

# Female brain size and parental care in carnivores

(mammal)

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Communicated by George C. Williams, February 24, 1994 (received for review October 12, 1993)

**ABSTRACT** Comparative studies indicate that species differences in mammalian brain size relate to body size, ecology, and life-history traits. Previous analyses failed to show intra-sexual or behavioral patterns of brain size in mammals. Across the terrestrial Carnivora, I find to the contrary. Differences in female, but not male, brain size associate with a fundamental ecological and evolutionary characteristic of female behavior. Other factors equal, females that provide the sole parental care have larger brains than those of biparental or communal species. For females, more parental investment accompanies larger brains. Future comparative studies of mammalian brain size must recognize that some patterns arise independently in the two sexes.

Among mammal species, brain weight reflects differences in body size, ecology, and life histories (1). Body size might be either a causal or constraining allometric variable of brain weight (2, 3). After removing the effects of body weight, brain weight is greater in dietary specialists across bats (4), rodents (5), and primates (6). Protracted gestation length coupled with small litter sizes is associated with large neonatal brain size, which in turn correlates with adult brain size (7). Two factors have eluded and confounded comparative study despite such consistent patterns across diverse taxa. First, patterns of variation need not be the same in males and females. Second, despite considerable effort to find behavioral correlates of brain size (1), no variables have emerged that are independent of phylogeny. By recognizing these factors, I show that relative female brain size is larger in species with strictly maternal care than in biparental or communal taxa. This finding is independent of allometry, ecology, neonatal development, phylogeny, and covariation of male brain size.

The terrestrial Carnivora exhibit three general forms of female parental care. (i) The majority of carnivore species, as in most other mammalian taxa, display solitary female parental care independent of a male or other adult helpers (8, 9). As exemplified by raccoons and all species of ursids (10, 11) and small felids (12, 13), a solitary female locates or builds a natal den site, nurses and grooms young, defends the young from potential threats, procures solid food after lactation, facilitates the development of food preferences and/or acquisition, and influences patterns and areas of dispersal. Further, given the amount of time necessary for young to reach age at independence in relation to female life-span, a single adult female typically spends 80% of her life attending young (14, 15). (ii) In biparental systems, as shown in many canids (16–19) and the brown hyena (20), mothers give similar care as in the solitary system, but assistance is provided by an attendant male who will feed, guard, and retrieve young as much as, and sometimes more than, the mother. (iii) In communal systems, such as observed in grey wolves (16, 17, 19), coatis (21), dwarf mongooses (22), spotted hyenas (23–

26) and African lions (27), a mother is assisted by multiple males and/or females. Communal duties include similar parental behaviors as shown in biparental systems, except that communal nursing is an added feature occasionally shown in some species. A crucial difference is that in both biparental and communal species, parental care by an adult other than the mother confers significant reduction in time and energy of maternal feeding, guarding, and den attendance (28–30). Of the three parental systems in carnivores, single female care reflects the most intensive behavioral and energetic demands.

Thus, assuming that brain size is associated with increased information processing (1, 4–6, 31), it is predicted that females of species that care for young exclusively on their own will have larger brains relative to their body weight than those in biparental or communal systems. Since other comparative studies of mammals indicate that dietary specialists have larger brains, dietary categories (meat-eating; omnivory; frugivory; insectivory) are examined across the Carnivora. Further, to allow for any possible effect of life histories on female brain size, particularly those that index precociality/altriciality in mammals (32), correlates of gestation length and the age at which eyes first open in neonates are also analyzed.

## METHODS

Brain-size measurements are from braincase volumes of adult females in 71 carnivore species and are presented elsewhere (14, 33, 51). Data on body weight, diet, and life histories are those of Gittleman (34–36); the data were logarithmically transformed before analysis. By use of information in the literature, each species was classified according to the above definitions of parental care (see the legend to Fig. 1). Autocorrelation and Moran's *I* statistics were used, respectively, for estimating (i) whether and (ii) at what taxonomic level cross-taxonomic variation in brain size is related to phylogenetic distance (37, 38). Many statistical methods are available for incorporating and/or removing phylogenetic pattern in comparative tests (37, 38). For continuous traits, two methods in particular are appropriate though different in statistical properties and assumptions concerning rates of trait evolution. The "phylogenetic autocorrelation" method assumes an autoregressive process whereby trait variation is correlated with phylogeny, and this correlation declines with phylogenetic distance (37–39). The "independent comparisons" method assumes a specific model of trait evolution by calculating expected contrast values in accord with phylogenetic distance (40, 41). Both methods are used in the present analysis as a conservative approach to presumed inaccuracy of phylogenetic information (42) and uncertainty of a model of trait evolution (39). A least-squares (model 1) regression is used to describe allometric relations. Even though this model is inappropriate with error variance in the *x* variable, it is acceptable in the present study because estimates of slope do not effect

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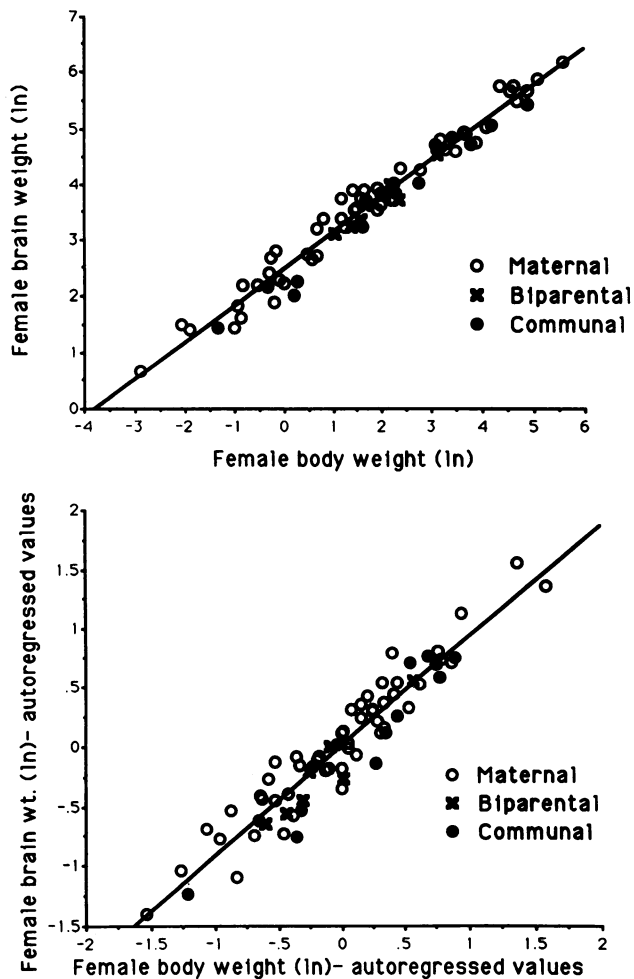


FIG. 1. Female brain weight regressed on female body weight (wt.) among different modes of parental care across the terrestrial Carnivora. Bivariate plots include original species data (Upper) and autoregressed data (Lower) that are statistically independent from phylogenetic correlation. Species classification of parental care are as follows. **Solitary female:** *Urocyon cinereoargenteus*, *Ursus arctos*, *Ursus americanus*, *Thalarchos maritimus*, *Selenarctos thibetanus*, *Melurus ursinus*, *Bassariscus astutus*, *Potos flavus*, *Procyon lotor*, *Ailurus fulgens*, *Ailuropoda melanoleuca*, *Mustela erminea*, *Mustela nivalis*, *Mustela rixosa*, *Mustela frenata*, *Mustela altaica*, *Mustela sibirica*, *Mustela lutreola*, *Mustela vison*, *Mustela putorius*, *Mustela nigripes*, *Martes americana*, *Martes pennanti*, *Gulo gulo*, *Tayra barbara*, *Taxidea taxus*, *Mephitis mephitis*, *Spilogale putorius*, *Lutra lutra*, *Lutra canadensis*, *Enhydra lutra*, *Genetta genetta*, *Arctitis binturong*, *Herpestes pulverulentus*, *Ichneumia albicauda*, *Atilax paludinosus*, *Paracynictis selousi*, *Hyaena hyaena*, *Proteles cristatus*, *Felis silvestris*, *Felis serval*, *Caracal caracal*, *Puma concolor*, *Lynx lynx*, *Lynx rufus*, *Panthera tigris*, *Panthera pardus*, *Panthera onca*, *Panthera uncia*, *Acinonyx jubatus*; **Biparental:** *Canis aureus*, *Canis adustus*, *Alopex lagopus*, *Vulpes vulpes*, *Nyctereutes procyonoides*, *Otocyon megalotis*, *Chrysocyon brachyurus*; **Communal:** *Canis lupus*, *Canis latrans*, *Canis mesomelas*, *Lycaon pictus*, *Cuon alpinus*, *Nasua narica*, *Meles meles*, *Mungos mungo*, *Crossarchus obscurus*, *Helogale parvula*, *Suricata suricatta*, *Hyaena brunnea*, *Crocuta crocuta*, *Panthera leo*.

comparative results with coefficients of determination about 0.90 (40).

## RESULTS

As with other studies, I find that continuous morphological traits tend to be conserved within phylogenetic lineages; an autocorrelation coefficient (37) reveals significant phylogenetic correlation at the 0.01 level ( $n = 71$ ) for all of the

following traits: female brain weight,  $r^2 = 0.63$ ; female body weight,  $r^2 = 0.49$ ; gestation length,  $r^2 = 0.65$ . Across taxonomic ranks, observed phylogenetic relations of brain weight are specifically due to correlation among species within genera ( $z$  values of Moran's  $I = 6.42$ ) and among genera within families ( $z = 5.37$ ), as expected with greater phenotypic similarity usually observed in more related taxa. These diagnostic statistics therefore indicate that it is necessary to apply the above-mentioned comparative methods for hypothesis testing.

Female brain weight increases significantly with increasing female body weight for absolute species data ( $y = 2.47x^{0.65}$ ,  $r^2 = 0.97$ ;  $n = 71$ ), autoregressed data ( $y = 9.29x^{0.92}$ ,  $r^2 = 0.90$ ;  $n = 71$ ), and independent comparisons ( $y = -0.05x^{0.64}$ ,  $r^2 = 0.89$ ;  $n = 20$ ); all analyses are significant at the 0.001 level. I remove these allometric effects by the regression of female brain size on female body weight and then use the residuals for the following comparative tests.

As predicted, carnivore species in which females exclusively take care of their young have larger relative brain sizes than females of species with either biparental or communal care [species data are  $F(2,68) = 5.20$ ,  $P < 0.008$ ; autoregressed data are  $F(2,68) = 6.72$ ,  $P < 0.002$ ; see also Fig. 1]. Mean deviations from a common slope (using autoregressed values) across the order show that exclusively maternal species have the highest elevation (0.28) followed by biparental ( $-0.52$ ) and communal ( $-0.60$ ) species. Pairwise comparisons reveal significant differences in deviation between the maternal and biparental species [ $t(28) = 2.21$ ,  $P < 0.05$ ] and maternal and communal species [ $t(32) = 3.25$ ,  $P < 0.01$ ]. Differences in relative female brain size are not observed among dietary categories across carnivores ( $F(3,61) = 2.06$ , not significant), nor do the relative life histories of gestation length ( $r^2 = 0.05$ ) or the days on which eyes first open in young ( $r^2 = 0.04$ ) correlate.

To employ the independent comparisons method, I coded types of parental care into numerical categories and examined their correlations with female brain size while controlling for body size (40, 41); the correlation coefficient is significant ( $r^2 = 0.28$ ,  $n = 20$ ;  $P < 0.05$ ).

## DISCUSSION

These results show that across the Carnivora, relative female brain size, after controlling for body size and phylogeny, is larger in species in which females solely provide parental care than in species where females share parental duties with other females and/or males. A potential confounding factor is that relative female brain size covaries with male size (brain and/or body) independent of differences in parental care. To examine this possibility, relative female brain weight was partially correlated with the three measures that comprise relative male brain size (i.e., male brain weight, male body weight, and relative male brain size). There were no significant correlations with the autoregressed values ( $n = 67$ ; male brain weight,  $r = -0.23$ ; male body weight,  $r = 0.31$ ; relative male brain size,  $r = 0.18$ ). Furthermore, in repeating the above analyses using relative male brain size, I found that modes of parental care were not associated with variation in male brain size [ $F(2,64) = 0.13$ , not significant; see Fig. 2].

In conclusion, these comparative results show that species differences in brain size contain intrasexual patterns that involve important evolutionary functions. Just as species-specific differences in mammalian brain size are adapted to the demands of particular ecological conditions, intrasexual variation relates to fundamental reproductive parameters. Specifically, as suggested elsewhere (43, 44), an increase in relative female brain size may enhance maternal investment and associated behaviors. Conversely, failure to find correlates of parental care and relative brain size in males may

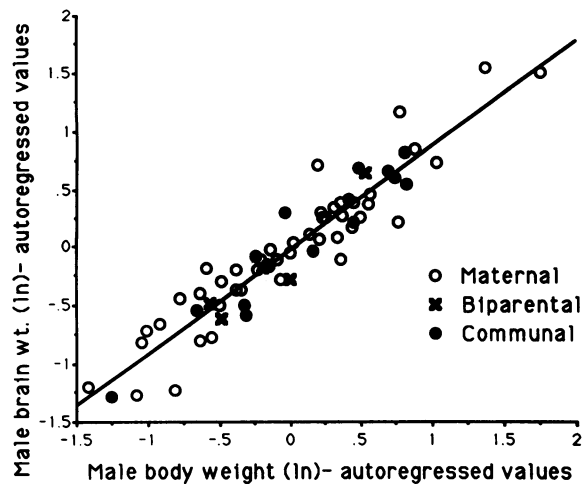


FIG. 2. Male brain weight regressed on male body weight among different modes of parental care across the terrestrial Carnivora. See text for definitions and details of analysis.

relate to the general pattern that male traits are more tied to sexual selection (45); for example, many solitary carnivore species are sexual dimorphic in which larger male size is related to increased mating abilities rather than parental duties. The cross-taxonomic trends of relative female brain size and parental care in this study parallel a growing number of brain studies showing sexual differentiation and behavioral variation (46–50). The present findings suggest that relative female brain size across other mammalian taxa should follow variation in modes of parental care.

I thank S. L. Pimm, G. M. Burghardt, A. C. Echternacht, K. E. Holt, A. Purvis, G. C. Williams, and two anonymous referees for helpful comments on the manuscript and H.-K. Luh and D. L. Bunting for assistance with the comparative analyses. This research was supported by the Department of Zoology and Science Alliance of The University of Tennessee (Knoxville).

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