbil	4.6	21	1	24	35	29	0.66	7
Tupaia	1.9	33	1	26	45	45	0.80	2.37
Domestic pig	8	55	5		180	158	7.02	5.70
Feral pig	6.2	30	5		170.5	134.5	4.89	6.33

IV. Applicability

The new approach, which calculates the optimal decision of "accepting" or "rejecting" a current brood of given size, is straightforward. It can be applied more easily and more broadly than WICKLER & SEIBT's optimality model. It does not require the calculation of probabilities of certain brood sizes. It has the advantage of including the current brood size (see above). Its applicability may be limited by strong deviations of the brood size frequency distribution from normality.

A common objection to mathematical arguments in animal behaviour is that they ignore the complexity of concurring variables and so are only applicable under special conditions rarely encountered in nature. The criticism is legitimate in the present case. The decision to rear a brood instead of abandoning, cannibalizing or absorbing it is probably not only a question of time costs and brood sizes, as modelled in this simplistic approach. Other important variables may include:

1. condition and age of a parent,
2. the variability of environmental quality with time (e.g. seasonal environments or temporary, unusual conditions, whether especially good or poor and dangerous; see HRDY 1979, p. 17),
3. the influence of rearing a brood on the quality of a subsequent one (e.g. weight; see FUCHS 1981, 1982) or, more generally, on the mother's reproductive value,
4. the trade-off between offspring number and quality within a brood, i.e. the reproductive value of young may depend on the number of nest mates (e.g. a single newborn gerbil with a survival chance of less than 2/3 that of young in an average brood should be rejected by its mother: $N^* = 0.66$, see above),
5. the physiological costs of rearing as a function of brood size, e.g. milk production for single young may be difficult in species with high average brood sizes. This may be why feral house mice, *Mus musculus*, raised only 27% of broods with 1 young, although their N^* calculated by equation (4) was about 0.8 (data from B. KÖNIG, pers. comm.), i.e. they should have raised all broods,
6. the energy a mother gains by "recycling" its young, either through intra-uterine or post partum cannibalism.

Some of these variables might be accounted for in a somewhat modified, more specific version of this approach (e.g. see 4., above), but at the cost of generality. Others may be hard to convert into interbirth interval and brood size measures and a more complex model would therefore be required.

There are cases, however, in which the above variables (1.—6.) may not be very important to a parent's filial cannibalism decision. These include many fish species, especially those with male care. Brood caring males of sticklebacks (*Gasterosteus aculeatus*, VAN DEN ASSEM 1967), bluegill sunfish (*Lepomis macrochirus*, DOMINEY & BLUMER, in press) and a Mediterranean wrasse (*Symphodus ocellatus*, own data) cannibalize or abandon complete clutches if they receive only a small number of eggs. This presumably reduces their "interclutch interval": the males start to attract females anew and may, on average, obtain a larger number of eggs in a shorter time. Blue gourami males (*Trichogaster trichopterus*, e.g. KRAMER & LILEY 1971; KRAMER 1973) also tend to cannibalize small clutches but readily care for large ones. It would also be interesting to examine female livebearers (Poeciliidae), some of which absorb embryos in their ovaries. Only environmental stress and embryonic death have been suggested as reasons for this (SCHULTZ 1961; HESTER 1964; MEFFE & VRIJENHOEK 1981). There are no quantitative fish data available to my knowledge for calculating the optimal decision of a parent with an unusually small clutch. Nevertheless, I suggest fish would be very appropriate for studying this question.

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