Mammary number and litter size in Rodentia: The "one-half rule"

(Cricetidae/Muridae/Sciuridae/lactation/reproduction)

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ABSTRACT Litter size and mammary number in the mammalian order Rodentia show a significant positive correlation. Mean litter size is typically one-half the number of available mammaries, while maximum litter size approximates mammary number. Similar relationships are found in the families Muridae, Cricetidae, and Sciuridae. The relationship of litter size to mammary number is significantly different between the arboreal and terrestrial squirrels, and between the hystricomorph and nonhystricomorph rodents. Mammary number may have operated as a selective constraint on litter size over evolutionary time.

Mammals are distinguished by the ability to nurse their young. Lactation has been a crucial factor in the evolution of mammalian parental investment and reproductive strategies (1–3), and potential constraints on lactation are therefore of great interest. Studies have implicated food supply, fat storage, and metabolic rate in the control of milk production (4). Curiously, little attention has been given to a potential anatomical limit on a female's nursing ability: the number of her mammary glands.

Aristotle recognized that the number and location of mammaries vary greatly between species (5). He also suggested that species-typical litter size tends to correspond to the characteristic number of teats, a claim reasserted in modern times by Cuvier (6). While some more recent authors have alluded to a positive correlation between litter size and mammary number (7–11), others have disputed it (12). The factual basis for both claims remains much as it was in antiquity—not rigorously quantitative, and based on small numbers of species in distantly related taxa. Thus, fundamental empirical questions remain unanswered: How does the number of offspring relate to the number of mammaries? Is the proportion constant across taxa and life-forms? There also remains an evolutionary question: Does mammary number limit litter size?

With their wide range of mammary number (from 2 to 14) and litter size (means from 1 to 8), the rodents (mammalian order Rodentia) are well-suited to such a study. From the literature, I collected litter size and mammary number data on 266 species representing 123 genera and 26 families. Primary sources were used whenever possible. The most frequently referenced journals were the *Journal of Mammalogy* (160 citations), *Australian Journal of Zoology* (9 citations), *American Midland Naturalist, Journal of Zoology (London), Mammalia* (6 citations each), *Canadian Journal of Zoology, Proceedings of the Zoological Society of London* (5 citations each), and *Zeitschift für Säugetierkunde* (4 citations). Nonperiodical references were also used (e.g., refs. 13–16).

Altogether, 566 litter size estimates were used, with a range of 1–27 estimates per species. When more than one estimate was available, the mean value was used for analysis. With few exceptions, mammary number in rodents is a species-typical invariant trait. When mammary number was disputed I resolved the point by examining museum study skins. If mammary number varied intraspecifically, the species was not used.

For the total sample ($N = 266$ species), mean litter size showed a significant positive correlation with mammary number ($P < 0.001$, $r = 0.72$). This relationship is described by the linear regression equation $L = 0.39 + 0.46 M$, where L = mean litter size and M = mammary number. The result may be characterized as a "one-half rule"—rodent species have on the average one-half as many offspring as they have nipples.

The litter size to mammary number scaling can be compared between species in different taxa. Separate regression equations were calculated for those families with adequate sample size (Cricetidae, Muridae, and Sciuridae) and for a group containing all other families (Fig. 1). In each case, litter size was significantly correlated with mammary number, and the slopes approximated 0.5. However, the four family slopes were significantly different [$F(3,258) = 7.31$; $P < 0.0001$].

The three nonsciurid slopes did not differ significantly from one another [$F(2,207) = 2.49$; $P > 0.05$]. Therefore, the overall difference among the four groups was due to the squirrel family Sciuridae, which had a steeper slope than the other families (Fig. 1). A comparison of the arboreal and terrestrial squirrels reveals that they have significantly different slopes [$F(1,49) = 10.52$, $P < 0.002$]. The flatter slope of arboreal forms indicates that, relative to ground dwelling forms, fewer young are born as mammary number increases across species. It might then appear that the arboreal squirrels use less of their reproductive capacity than terrestrial forms. However, the ability to breed by postpartum and lactational estrus (an indicator of high reproductive effort) has been found only in the arboreal squirrels (17). These features of sciurid breeding biology may belie differences in reproductive strategy. Arboreal species can simultaneously nurse and gestate two litters, each of which use proportionally fewer mammaries. In contrast, terrestrial squirrels produce litters one at a time, and these litters make relatively greater use of mammary capacity. This finding adds a new dimension to previously documented differences in reproductive tactics between arboreal and terrestrial squirrels (18).

Species of the suborder Hystricomorpha have been characterized as relatively slowly breeding rodents (19). This evaluation was confirmed and extended by the present analysis. Hystricomorph species ($L = 0.98 + 0.25 M$) have a significantly flatter slope than nonhystricomorphs [$L = 0.34 + 0.47 M$, $F(1,262) = 7.38$, $P < 0.01$]—i.e., they have fewer additional pups for each interspecific increase in mammary number.

It has been argued recently that congeneric species should not be treated as independent data points in bivariate regression analyses (20): clusters of such points may represent

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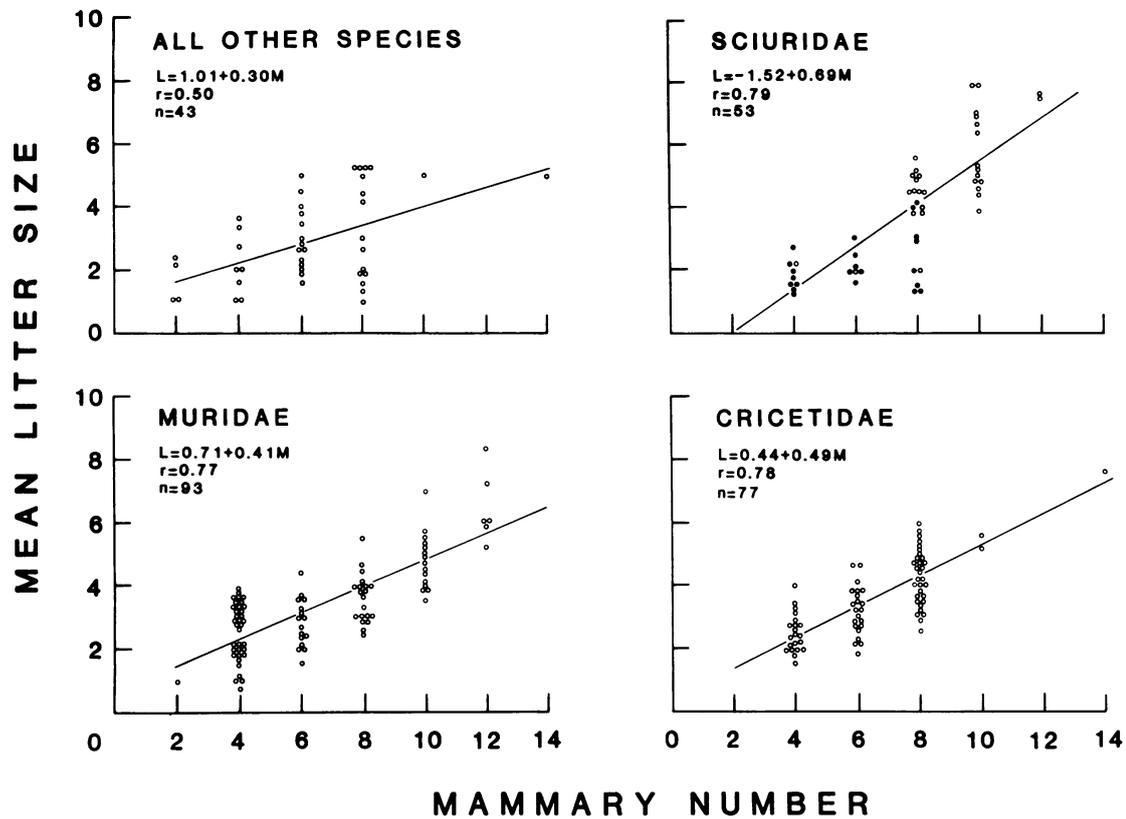*Proc. Natl. Acad. Sci. USA 83 (1986)* 4829

FIG. 1. Scatterplots of mean litter size versus mammary number for the species in the three largest rodent families, and a category containing all remaining species. Within the Sciuridae, the regression equation for the arboreal squirrels (solid circles) was ($L = 1.09 + 0.18 M$; $r = 0.38$; $n = 22$), and for the terrestrial squirrels (open circles) it was ($L = -1.36 + 0.72 M$; $r = 0.73$; $n = 31$).

common ancestry more than common selective pressures and therefore may distort the analysis. This possibility may be avoided by using generic data points (the mean value of the species within each genus), although this risks possible bias from overvaluing monotypic genera. Nevertheless, all analyses presented here were repeated with generic data. The results were substantially similar.

Given the reliable empirical relation between these variables, it is possible to ask: Does mammary number limit a female's nursing ability and therefore act as a constraint on litter size? The answer depends on which of two distinct senses of limit is meant—a contemporary limit or a limit over evolutionary time.

In a contemporary sense, the more mammaries a female has, the greater the number of pups she can nurse simultaneously. Pup rotation during nursing has been reported (21–23) implying that females can nurse litters more numerous than their mammaries. However, many observers report sharply increased pup mortality when litter size exceeds mammary number (22, 24–28). Thus, mammary number may be among the contemporary factors operating on rodent litter size, but its role is not well understood.

Mammary number may limit litter size in an evolutionary sense. This can be assessed by analyzing maximum litter size. An offspring/mammary ratio (OMR) was calculated by using maximum litter size. This maximum OMR (mean ± SEM) was 0.92 ± 0.02 ($n = 247$)—i.e., maximum litter size was nearly equal to nipple number. In comparison, a similar ratio calculated from mean litter size was 0.53 ± 0.01 ($n = 266$), a reflection of the one-half rule. The one-half rule can be interpreted as a statistical consequence of the frequency distribution of litter sizes. These distributions typically have a lower boundary of one and an upper boundary equal to the mammary number. Because the modal litter size of most

species is an intermediate value, the result is that mean litter size falls halfway between one and the mammary number.

One interpretation of these results is that natural selection has favored mammary numbers adequate for the occasional extreme rather than the more frequent typical litter size. Over evolutionary time, therefore, mammary number may be an important factor in the evolution of litter size. This inference is supported by two lines of evidence. Selective breeding experiments with mice show that litter size can be substantially increased within a few generations (29). However, an attempt to breed for supernumerary mammaries in sheep encountered only limited success (30, 31). Based on these sets of data, the additive genetic variance appears to be less for mammary number than for litter size. Thus, in an evolutionary sense it is more likely that mammary number constrains litter size rather than vice versa.

The possible adaptive significance of interspecific variation in mammalian litter size is a question of long-standing interest to evolutionary theorists. Covariates of litter size such as latitude (18, 32), length of breeding season (18), and body size (3, 33) have been examined by many investigators. Mammary number has not previously been linked to quantitative differences in parental investment—earlier research on the evolutionary implications of variation in mammary number (34, 35) was primarily concerned with questions of phylogeny. Whatever the causal direction of the correlations reported here, it has now been established that mammary number is a significant covariate of rodent litter size and a factor that deserves further attention in quantitative studies of female reproductive strategies.

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