A COMPARISON OF BETWEEN AND WITHIN SPECIES REPRODUCTIVE AND TOTAL LIFE CYCLE EFFICIENCIES

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SUMMARY

The agreement between the genetic logregression slopes, estimated from selection experiments, for intake rates or litter weaning mass on body mass and between species estimates gives confidence that these estimates may be generally applicable to most mammalian species. Main components of fitness do not show such agreement and may show or induce an intermediate optimum for body mass within populations. Evidence is presented and the conditions specified for the constancy of reproductive and growth feed conversions over species. The genetic logregression slopes for intake rates (MJ/d) may, at present, probably be regarded as constant at either 0.7 or 0.8, while periods of lactation or growth may be modifiable under managerial or nutritional improvement. This may allow a short-circuiting of the constancy of feed conversion for animals of different body sizes, as such constancy depends on longer duration of developmental times for larger animals.

INTRODUCTION

The allometric or power function \( y = ax^b \) (1) has been widely used in biology for comparison between species. According to Lande (1979), Huxley (1932) noted a frequent close correspondence between individual and interspecific allometries, which he felt would be equivalent when natural selection acted only on general body size. From a comparison of genetic logregression coefficients from a mouse selection experiment to between species logregression coefficients Lande (1979) concluded, for example, that the differentiation of brain and body sizes in closely related mammalian forms resulted either from directional selection mostly on body size with changes in brain size largely a genetically correlated response, or from random genetic drift. It is the purpose of this paper to show that a similar conclusion can be sustained for some reproduction and production traits in mammals.

MATERIALS AND METHODS

Intake and reproduction data for 8 species were obtained from the literature together with sheep and rat data from our Institute. The 10 species consisted of two voles, two mice, two rats, rabbits, pigs, sheep and cattle; the last being data from heifers for purpose of comparison with other species where pregnancy and lactation do not normally coincide. In most species mother body mass at weaning of offspring was available and used in calculations. The slope and logintercept of equation (1) was calculated by ordinary regression procedures.

The mouse selection experiment data used in this analysis are from Eisen and Durrant (1980 a,b), Hörstgen-Schwark et al. (1984 a,b) and Eisen et al. (1984), and consisted of evaluations of the line selected for 6 wk body mass (\( W^+ \)) and the control line (K). The logregression slope (b) was estimated unbiasedly by \( (\ln \bar{y}_1 - \ln \bar{y}_2)/(\ln \bar{x}_1 - \ln \bar{x}_2) \) where \( y_1 \) and \( y_2 \) are the arithmetic scale means of a given trait for lines \( W^+ \) and \( K \) respectively and \( x_1 \) and \( x_2 \) are the means of two lines for maternal body mass at weaning of offspring. An estimate of \( a \) was obtained from \( \exp (\ln \bar{y} - b \ln \bar{x}) \). Estimates of \( a \) and \( b \) for the reproduction traits are given in Table 1. Where a trait was evaluated in more
than one source a least variance combined estimate is given; intercepts were calculated from Eisen and Durrant (1980 a,b). It was judged that the mice received a diet of metabolizable energy (ME) concentration of 13.6 MJ/kg feed.

RESULTS

TABLE 1: Estimates from a mouse selection experiment for 6 wk body mass, of genetic log regression slopes (b) and of intercepts (y=a;x=1); for reproduction traits regressed on maternal body mass (kg) at weaning, compared to similar between species estimates (n=10).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Unit</th>
<th>Selection experiment</th>
<th>Between species analyses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Maternal 6 wk body mass</td>
<td>kg</td>
<td>0.61</td>
<td>0.96</td>
</tr>
<tr>
<td>Intake during gestation (ME)</td>
<td>MJ/d</td>
<td>0.79</td>
<td>0.67</td>
</tr>
<tr>
<td>Intake during lactation (ME)</td>
<td>MJ/d</td>
<td>2.78</td>
<td>0.71</td>
</tr>
<tr>
<td>Intake from conception to weaning (ME)</td>
<td>MJ/d</td>
<td>1.78</td>
<td>0.70</td>
</tr>
<tr>
<td>Intake 1-12 days of lactation (ME)</td>
<td>MJ/d</td>
<td>1.69</td>
<td>0.61</td>
</tr>
<tr>
<td>Intake 13-21 days of lactation (ME)</td>
<td>MJ/d</td>
<td>4.52</td>
<td>0.81</td>
</tr>
<tr>
<td>Litter birth mass</td>
<td>kg</td>
<td>0.28</td>
<td>0.79</td>
</tr>
<tr>
<td>Litter weaning mass</td>
<td>kg</td>
<td>3.02</td>
<td>0.91</td>
</tr>
<tr>
<td>Individual weaning mass</td>
<td>kg</td>
<td>0.09</td>
<td>0.60</td>
</tr>
<tr>
<td>Number offspring born</td>
<td>no</td>
<td>67.04</td>
<td>0.52</td>
</tr>
<tr>
<td>Number offspring weaned</td>
<td>no</td>
<td>40.33</td>
<td>0.38</td>
</tr>
<tr>
<td>Interval from exposure to parturition</td>
<td>d</td>
<td>42.86</td>
<td>0.21</td>
</tr>
<tr>
<td>Duration of pregnancy</td>
<td>d</td>
<td>19</td>
<td>0</td>
</tr>
<tr>
<td>Duration of lactation</td>
<td>d</td>
<td>21</td>
<td>0</td>
</tr>
<tr>
<td>Duration of pregnancy+lactation</td>
<td>d</td>
<td>40</td>
<td>0</td>
</tr>
<tr>
<td>No of litters</td>
<td>no/yr</td>
<td>Calder (1984)</td>
<td>1.59</td>
</tr>
</tbody>
</table>

Conclusions from a comparison between the two sets of estimates in Table 1

1. The slopes of the litter mass and intake rate traits agree remarkably well between the mouse experiment and between species; the difference is often of the same magnitude as the standard errors of the estimates.

2. The slopes of individual offspring body masses and the fitness traits (numbers born and weaned) of the mouse selection experiment do not agree with the between species slopes.

Conclusions from the between species analyses in Table 1

1. The total ME intake from conception to weaning per kg litter weaned is nearly constant over species:

\[ 1.04 M^{0.68}_0 \times 74.63 M^{-0.23}_0 / 1.06 M^{0.88}_0 = 73 M^{0.03}_0 \text{ MJ/kg} \] (2).

2. The total ME intake during lactation per kg litter weaned is a constant for the species under consideration:

\[ 1.41 M^{0.68}_0 \times 32.61 M^{-0.20}_0 / 1.06 M^{0.88}_0 = 43 \text{ MJ/kg} \] (3).

Preliminary conclusion from the mouse selection experiment

Selection for body mass had, as a correlated response, an advantage in reproductive feed conversion for heavier mice; total feed intake (ME) from conception to weaning per kg litter weaned; 40 x 1.76 M^{0.70}_0 / 3.02 M^{0.91}_0 = 24 M^{-0.21}_0 \text{ MJ/kg}(4). Although the mouse experiment and the between species analysis gave similar slopes for intake rates, this result (eq. 4) is in contrast to the situation between species(2) and follows from the apparent canalization of gestation time within species as well as the constancy of lactation duration imposed by
The effect of prolonged selection for body mass on reproduction in terms of Fisher's fundamental theorem

Roberts (1961) evaluated lifetime reproduction in mice selected for body mass and measured early productivity for the different lines by the masses of total number of offspring weaned by 183d after first joining. These body masses have been used, together with the assumptions of constant % mortality per litter per parity and constant body mass per offspring through all parities, to construct Table 2 from Roberts' graphs and figures. These assumptions on mortality and body mass appear reasonable from Table 12 of Nagai et al. (1980). Estimates of genetic logregression slopes are also given for each trait regressed on 6 wk male body mass.

TABLE 2: Data and estimates of logregression slopes of averages of reproduction traits regressed on 6 wk male body mass.

<table>
<thead>
<tr>
<th>Lines</th>
<th>6 wk male body mass (g)</th>
<th>No weaned per litter</th>
<th>No litters till 183d</th>
<th>No offspring weaned till 183d</th>
<th>Mass of offspring till 183d (g)</th>
<th>Litter Total mass till 183d (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NF (up)</td>
<td>33.4</td>
<td>4.29</td>
<td>3.65</td>
<td>15.7</td>
<td>9.39</td>
<td>40.3</td>
</tr>
<tr>
<td>NC (control)</td>
<td>24.2</td>
<td>4.80</td>
<td>4.64</td>
<td>22.3</td>
<td>8.93</td>
<td>42.9</td>
</tr>
<tr>
<td>NS (down)</td>
<td>15.4</td>
<td>3.77</td>
<td>4.24</td>
<td>16.0</td>
<td>7.08</td>
<td>26.7</td>
</tr>
<tr>
<td>Slope up selection</td>
<td>-0.35</td>
<td>-0.74</td>
<td>-1.10</td>
<td>0.16</td>
<td>-0.19</td>
<td>-0.94</td>
</tr>
<tr>
<td>Slope down selection</td>
<td>0.53</td>
<td>0.20</td>
<td>0.73</td>
<td>0.51</td>
<td>1.05</td>
<td>1.25</td>
</tr>
<tr>
<td>Slope combined</td>
<td>0.19</td>
<td>-0.17</td>
<td>0.02</td>
<td>0.37</td>
<td>0.57</td>
<td>0.40</td>
</tr>
</tbody>
</table>

For the purpose of comparison with Table 1, consider a system of management associated with early accurate testing of pregnancy so that non-pregnant females can be replaced without appreciable loss. Then, to a first approximation reproductive feed conversion, estimated from the slope calculated from the up-selection and control lines, would be proportional to total amount of food eaten by the mother/biomass produced at weaning, or $M^{0.70} / M^{0.19} = M^{0.89}$ (5). Note that in contrast to equation (4) the positive exponent (0.89) indicates an advantage to smaller mice. Hence, the conclusion would be either to stop or to reverse selection for body mass. Reproductive feed conversion estimated for the down selection line versus the control would be proportional to $M^{0.70} / M^{0.05} = M^{0.35}$ (6). Indicating, like equation (4), an advantage to larger mice. An indication for an intermediate optimum in body mass for reproductive efficiency therefore emerges; above the control population the indication is that smaller mice would be more efficient and below that larger mice would be more efficient. It is evident that the same conclusion would follow if reproduction till 183d after joining was considered.

Laboratory rats and mice are probably mostly allowed to complete about 4 parities before being discarded as reproduction rate often starts to decline drastically afterwards. Furthermore, from conception to weaning is the most hazardous period by far in the early lifecycle of mammals. Hence, the number of offspring weaned to about 183d after first joining of males and females is a first approximation to fitness in laboratory mice and rats. In practical terms Fisher's fundamental theorem as formulated by Ginzburg (1983) says that natural selection will cause population mean fitness to increase almost all the time until either a maximum or equilibrium point is reached. Hence, one would expect that artificial selection for almost any trait would cause an
eventual decline in fitness, since inevitably gene frequencies would eventually be moved away from the equilibrium or maximum point.

The applicability of the above remarks becomes clear from an examination of the trait, number of offspring weaned till 183d, in Table 2. Here the control population weaned more offspring than both the up and down selected lines and probably is near to a local point of maximum fitness for the N-lines. This can also be deduced from the change of sign from the up to the down selection slopes and the near zero combined slope. To clarify the situation for the other traits in Table 2, the genetic relationships between fitness and its components derived by Robertson (1955) could be considered.

That the results on intermediate optima in body mass deduced from Roberts (1961) are not an isolated instance, is shown by figures in Table 3 obtained from Nagai et al. (1984), with \( \text{Up} \) and \( \text{Uq} \) indicating the body mass plus lines and \( \text{ Cp} \) and \( \text{Cq} \) the control lines, from the P and Q stocks respectively.

**TABLE 3**: Reproduction traits of the P and Q lines.

<table>
<thead>
<tr>
<th></th>
<th>\text{Up}</th>
<th>\text{Cp}</th>
<th>\text{Uq}</th>
<th>\text{Cq}</th>
</tr>
</thead>
<tbody>
<tr>
<td>No of litters till 155d of cohabiting</td>
<td>4,13</td>
<td>5,00</td>
<td>3,50</td>
<td>4,60</td>
</tr>
<tr>
<td>Average no weaned per litter</td>
<td>7,53</td>
<td>7,28</td>
<td>9,40</td>
<td>9,83</td>
</tr>
<tr>
<td>No offspring weaned after 155d of cohabiting</td>
<td>31,5</td>
<td>36,4</td>
<td>32,9</td>
<td>45,2</td>
</tr>
<tr>
<td>Average litter mass (g)</td>
<td>84,00</td>
<td>70,11</td>
<td>95,32</td>
<td>102,82</td>
</tr>
<tr>
<td>Total mass weaned after 155d of cohabiting</td>
<td>346,9</td>
<td>350,5</td>
<td>333,5</td>
<td>472,6</td>
</tr>
</tbody>
</table>

The conclusion from Table 3 seems clear: \( \text{Uq} \) is above the optimum body mass for maximal reproduction in the Q-line, while \( \text{Up} \) is below the optimal body mass for the P-line in number of offspring per litter, and above it for number of offspring weaned after 155d of cohabiting.

In the situation of selection experiments with mice Falconer (1973) argued that number of offspring at weaning per first mating (defined as productivity) is the first approximation to fitness. Falconer found that for the first 5 generations the Large lines gained a small initial advantage in productivity over the Controls, but definitely fell slightly below the Controls by the 10th generation and ended the experiment by the 23rd generation with 6,5 offspring/mating vs 7,4 for the Controls. The productivity of the Small lines dropped more rapidly and continuously to a final level of 4,4 offspring/mating.

Ginzburg (1983) points out that exceptions to the general increase in fitness predicted from Fisher's fundamental theorem, occur when the effects of linkage and genic selective advantage are of the same order of magnitude near equilibrium points. This could explain the difference between Table 1 and Tables 2 and 3, as well as the initial advantage in productivity (fitness) of Falconer's (1973) Large lines over the Controls.

The genetic regression between feed intake and body mass during growth and non-reproductive maturity.

The method associated with the mouse selection experiment of Table 1, was employed to estimate the genetic relationship of ME intake rate (MJ/d) to end of test period body mass during active growth, from rat and mouse selection experiments for the traits: end of test period body mass or body mass gain to end of test. The values of the exponents tended to cluster around two values,
independent of selection for gain or body mass, species or experimental procedure:

\[
\text{Intake (MJ/d)} = 1.47M^{0.81} + 0.012 \quad (7)
\]

\[
\text{Intake (MJ/d)} = 0.98M^{0.69} + 0.012 \quad (8)
\]

with \( M \) equal to body mass, kg.

For purpose of comparison, both intercepts were calculated from Hörstgen-Schwark et al. (1984a).

It is of interest to note that the high slope corresponds in magnitude to the intake slope during peak lactation (13–21d) in the mouse experiment of Table 1. It may, therefore, be associated with some sort of physiological maximum. The second estimate is in line with: \( \text{Intake (MJ/d)} = 0.98M^{0.70} + 0.013 \quad (9) \) for mature mammals from Farlow (1976).

**GENERAL DISCUSSION**

Calder (1984) gives evidence that mammalian developmental times are proportional to \( M^{0.29} + 0.08 \). Hence, from eqs. (8,9) growth feed conversion, defined as total feed ingested per unit body mass, must at physiologically equivalent ages be proportional to \( M^{0.70}M^{0.29} = M^{-0.01} \) \( (10) \); i.e. it must be approximately constant over species. In contrast to this the 3-6 wk feed conversion for mice is equal to \( 21 \times 0.98M^{0.68}/M = 20.6M^{-0.31} \) MJ/kg \( (11) \), giving a distinct advantage to larger mice.

Note that the intercept for intake from conception to weaning in Table 1 do not differ much, for the between species analysis, from the intercepts valid during growth and maturity, eqs. (8,9). It follows that intake per year can be estimated by \( 365 \times 1.04M^{0.68} \) MJ regardless of life phase. An estimate of the number of offspring per year, from Table 1, is \( 1.59M^{0.19} = 4.39M^{-0.11} \). Hence, it follows that intake per kg mother per offspring is equal to \( 365 \times 1.04M^{0.68} \times M^{-1.68} = 54M^{-0.02} \) MJ/kg/offspring \( (12) \). Together with equations (2) and (3) this is an expression of the proposition that, over species, reproductive feed conversion is constant.

By the arguments employed to establish the local maxima associated with Table 2, number of offspring at weaning must be proportional to \( M^{0.7} \) at the point of maximum fitness of a population. Hence, total life cycle feed conversion for a given population at maximum fitness will be proportional to \( M^{0.7}/M^{0.7} = M^{0.3} \) \( (13) \) in agreement to the growth feed conversion of \( (11) \). The indefinite validity of constant period testing must, however, be in doubt. From Table 1 intake from mating exposure to parturition can be estimated by \( (0.79M^{0.67}) \) \( (42.86M^{0.21}) = 33.86M^{0.88} \) MJ \( (14) \). Furthermore, any prolongation of suckling of the young would be an extension of the period 13-21d in Table 1. Assume that this is proportional to \( M^{0.20} \), the between species exponent. Then the dominating term for lactational intake would become proportional to \( M^{0.81}M^{0.20} = M^{1.00} \), which could easily average with 33.86 \( M^{0.88} \) to near \( M^{0.91} \) for litter weaning mass. As a consequence the fixed period feed conversion would become inapplicable after considerable progress in body mass.

On the other hand, it has been shown that an intermediate optimum for body mass for reproductive fitness can be expected, if not initially, then amplified or induced by selection for body mass according to the pattern suggested by Robertson (1955). Experimental evidence is presented indicating that this may eventually be severe enough by itself to cancel any initial constant period advantage in reproductive feed conversion. Hence, the advantage of larger animals, obtained by selection for body mass or gain, in growth feed conversion for constant time period or constant body mass intervals, may generally not
hold for reproduction or lactation feed conversion, in natural production systems. A system of early weaning, feasible in pigs, for example, may again tilt the balance in favour of larger animals, since the high energetic cost of lactation is circumvented. However, if veterinary and management costs are taken into consideration, the advantage of intermediate body masses may again become apparent from the increased importance attached to number of piglets per mating weaned alive, in Tess et al. (1983). For the final conclusions in a nutshell, see the Summary.

REFERENCES


