

litter size should be a criterion for classification of neonate development.

Classifying species as altricial versus precocial based on differences in litter size introduces a serious confounding effect not discussed by Martin and MacLarnon¹. In particular, we note that fetal growth parameters for precocial taxa are essentially standardized for constant litter size as most of these taxa have only one young per litter (by Martin and MacLarnon's definition). By contrast, we find a great variability in litter size among altricial species (again, using their definition). That litter size is inversely correlated with adult body size among mammalian species⁶⁻⁸ confounds Martin and MacLarnon's analysis of how fetal growth relative to body size differs between altricial and precocial species. A larger litter size results in each individual offspring obtaining a relatively smaller fraction of the mother's total parental investment at birth⁹. Growth rates of such offspring might be comparatively high simply to increase survivorship.

If a more rigorous consideration of neonatal status is used²⁻⁴, the discreteness of altricial and precocial taxa is not as great as suggested by Fig. 1 of ref. 1. Related to this, we find the legend to Fig. 2 inappropriate because it is not obvious that an "overall best-fit line of fixed slope 0.1" essentially constitutes a linear discriminant function between the 'altricial' and 'precocial' taxa. Their discriminant function with a 0.1 slope is as effective with a slope of 0; there are about five misclassified points using either slope. This suggests that Martin and MacLarnon's altricial and precocial categories are more explicitly defined as groups of short versus long gestation period. Realization of this leads us to question seriously the relevance of Martin and MacLarnon's use of this 0.1 slope as an allometric coefficient, as in their equations (6) and (8)¹, since it has no biological basis.

Allometric pattern is often presumed to reflect physiological constraints to life history alternatives. Although we recognize that such constraints certainly exist, we caution that sampling bias might be present because the representation of mammals of various body sizes is seldom independent of environmental variation. Large mammal species are most numerous in regions of pronounced seasonality¹⁰. We suggest that natural selection may favour rapid growth rates in highly seasonal environments to ensure that the young attain adequate size during the limited growth season to enhance survival through the oncoming winter or seasonal drought. This implies that environmental seasonality selects for a suite of life-history attributes which increase survival during periods of resource shortage, but which capitalize on abundant resources during the growth season^{11,12}. Such a sampling bias may well account for the positive

correlation between "fetal growth factor" and body mass as described by Martin and MacLarnon¹.

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MARTIN AND MACLARNON REPLY—
The points raised by Zeveloff and Boyce indicate the need for further clarification of issues raised by our paper¹, and we are glad of the opportunity to comply.

There is, indeed, potential confusion surrounding the definition of 'maternal investment'. In our paper, we implicitly used this term in relation to the mother's investment per unit time in the growth of an individual fetus. In order to convert this to total investment per unit time during pregnancy, it would, of course, be necessary to multiply each fetal growth factor by litter size for the species. Thus, the distinction between altricial and precocial mammals in this respect is far more marked than indicated in our Fig. 3. However, we recognize that maternal investment could be defined as total investment in individual neonates, regardless of the time over which the investment is spread. By such a definition, mothers clearly invest more in precocial neonates than in altricial neonates. We would defend our definition on the grounds that it relates to the mother's division of her total resources (which are heavily influenced by her body size) between reproduction and other functions during pregnancy. Clearly, accurate calculation of total maternal investment by any definition would require data on lifetime reproductive performance.

The double criterion that we used to define altricial as opposed to precocial mammals (combining time of eye opening and litter size) was a quantitative translation of two features originally emphasized by Portmann² in his pioneering studies separating 'Nesthocker' from 'Nestfluchter' in both birds and mammals. While we accept that some gradation exists (and, in fact, we allowed for it in our paper—

intermediates), the important point is that a clear bimodal distribution among mammals emerges when gestation period is considered in relation to body size, closely matching the distinction between altricial and precocial categories. Incidentally, although human infants are often described as 'altricial', they are precocial both by Portmann's definition and by ours. It has been shown that the relative helplessness of the human neonate is a special condition, unique among mammals, related to an unusual pattern of postnatal brain development^{3,4}.

The fixed slope value of 0.1 used to derive the histogram in our Fig. 2 was initially determined by the average empirical value for major mammalian groups with a single neonate type (our Table 1). The iterative technique reported was used as an additional approach, primarily to investigate the distributions of residuals generated with different slope values. As Zeveloff and Boyce point out, altricial and precocial mammals (as defined by us) are to a large extent separated by gestation period even without taking maternal body size into account (that is, slope value of 0). This, surely, is one of the most convincing indications that there is an underlying split between altricial and precocial mammals. The histogram of residuals in fact becomes trimodal when a slope value of 0 is used for all gestation periods, as certain large-bodied altricial mammals (for example, some carnivores) overlap with certain small-bodied precocial mammals (for example, some primates, and some hysticomorph rodents). This overlap is largely eliminated when a slope value of 0.1 is used, and an order-by-order analysis of residuals (unpublished) shows that the resulting pattern is entirely in accord with Portmann's interpretation of the altricial/precocial division.

As Zeveloff and Boyce themselves produce a separation of mammals into two groups that are 80% in agreement with our altricial/precocial division, despite an entirely different approach, there would seem to be an underlying biological reality in such distinctions, regardless of any disagreement about finer details. It is important that debate about the details should not obscure this fact.

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