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Phylogeny, Behavior, and Ecology in the Mammalia

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I. Introduction

In a review written some 11 and published 9 years ago, I attempted to summarize the literature concerning mammalian social behavior and then proceeded to discuss two major issues: (1) the relationship of social structure to the species' habitat and economy, and (2) the influence of evolutionary history on the form of social organization displayed (Eisenberg, 1966). The almost exponential increase of information during the last decade concerning mammalian social behavior and ecology, as well as the founding of social ecology as a subdiscipline (Crook, 1970), have rendered my earlier review out of date. My co-workers and I have recently attempted two reviews, one for primates, the other for selected carnivores (Eisenberg *et al.*, 1972; Kleiman and Eisenberg, 1973). The problems of correlation and reconstruction remain as challenging as ever.

In the fields of animal behavior studies and the ecological aspects of behavior, there are at least three types of questions which one may pose regarding phenomena observed in nature. One may seek an historical answer. Such a question involves a fusion between formism and organicism (see Pepper, 1961). The question may be stated: "From whence was such a behavioral pattern derived?" And in order to explore this, one needs to

employ the comparative approach and to attempt to trace the historical steps in the appearance of the pattern.

One may seek a casual answer which is more strictly mechanistic. The question may be posed: "What are the casual events antecedent to the appearance of a given phenomenon?" In this case it is generally the procedure to set up experiments to isolate the variables giving rise to the expressed pattern.

Finally, one may ask the question: "How does this particular behavior pattern function in nature?" This is an ecological or adaptive question and falls under the category of contextualism (see Pepper, 1961). We must be careful to distinguish between the anthropomorphic answer to such a question and an objective answer. An anthropomorphic answer would imply a final cause in an Aristotelean sense. What we wish to imply is that goal-directed behavior results from neurophysiological mechanisms that are patterned in a particular way because the animal in question is the progeny of forms which have survived in competition with other forms in the same context or environment. Survival of a genotype is the outcome of reproductive success, and reproductive success is the result of a successful preceding adjustment on the part of the parental stock to environmental variables and success will vary as the genotype varies.

In essence, behavior patterns must be viewed as sets of muscular movements utilized by the organism to ensure its survival and the maintenance of its genotype. The study of behavior is in fact the study of sense organ, nerve, muscle, and endocrine relationships as reflected in movements and postures. Behavior patterns involved in intraspecific interaction are generally referred to as social behavior patterns, while a subset of these may be termed signals and as such an aspect of animal communication (Marler, 1961).

Since behavior patterns are the dynamic reflection of neuromuscular relationships, it seems logical that many relatively stereotyped behavior patterns may be treated as "structures" with a temporal dimension. Rules for comparison and determination of homology were developed by Wickler (1961) who drew heavily from Remane. One of the problems in applying Wickler's criteria to mammalian behavior patterns has been the lack of a framework defining a basic or fundamental mammalian repertoire. Another difficulty centers on the fact that Wickler's criteria grew out of a consideration of the displays of fishes and birds. In these taxa such displays are often rather stereotyped, but comparable displays are rare in many but not all groups of mammals. Andrew (1963, 1964) rather successfully provided an evolutionary perspective to the displays of primates, and he creatively departed from classical motivational models and developed a new theory of signal genesis, i.e., "stimulus contrast."

While some discrete patterns of behavior may be treated as structures and compared from one taxon to another, whole complexes of behavior are often not comparable. Although the units of behavior within, for example, a courtship bout may be compared from one species to another, whole adaptive complexes do not permit themselves to be treated as unitary phenomena. The comparison of social structures at best may involve the comparison of analogs. Working from a rather limited data base and without attempting to clearly delimit homologous behavior patterns, a recent series of facile comparisons has been published by various authors. Recently I attempted to point out the existence of behavioral analogs and convergences in the evolution of social structures

(Eisenberg, 1973), and I will not attempt to repeat the same line of reasoning here. Rather I wish to explore several questions of behavioral evolution by examining four radiations, the Tenrecidae, Edentata, Marsupialia, and Menotyphla,* and then proceed to a brief scheme for interpreting the phylogenetic sequences in the evolution of mammalian behavior. Obviously this essay is speculative and does not pretend to be a comprehensive review. I do hope to highlight some aspects of the interrelationship between mammalian behavior and ecology.

II. Lessons from the Tenrecidae

The tenrecid insectivores represent a unique eutherian radiation. Isolated on Madagascar since the Eocene or earlier (Simpson, 1940), this taxon has co-evolved with lemuriform primates, viverrid carnivores, and nesomyine rodents which apparently colonized Madagascar at somewhat later dates (Petter, 1972). In terms of trophic specializations, the family has not advanced beyond the level of insectivore/omnivore. In general the species are terrestrial or semiarboreal with one exception, *Limnogale mergulus*, which is aquatic. When the various genera are compared, some of the more profound differences in morphology can be related to either feeding or antipredator mechanisms (Eisenberg and Gould, 1970). Great similarities in reproductive behavior, vocalizations, and maintenance behaviors reflect the morphological and phylogenetic unity of this group. Given their morphological conservatism and relatively isolated status on Madagascar, it may be reasonable to assume that this adaptive radiation expresses the current limits of variation within a conservative morphological framework (Fig. 1).

Specializations are manifest. The eye is relatively reduced in size, as is the tail in the Tenrecinae. Facultative hypothermia may be viewed as a special adaptation in the Tenrecinae, but of rare occurrence in the Oryzoricinae. The complex communication mechanism of the genus *Hemicentetes* involving a stridulating organ is surely a very specialized adaptation (Eisenberg and Gould, 1970).

As outlined in previous publications, this family probably shows some enduring, conservative behavioral traits. Echolocation of a simple nature has been demonstrated in the Tenrecidae by Gould (1965). This ability probably evolved early in mammalian history in conjunction with nocturnal adaptations. The auditory, tactile, and chemical senses are uniquely developed in the Mammalia. If the early mammals did initiate their evolutionary history as nocturnal forms, then the three previously mentioned sensory systems undoubtedly achieved great emphasis. Indeed, Jerison (1973) argues convincingly that the initial selective pressure favoring large brains in mammals (relative to reptiles) may have derived from the need to store, retrieve, and compare the information received from the cochlea.

The possession of a cloaca and the absence of a scrotum in the male tenrec probably represent conservative characters. The prolonged courtship attention of the male which

* Use of this taxonomic category in this paper does not imply a belief by the author in the close affinity of the tree shrews and elephant shrews, but rather the term serves as a convenient reference category.

induces final ovulation by the female is probably also a conservative feature (Poduschka, 1974). Copulation is prolonged with intromission lasting 7.5 min (*Microgale dobsoni*) to 90 min (*Setifer setosus*). Spontaneous ovulation and brief mount durations are considered specialized attributes (Asdell, 1965). Gestation is rather long for the size class of this family (55–66+ days). If the time from birth to eye opening is added to the gestation, the range for the family is 65–80 days. The extended gestation nevertheless results in the production of altricial young and, although the eyes open at an earlier age postpartum than the eyes of many soricoids (Gould and Eisenberg, 1966), their overall developmental time is longer than that of soricoids of equivalent weight classes with comparable litter sizes. The longer gestation of the tenrecids does appear to shorten the postpartum development time for their young, but the long gestation may also reflect metabolic differences between soricoids and tenrecs which do not necessarily bear on phylogenetic arguments.

Litter size varies widely from over 30 in *Tenrec ecaudatus* to 1 or 2 in *Microgale talazaci*. Litter size reflects predation levels and survivorship as well as potential longevity and does not offer any light concerning “primitive” characteristics. It is noteworthy that of rainforest-adapted tenrecids, *Microgale talazaci* holds the record for longevity in captivity at 5 years 6 months, while *Hemicentetes semispinosus* has survived for only 2 years 7 months. The long-lived *Microgale* not only has the smallest litter size but also the

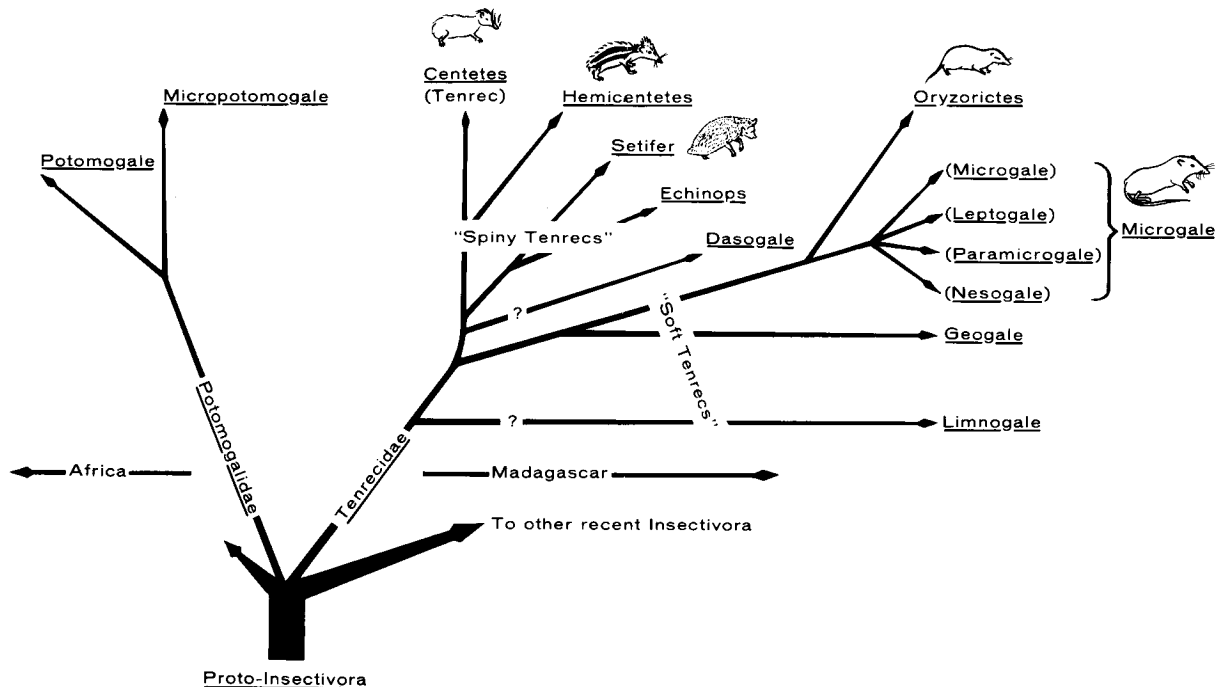


FIG. 1. Dendrogram illustrating probable relationships of the tenrecoid insectivores. The Tenrecinae are referred to as “spiny tenrecs” and the Oryzoricinae as “soft tenrecs.” The status of *Dasogale* is uncertain. The genus *Microgale* is broken into 4 subgenera which probably represent a recent radiation. The Madagascar radiation shows the greatest range of adaptations. Although the early radiation on Africa may have been equally diverse, the fossil record is not complete enough to fill in the picture.

longest developmental time, and the highest encephalization quotient (EQ) for any terrestrial tenrecid (Jerison, 1973). This correlation of brain development, litter size, parental care, and longevity is a complex which shows itself again and again in other taxa having evolved convergently in response to several interrelated selective pressures.

Finally, a word about brain and behavior. As pointed out in a recent review (Eisenberg, 1973), the gross behavioral repertoires of most mammals are roughly equivalent in complexity. Maintenance behaviors as well as postures, sounds, and movements involved in social interactions are of a similar level of magnitude when primates are compared with insectivores. It remains to be proved, however, whether primates utilize more of the potential information contained in social exchanges than do insectivores. What is of interest is the fact that small insectivores, such as *Hemicentetes semispinosus*, can accomplish much integrative behavior with an extremely small brain. Some tenrecids share with didelphid marsupials and soricoid insectivores the lowest brain-body-weight ratios of living mammals (Bauchot and Stephan, 1966; Jerison, 1973). Among the tenrecs, the genera *Hemicentetes*, *Tenrec*, *Setifer*, and *Echinops* are considered to possess a basic brainstem structure irrespective of EQ (Bauchot and Stephan, 1966). Thus, it seems reasonable to assume that these particular genera represent an eutherian base line in terms of brain structure. Yet the behavior repertoire and signaling system of *Hemicentetes* is among the most specialized of all the Tenrecidae. The littermate group may not leave the mother and, since her daughters can conceive at 35 days of age, the possibility for a multigeneration extended family utilizing the same burrow is ever present in this species. The use of stridulating quills as a means of coordinating the movements of the mother-juvenile foraging group is certainly a specialized communication system (Eisenberg and Gould, 1970).

Thus a corollary to our review of the Tenrecidae would include the principle that possession of a low EQ does not necessarily set limits on the complexity of coordination mechanisms or signal systems, nor does it set limits on the size of social groupings. What it may mean, however, is that an animal with a low EQ is more limited in the plasticity of its behavior and most nearly approaches the "Cartesian ideal of classical ethology" (Jerison, 1973).

III. Lessons from the Edentata

The living edentates represent the last survivors of an ancient lineage well documented by Patterson and Pasqual (1972). The radiation of the Edentata was confined to South America in relative isolation from the extensive eutherian radiations of the northern hemisphere and Africa. Starting from a generalized insectivorous ancestral form, the edentates radiated to fill herbivore niches. The successful terrestrial herbivores included the ground sloths (Megalonychoidea and Mylodontoidea) of the infraorder Pilosa and the Glyptodontidae of the infraorder Cingulata. All these taxa were extinct or nearly so by the end of the Pleistocene (Patterson and Pasqual, 1972). The three surviving families, Dasypodidae, Bradypodidae, and Myrmecophagidae, represent three rather separate adaptations. The Dasypodidae (armadillos) are the most diverse with respect

to feeding habits, antipredator mechanisms, and litter size (Kühlhorn, 1936; Moeller, 1968b). In general they are insectivores or omnivores adapted for a terrestrial life with reduced climbing ability. Some forms are almost entirely fossorial (e.g., *Burmeisteria*), and have occupied a niche similar to that of the Holarctic Talpidae.

The Myrmecophagidae (anteaters) are specialized for feeding on ants and termites. The three living genera are graded in size and arboreal ability and represent niche specializations comparable to the African pangolins (*Manis*) described by Pagès (1970, 1972a,b).

When we consider the Bradypodidae (sloths), we encounter a set of specializations which are duplicated in all the other major continental radiations of mammals. The sloths have evolved dental and gut adaptations permitting the use of plant cellulose as a nutrient source (Goffart, 1971). To be a browsing herbivore in the canopy of a rainforest permits a species to reach extremely high densities. The biomass of sloths in neotropical rainforests may be the major component of the mammalian fauna (Eisenberg and Thorington, 1973). This trend is paralleled in the evolution of colobine primates in Africa and Asia (Eisenberg *et al.*, 1972).

Another concept may be introduced from a study of living edentates; this involves a consideration of r and K selection (MacArthur, 1972). If we consider the equation which describes the natural growth of a population as:

$$\frac{dN}{dt} = rN \left(\frac{K - N}{K} \right),$$

where N is the population number at time t and dN/dt is the unit change per unit time, then r represents the intrinsic rate of population increase if unchecked and K represents the maximum density compatible with sustained resource utilization (i.e., the carrying capacity). When two alleles in a population or two populations are under selection and the effect of selection is to increase r , then the population is said to have undergone r selection. On the other hand, selection favoring a population which does not increase r or has a lower r is said to be K selected. The concept has great heuristic value, but also certain limitations (for a full discussion, see Pianka, 1972). For example, a species, such as *Dasypus novemcinctus*, reproduces at an early age and typically has 4–8 young. Many members of the tribe Dasypodini have similarly high reproductive rates. This suggests that these species are adapted to make use of transient resources which have rapidly fluctuating densities. The specialized armadillos of the genera *Tolypeutes* and *Priodontes*, as well as the highly specialized Myrmecophagidae and Bradypodidae, typically have a single young. The latter two families show a prolonged gestation, and a long period of intensive parental care. In both their capacity to reproduce and their potential longevity, sloths and anteaters suggest a K strategy in which a species is adapted to a stable niche and there is no special advantage to having a high reproductive rate. Instead, emphasis is placed upon the ability of an individual to retain a home range for its long-term use. In brief, then, reproduction is geared to maintain the population at a stable carrying capacity.

As recently shown (Montgomery and Sunquist, 1975), each individual 3-toed sloth (*Bradypus infuscatus*) has a set of trees in its home range which it visits with varying

frequency. Over 40 species of trees and vines may be involved in the diet of the sloth and in some manner the sloth retains a memory of the location of its "modal" feeding trees and visits them on a schedule which is yet poorly understood in a causal sense. Although sloth home ranges overlap, each sloth tends to move and feed alone unless paired for mating or in the special case of a mother accompanied by her dependent young (Montgomery and Sunquist, 1975).

The mode of tree use suggests that the sloth is able to remember characteristics of its home range permitting it to move to preferred feeding trees in an orderly fashion. It is not surprising that sloths have a respectable brain size which no doubt reflects the necessity for integrating considerable information concerning spatial location of trees that provides for the effective utilization of its home range for a period of many years (Britton and Kline, 1939). It is entirely possible that in the wild, once established as adults, sloths live for a period exceeding 15 years, perhaps even longer.

The arboreal anteaters, *Tamandua* and *Cyclopes*, similarly must navigate in a 3-dimensional environment feeding on ant and, to a lesser extent, termite nests in a rotational fashion. This presupposes an ability once again to retain masses of individually acquired information concerning the structure of food sources within their home range. When the Edentata are compared with respect to brain size, sloths and anteaters have larger brains relative to their body weight than do armadillos (Eliot-Smith, 1898; Röhrs, 1966). This may very possibly reflect the particular needs for such long-lived animals as anteaters and sloths to acquire and store information concerning the location of food within the discrete 3-dimensional structure of their home range. Note again the correlation between small litter size, long life, and relatively high EQ (Fig. 2).

Undeniably, the Edentata are conservative in certain aspects of their morphology and physiology. They have a lower basal metabolic rate than more "advanced" eutherians, the sloths much more so than the anteaters. Certain features of the reproductive system in sloths may be considered morphologically conservative (Goffart, 1971). In none of the Edentata do we find specializations for great visual acuity, although their auditory systems appear to function about as well as many other eutherian mammals (Peterson and Heaton, 1968). The olfactory system is apparently well developed and, in the case of *Tamandua*, hunting by scent trailing is the major feeding strategy (Montgomery and Lubin, personal communication). If this order be considered somewhat morphologically conservative, surely all the members represent certain degrees of specialization. It is interesting to note that, in their adaptive radiation, they have replicated trends observable in other mammalian radiations in the Old World tropics.

IV. Lessons from the Marsupialia

In isolation from the major eutherian radiations, Australian marsupials and to some extent the South American marsupials adapted to fill a multiplicity of niches. In Australia the radiation reached its maximum flowering and, although many larger herbivorous marsupials are now extinct, the record would indicate that in Australia marsupials showed a range of diversity parallel in complexity to early eutherian radiations in the

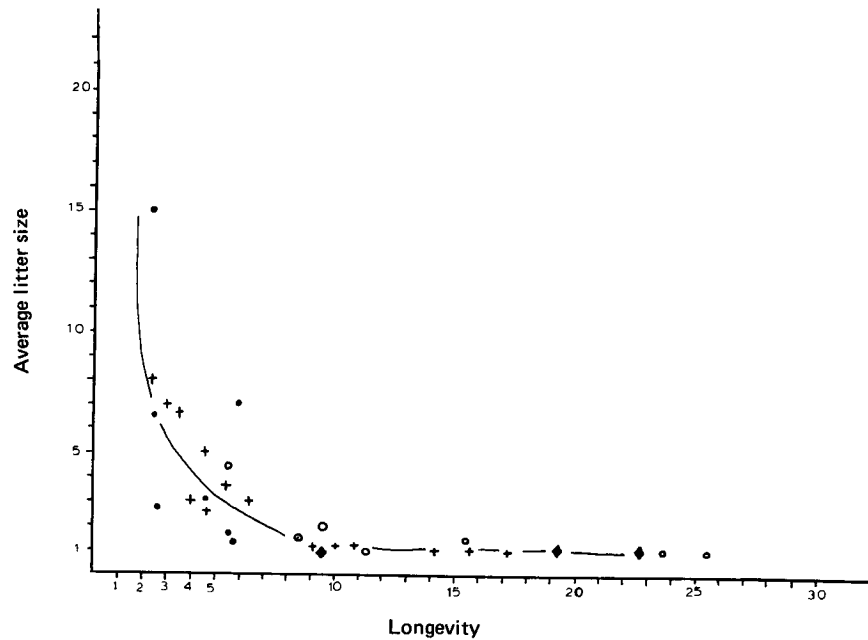


FIG. 2. Relationship between litter size and longevity for selected mammals. \blacklozenge = Monotremata, $+$ = Marsupialia, \circ = Edentata, \bullet = Tenrecidae, \odot = *Solenodon*. Data concerning reproduction and longevity in the Monotremata and Marsupialia taken from Collins (1973); data for the Tenrecidae and Solenodontidae taken from the publications of Eisenberg and Gould; data for the Edentata come from unpublished records of the National Zoological Park. Longevity records are in most cases based on averages of 3 or more individuals. Two-toed sloths (*Choloepus*) have reproduced when at least 22 years of age in captivity. Maximum longevity records for members of the family Tachyglossidae have exceeded 49 years in captivity.

more continuous land masses. As Tyndale-Biscoe (1973) has documented in his recent book, marsupials should not be thought of as an inferior type of mammal. Rather, they have gone about the business of adaptive radiation with a slightly different basic body plan. The Australian marsupials apparently show a lower metabolic rate than their eutherian counterparts (MacMillen and Nelson, 1969). Certainly, the reproductive system of marsupials is their most unifying morphological and physiological feature, and their process of producing young is somewhat different from that developed by eutherians (Sharman *et al.*, 1966; Wooley, 1966). Yet when reproductive patterns of living marsupials are compared, the following trends in the evolution of marsupial viviparity can be noted. When we compare morphologically conservative forms in so-called conservative niches with more advanced forms, then specialization often shows that: (1) the number of ova shed from the ovary is reduced, (2) the number of young is reduced, (3) the weight of the neonatus is increased, and (4) the gestation period is lengthened (Sharman, 1965). These trends were convergently followed in many eutherian orders, if one accepts the proposition by Portman (1965) that the "primitive" reproductive methods of eutherians involved the production of several rather altricial young initially reared in a nest.

Without doubt most modern marsupials trace their lineage to a common ancestor strongly adapted for arboreality. This appears to be true of both the New World and Old World radiations (Dollo, 1899; Gregory, 1951). Although New World marsupials adapted to fill a semiherbivorous niche in the extinct Polydolopidae (Patterson and Pasqual, 1972), the use of plant cellulose as a food base has strongly evolved at least twice within the Australian marsupials (e.g., the Phalangeridae and Macropodidae). The evolution of adaptations for feeding on grasses in macropodid marsupials was accompanied by a trend toward the formation of cohesive social groupings as well as larger, temporary groups forming from more cohesive subgroups based upon a female and her descendant offspring. Such trends in the structuring of group size also accompanied the evolution of grazing in the Artiodactyla (Eisenberg, 1966; Kaufmann, 1974).

Some aspects of marsupial behavior which appear to be unique center around the profound differences between the marsupial and eutherian mode of reproduction. Marsupials are characterized by having a rather short gestation period relative to their size, followed by a prolonged period where the young are helpless and completely dependent upon female transport and nutrition. As is well known, the altricial marsupial young transport themselves to a pouch or marsupium (or teat area in the case of some Dasyuridae and Didelphidae). Attachment to the teat and further development outside the female reproductive tract may be prolonged, and in general the developmental rate of young marsupials is somewhat slower than that of comparably sized eutherians (see Fig. 3). The evolution of litter size within the order Marsupialia shows trends similar to those displayed by continental eutherians. Large litters are characteristic of small insectivorous and carnivorous forms; smaller litters are typical of larger herbivorous forms, with the smallest litters produced by the arboreal folivore, *Phascolarctos*, and the large grazing macropodids, *Megaleia* and *Macropus*.

During the neonatal and early postnatal developmental stages of the young marsupial, there is an intimate association with the mother. The young are attached to teats in the pouch or teat area. When the sense organs (i.e., eyes and ears) of the young become functional, the mother's body is the primary environment for the young. Although the mother may have a nest into which she retires, it is not the nest, but her body, which has a strong valence for the young. During the period subsequent to development of the sense organs, often termed the "socialization period" in eutherian mammals, young marsupials become capable of some independent locomotion. The young now may still be transported at times on the mother's body or in the pouch, although in the case of dasyurid marsupials the young often remain in the nest when the mother forages. Even so, the female dasyure will still continue to nurse the young in the nest and the young may ride on her for short periods (Collins, 1973; Ewer, 1968).

The mother marsupial is, in a sense, the "nest" during the initial phase of development for the young. It is only when the young reach the stage of socialization that they begin to approximate the eutherian condition and, in the case of nest-building forms, the nest attains an importance as a source of conditioning stimuli. Littermates serve as social partners during development while the mother is an important source of socializing stimuli in the larger macropodids which bear a single young (Russell, 1973).

In terms of the development of brain and sense organs, marsupials exhibit trends

similar to those of eutherians. While it is true that living didelphids do not show brain development beyond the level of that attained by tenrecid insectivores, the carnivorous Dasyuridae of Australia do show brain development at a much higher level. Nevertheless, the Australian carnivorous marsupials show levels of brain development below those of eutherian carnivores in comparable niches in the main continental areas (Moeller, 1968a; Wirz, 1950). Similarly, the grazing macropodids of Australia show the lowest brain-body weight ratios of any terrestrial herbivore. These latter comments on the brains of marsupials give rise to two major points:

1. When a morphologically conservative species specializes for a niche with certain key demands for information storage and retrieval and muscular coordination, the brain undergoes appropriate selection and increases to the size necessary for receiving, inter-correlating, and retrieving data from the relevant sense organs. Thus, carnivores that pursue fast, mobile prey generally tend to have larger brains than insectivores which feed upon abundant, slow or stationary prey which are located by chemical or tactile means. (An exception, of course, would be bats which must locate winged insects using echolocation data.)

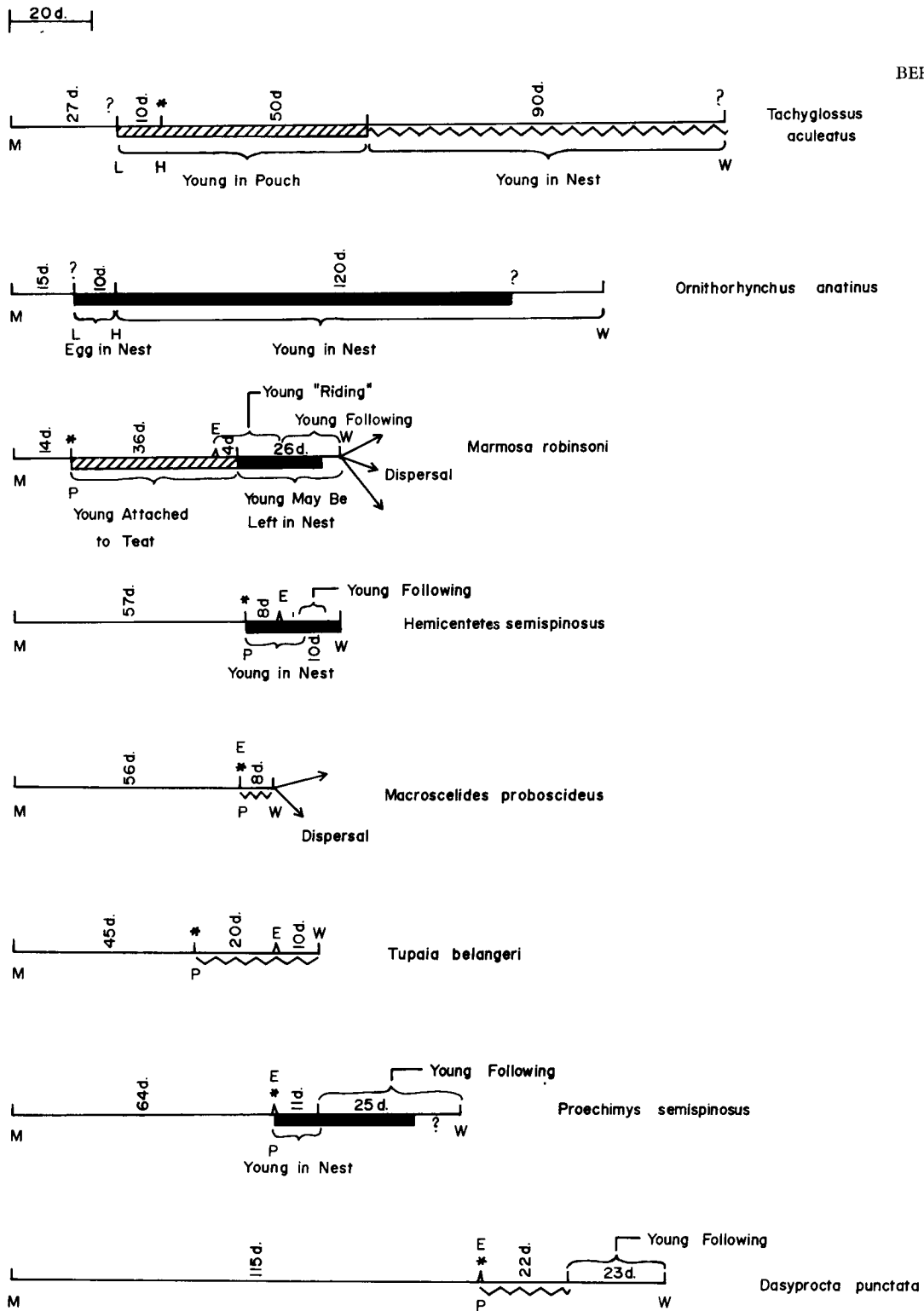
2. Morphologically conservative forms in relative isolation often evolve brain size at slower rates; thus, the Marsupialia and Tenrecidae exhibit brain-body ratios and brain structures which are more conservative than those of mammals in comparable niches on the continental land masses (Andrew, 1962; Jerison, 1973).

V. Lessons from the Tupaiidae and Macroscelididae*

The tree shrews and elephant shrews represent specialized taxa which share many conservative morphological characters found in the classical lipotyphlan insectivores (Weber, 1928). Both taxa show certain parallel trends in brain and sense-organ structure departing from the patterns of the lipotyphlan insectivores, yet neither family is closely related to the other (Patterson, 1965). If we assume that early eutherians were nocturnally adapted, then it follows that olfactory, tactile, and auditory senses were most important for obtaining information about their external environment. The eye would be of reduced utility, although our hypothetical ancestral mammal may, in fact, have had moderately sized eyes with a rod retina. Nevertheless, as a distance receptor, the ears, eighth cranial nerve, and all associated projection areas for the eighth nerve, began to assume primary importance.

* I do not consider the Tupaiidae as a family of the order Primates; see McKenna (1963) and Van Valen (1965).

FIG. 3. Maternal care patterns for selected mammals. M = mating; L = laying; H = hatching; P = partus; * = beginning of lactation; W = end of weaning period; E = eye opening; d = days; // // // // = period of teat attachment; ■■■■ = period of female and young in same nest; and ~~~~~ = period of absentee parental care. Data for Monotremata and Marsupialia taken from Collins (1973); data for *Hemicentetes* from Eisenberg and Gould (1970); data for *Macroscelides* from Sauer and Sauer (1972); data for *Tupaia* from Martin (1968); and data for caviomorph rodents from Kleiman (1974). The sequences for certain events in the Monotremata are imperfectly known, but the "absentee system" for *Tachyglossus* is established. Question marks indicate uncertainties in the timing of events (see Collins, 1973).



The tupaiids and macroscelidids took two routes in their evolution. On the one hand, the elephant shrews retained a terrestrial niche, whereas the tupaiids began to develop increasing specializations for arboreality. In both lines, however, the animals show trends toward reliance on vision, if nocturnal, and ultimately specializations of the eye during the invasion of diurnal niches. Becoming diurnal must have placed demands upon the eye as a receptor of more and more fine-grained detail. Central projection areas for visual information began to become more important, a sequence that can still be seen when *Ptilocercus* is compared with *Tupaia*. With this dependence on visual information, a corresponding increase in brain size relative to body weight can be demonstrated together with the development of appropriate projection areas in the neopallium (Clark, 1924, 1926).

The diurnal tupaiids began to utilize much more information concerning depth perception and the structure of the 3-dimensional, arboreal world that they were invading; this may again have accounted for some of the increase in brain size which they show. Certainly an increased brain size in correlation with diurnality and arboreality is reflected in the evolution of the brains of sciurid rodents (Pilleri, 1959; Wirz, 1950). It is difficult, however, to tease these two variables apart unless by inference we assume that the demands of navigation in a 3-dimensional environment always presuppose some increase in brain size relative to body weight as is reflected in the rather large brains of the aquatic insectivores *Potomogale*, *Limnogale*, *Desmana*, and *Galemys*, all four of which do not show any extraordinary development in eye size, but do show increased development in the cerebellum and cerebral cortex (Bauchot and Stephan, 1966). A similar argument could be applied to the Pinnipedia and Cetacea. The latter also evolved an echolocation ability which parallels the bats. Dependence on such auditory integration may account for the initial increase in brain size of the Cetacea (Jerison, 1973) (see Fig. 4).

It would seem that, in an attempt to understand the steps from nocturnal life to diurnal life and all that this entailed in the evolution of mammals, one should look more closely at the behavior, reproductive biology, thermoregulation, and trophic specializations of *Ptilocercus*, for it truly is a connecting link between *Tupaia* and whatever ancestral form gave rise to them. Speculations concerning the ancestors of tupaiids and primates are perhaps best deferred until the biology of *Ptilocercus* is better understood.

Certainly no speculations concerning the evolution of the tupaiid way of life should be made without reference to parallel developments in the Macroscelididae. The unique method of parental care demonstrated by Martin (1968) in *Tupaia* has now been confirmed for *Macroscelides* by Sauer and Sauer (1971, 1972). In *Tupaia*, nests are constructed by both the male and female, although the female specifically constructs a natal nest into which the young are *altricially* born. While nesting separately from the male, the female only returns to the natal nest to nurse the young at intervals of 24–48 hr. In *Macroscelides*, the female gives birth to 2 *precocial* young in a secluded spot, returning to nurse them at 24-hr intervals. This demonstrated behavioral similarity need *not* be homologous. Similar forms of maternal care are demonstrated in the Monotremata (Tachyglossidae), Lagomorpha (Leporidae), Artiodactyla (Cervidae, Antilocapridae, and some Bovidae), Perissodactyla (Tapiridae), and Rodentia (*Dasyprocta*, *Pediolagus*, and *Myoprocta*)

(Kleiman, 1972, 1974; Lent, 1974). It would appear that the trend toward the production of precocial or semiprecocial young often involves the evolution of the "absentee system" of parental care. The unique attribute of the *Tupaia* system is that it involves relatively altricial young (Martin, 1968) (see Fig. 3).

It has been suggested (Martin, 1968) that the lack of a retrieval pattern shown by the female *Tupaia* plus the "absentee" maternal care system could be part of a conservative mammalian pattern of reproductive behavior. If *Macroscelides* and *Tupaia* are indeed only distantly related, then the possibility exists that the "absentee" parental care system is a plesiomorph character. Yet the presence of maternal retrieving behavior plus a conventional nesting attendance phase by such ecologically and morphologically

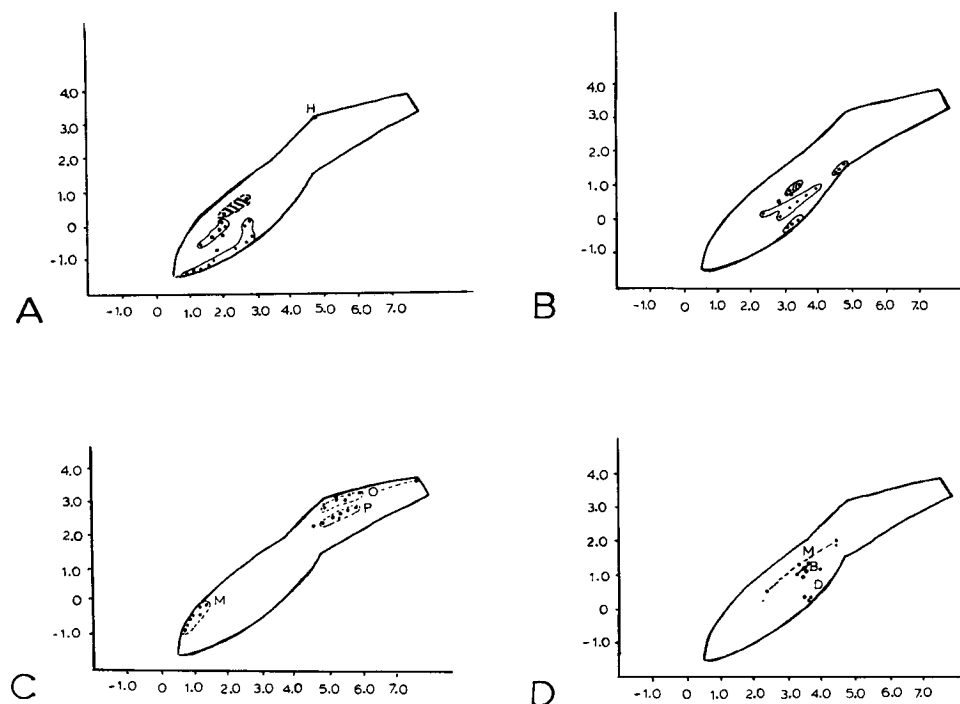


FIG. 4. Brain-body weight relationships for selected mammals. Ordinate = brain weight (E_c) in grams expressed as \log_{10} . Abscissa = body weight in grams expressed as \log_{10} . Boundary of diagram outlines the total set of brain-body weight points for the class Mammalia. Method of plotting adapted from Jerison (1973). All absolute brain weights converted to E_c where $E_c = \text{absolute brain weight } (E) \text{ minus } E_v \text{ and } E_v = (0.03) \times (\text{body weight})^{0.66}$ (see Jerison, pp. 78-81). The transformation in no way effects the relationships as shown here. (A) Brain-body weight relationships for insectivores, tree shrews, and elephant shrews (the latter two groups are cross-hatched). Points adjacent to the cross-hatching represent the set including the aquatic insectivores, *Limnogale*, Potamogalidae, and Desmaninae. H is the average point for the genus *Homo*. (B) Brain-body weight relationships for monotremes and marsupials. The cross-hatched set is the Monotremata. (C) Large brains for rapid navigation in three dimensions. M is the set for several Microchiroptera; O encloses selected species of the Odontoceti; P bounds several species of Pinnipedia. (D) Brain-body weight relationships for the Edentata. M denotes the Myrmecophagidae (connected by a dotted line). B shows three values for the Bradypodidae (connected by a solid line). D includes several points for the Dasypodidae. Note that the long-lived Euphractini (open circles) approximate the Bradypodidae.

conservative mammals as the edentate genera *Euphractus* and *Chaetophractus* and all genera of the Tenrecidae render the plesiomorph hypothesis dubious (Encke, 1965; Gucwinska, 1971; Eisenberg and Gould, 1970).

VI. The Evolution of Mammalian Patterns: Attempt at a Reconstruction

The brilliant synthesis by Pearson (1964) clearly indicates a marked climatic deterioration at the close of the Cretaceous followed by return to widespread tropical conditions in the early Tertiary. Subsequent to that time, there is evidence of continued change in climate accompanied by alterations in vegetation. Several cyclic patterns of climatic change have been proposed. With the decline of the reptiles at the end of the Cretaceous, the ancestral Eutheria and Marsupialia were offered the opportunity of filling unoccupied ecological niches (Olson, 1961). With such a changing pattern of selection pressures, rapid radiation occurred with the ordinal groups of mammals becoming clearly established in the Paleocene. Superimposed on the initial mammalian radiation was the concomitant breaking up of the earth's land masses which contributed to the geographical isolation of certain key groups of morphologically conservative mammals (Fooden, 1972). Australia, South America, and Madagascar were able to develop mammalian faunas which were distinctive until more recent invasions of eutherians from the more contiguous land masses.

Subsequent to this initial radiation, some living mammals existing in present-day tropical forests are relatively unmodified morphologically when compared with their ancestral stocks. This conforms to the hypothesis advanced by Simpson (1944) that bradytely or persistence of slowly evolving taxa results from an original adaptation of a widespread population to a relatively homogeneous environment, which may then persist through time as isolated populations in those areas which undergo little environmental modification. Thus, it seems legitimate to infer that certain morphologically conservative species inhabiting niches in the tropics represent forms that are, in a sense, adapted to a "conservative niche." Therefore a phylogenetic reconstruction of mammalian behavioral evolution must use as its starting point generalizations developed from a comparison of morphologically conservative forms occupying what might be considered to be the niches of the Paleocene-Eocene boundary (Jerison, 1973).

If we assume a polyphyletic origin of mammals (Simpson, 1959), it is even more difficult to reconstruct the probable evolutionary steps leading back from the pantotheres to the divergence from the stock giving rise to the monotremes. No doubt the trend away from oviparity and the evolution of mammary glands in the monotremes indicates either a parallel analogous with developments which took place in the stock giving rise to marsupials and eutherians or a primitive mammalian condition representing the ancestral pattern for both Metatheria and Eutheria. Concomitant with the evolution of mammary glands came a reorganization in methods of parental care. A comparison of the eutherian and marsupial lines indicates that parallel developments may have taken place in the evolution of reproductive patterns. The stock for both lines must have

diverged from a precursor which possessed mammary glands to nourish the neonate by means of milk rather than by a large store of maternally derived yolk. The therian ancestor had departed from the pattern of laying large-yolked eggs and was either laying smaller eggs with little yolk or was ovoviviparous with a choriovitelline placenta (see Luckett, this volume).

If we agree that the early niches exploited by eutherians and marsupials were in forested habitat with a moderately stable climate, that the activity patterns of these mammals were confined to darkness, and further, that the animals were specialized as insectivores, then it follows that the evolution of thermoregulation and the reliance on audition for gaining distance information went hand in hand with the exploitation of a nocturnal niche. Invasion of an arboreal niche, and yet remaining nocturnal, perhaps placed further demands on the eye as an additional source of distance information. This would be especially true of nocturnal forms that moved rapidly in a 3-dimensional environment and employed leaps to get from one position in space to another. Either the echolocating ability would have to be refined so that a spatial map could be constructed based on echo information as in the case of the Chiroptera, or the eye would have to assume additional importance as a distance receptor, as is the case with the Phalangeridae, Lorisidae, and Lemuridae, to mention only a few. The most dramatic departure, then, once mammals had evolved to this point of agile use of trees and enhanced auditory and visual perception, would be for the organism to undergo selection to occupy diurnal niches with the eye continuing to be refined as a distance receptor. No doubt the Chiroptera passed through a stage of reliance on the eye while springing in trees at night. Sophisticated use of echolocation for maneuvering around obstacles or catching prey could only come *after* the development of some controlled flight. Presumably echolocation in the buoyant aquatic realm was accomplished much easier in the evolution of Cetacea.

The evolution of physiological and morphological adaptations for obtaining plant material and processing it in order to extract energy from cellulose with the aid of bacterial symbionts was another great step forward taken convergently by the Marsupialia and Eutheria. Convergent and/or parallel trends are widespread in modern taxa. Terrestrial use of plants dominates the evolution of the Artiodactyla and Perissodactyla in the Eutheria and the Macropodidae in the Marsupialia. Arboreal browsing as an alternative route for the exploitation of plants reaches its height in the colobine primates, bradypodid edentates, and phalangerid marsupials. Such evolutionary steps in the different mammalian lines often involved alternative solutions to the same problem. At the same time, when such similar niches are occupied by representatives of different radiations, we see repeated convergences in methods of antipredator behavior, rearing of young, and form of social structure.

The validity of comparative studies utilizing behaviors as phenotypic expressions of genotype (for the reconstruction of phylogenies extending back over 60 million years) is severely limited when the investigations of modern-day forms are used as points of reference. Comparative studies of behavior are most useful at the present stage of our understanding when they are confined to closely related species in taxa well defined on morphological grounds.

In order to assess what restrictions the phylogenetic heritage of a given radiation places upon the forms of the adaptations that it evolves, one must continue to analyze the various aspects of ecology and behavior of those species which have evolved in relative isolation from the competition of many species which has been imposed on the evolution of the Eutheria within the contiguous continental land masses. Thus, the analysis of behavior in the Malagasy tenrecids and Australian marsupials becomes more pressing and relevant.

To summarize some of the foregoing conclusions, I offer the following set of hypotheses:

A. Brains and Perceptual Worlds

Throughout the text I have made reference to various indices of brain enlargement. It is true that mammals and birds have larger brains in proportion to their body weight than do reptiles and amphibians (Jerison, 1973). The causes for this difference are imperfectly understood, but the differences are readily available for empirical verification. Furthermore, Jerison (1973) argues rather successfully that there has been a progressive trend in the enlargement of the brain throughout the history of the Mammalia. This increase in absolute and relative brain size has not occurred at equal rates in all taxa, but seems to accompany increasing specialization and refinement in the occupancy of new niches. Thus certain groups of mammals, such as tenrecid and soricoid insectivores, may retain brain structure essentially little modified from the brain structure of Cretaceous mammals.

Increase in brain size need not be confined to only one area of the brain. An increased brain size in one taxon may not reflect increase in the size of the neocortex, but only increase in the size of some subcortical structures. Those areas of the brain that do increase in size are often related to specializations in certain sense organs and thus correlate with the collection, storage, and retrieval of specific kinds of data relevant to the niches which the animals exploit. This principle is extremely well illustrated in the publication by Mann (1963) concerning the brain of the Chiroptera. He points out that "the cortical circuits are not empowered to replace advantageously, in every case, the subcortical mechanisms. Specialized phylogenetic trends may involve, therefore, increase of such subcortical centers without a corresponding increase in the neocortex" (Fig. 4).

B. Arboreality

Specialization for arboreal niches may have come early in the case of the Marsupialia and somewhat later in Eutheria. To be arboreal and nocturnal need not require any great specializations in the sense organs beyond the primitive mammalian level if the organism locomotes slowly and carefully in the branches and is specialized for capturing slow or relatively immobile prey. Great specialization in vision and hearing seem to accompany departures in locomotion which involve springing from one point to another in a truly 3-dimensional environment. The range of adaptations and morphological correlates has been reviewed by Cartmill (1972).

C. Diurnality

The evolution of diurnal habits seemed to involve greater reliance on vision as a means of obtaining information concerning distant objects. As they evolved in the Mammalia, the neural mechanisms for the integration of visual information in the central nervous system seemed to involve structural parallels with the mechanisms by which auditory data from the eighth cranial nerve were organized at the subcortical and cortical levels. This parallel development of brain mechanisms involving the second cranial nerve resulted in a greater encephalization by all those mammals which became diurnal (Jerison, 1973).

D. Herbivory

Utilization of plant cellulose as a food substrate occurred in every major mammalian radiation. Yet these tasks of trophic adaptation were in some cases parallel, e.g., the Rodentia (Vorontsov, 1960), or convergent, e.g., Marsupialia and Eutheria. The consequences of becoming a terrestrial herbivore and, in particular, utilization of grasses resulted in convergent evolution of social tolerance mechanisms which permitted formation of larger cohesive groupings. Such trends have been reviewed previously (Eisenberg, 1966).

E. Longevity and Litter Size

Increase in length of life and, in particular, effective reproductive life always seems to accompany reduction in litter size. Yet reduction in litter size may be a response to relatively short-term selective pressures. In the invasion of certain niches, such as the grazing niche, we have seen a convergent trend in reduction of litter size and the production of relatively mobile young; for example, when the leporid lagomorphs or caviomorph rodents are compared with bovid ungulates (Kleiman, 1972). Adaptations for these types of niches, then, do involve some predictable trends in litter size, but these are convergences at best and more often than not the longevity-litter size correlation is the result of particular factors related to the relative efficiency of replacement which vary greatly from one taxon to another. The importance of so-called *K* and *r* selection is related to a host of factors which does not permit the establishment of anything but trends and simple correlations among closely related species.

F. Parental Care

Viviparity and the production of altricial young demanded some form of parental care for maintenance of a high temperature for the developing young and provision of extrauterine nourishment. In the Marsupialia both objectives were accomplished with the evolution of the marsupium; in the Eutheria, apparently the first objective was obtained by bearing the young in a protected nest site where the parent could "brood" them. The latter problem was solved in the same manner as in the Marsupialia, i.e., by the evolution of the mammary gland-teat complex.

Without any necessary reduction in the complexity of parental care, more precocial young could be produced, thus shortening the time necessary for the parent to maintain a high temperature within a nest for the developing young. If the young were born precocial enough to maintain their own body temperature or born in a sufficiently insulated nest, the parent need only tend the young during periods of lactation. The so-called "absentee" system of parental care (Martin, 1968) could then have evolved in a convergent or parallel manner many times. If the young were born precocial enough to follow the mother, the absentee system could be eliminated almost entirely, provided the young were agile enough to participate in appropriate antipredator responses (see Fig. 3). This condition has been attained in some Artiodactyla.

On the other hand, bearing young in an arboreal habitat presents special problems. The young must have sufficient muscular coordination so that they will not fall before they leave the nest area. If a trend toward precocial young should be selected for, then the transition phase must be bridged from, at one extreme, a young that can immediately follow the mother to, at the other extreme, a young that is helpless in a nest. In general, this has been done either by retaining a nest phase in the rearing cycle of the young or eliminating it by producing a small number (e.g., 1-2) of very precocial young which can cling to the mother. The mother thus assumes the function of a "moveable nest." A convergent solution to the problem is seen in arboreal marsupials, but this shows only functional analogs since in this case altricial young transfer themselves to a pouch area and in this manner the mother becomes a "moveable nest."

G. The Formation of Social Groupings

Incipient pair-bond formation can be seen in many morphologically conservative mammals, such as the insectivores *Cryptotis parva* and *Microgale talazaci*. Such pair bonds are probably formed because of greater efficiency in mating when the presence of the opposite sexed partner is known and available to the other. This system is permissible in those conditions where a given pair can occupy and exploit resources efficiently in the same home range. Where joint exploitation is not possible or is less efficient, permanent pair bonds do not seem to exist and separate foraging areas for the male and female are the rule (Smith, 1968).

Where the male and female occupy the same home range and show some tolerance for their progeny, the possibility exists for the formation of small temporary inbreeding groups. Such units of population may provide the beginnings of group selection (Wilson, 1973). That such systems evolve in response to the peculiarities of each exploitation system is no doubt the case. Behavioral convergences in the form of social structure occur again and again in the Mammalia and only a generalized phylogenetic pattern can be detected (Eisenberg, 1966; Eisenberg *et al.*, 1972). Trends can be discerned, however, although the correlations apply only to cases where the evolutionary history of the group is reasonably well known (Kleiman and Eisenberg, 1973). Differences between mammalian social systems surely reflect overall adaptations to the physical habitat and the species' mode of exploitation.

The home range or area which an animal utilizes is very much a function of the distribution pattern of its foodstuffs (Altman and Altman, 1970), and home-range size is roughly correlated to the size of the species in question. But, even within body-size ranges that are similar, vast differences exist between home-range size for, let us say, carnivores on the one hand and herbivores on the other (McNab, 1963).

The form of social organization is often profoundly influenced by the nature of the shelter that the animal constructs. If a shelter is constructed and a considerable amount of energy is expended in the construction of such shelters, then defense of the shelter against a conspecific competitor is most essential. In addition to shelter construction, one must also consider the caching of foodstuffs. The formation of a food supply in space for later utilization by the assembler or its progeny very often involves an intraspecific defense system so that use of such an assemblage of food is restricted.

The mobility of a species has a profound influence on the form of its social organization (Eisenberg and Lockhart, 1972; McKay and Eisenberg, 1974). For example, a top carnivore may still form social groups, if the group itself possesses a sufficient ability to allow movement over a wide enough home range to effectively utilize its resources without overcropping (Kleiman and Eisenberg, 1973). Finally, antipredator behavior of prey animals profoundly influences whether or not groups can be formed. Small forms whose most adequate predator defense is inconspicuousness cannot afford to form groups which render their concealment impossible. Such species may become communal and utilize the same resources as long as they can do so while at the same time remain relatively invulnerable to predation (Eisenberg and Lockhart, 1972; Eisenberg and McKay, 1974).

To sum up then, in general those morphologically conservative mammals which are alive today exhibit the following trends in ecology and social behavior: They require a high energy content in their diet and are either specialized as small carnivores, insectivores, or generalized omnivores. As a result, they tend to range over a wide area relative to their body size and some spacing mechanisms are necessary to promote efficient utilization of habitat and further to reduce overutilization of restricted food sources. A given male and female may show overlap in home range and yet show very limited contact except at the time of mating. Parental care may fall entirely to the female; nevertheless, the same male and female may mate during consecutive seasons as the result of the proximity of their home ranges and as a result of their own agonistic tendencies toward conspecifics of the same sex. The adult female repels other females and the male repels contending males. Through such a behavioral mechanism the dispersal of their own progeny is assured. However, if family clustering is to be promoted and some selective advantage is retained by such a group (e.g., *Hemicentetes semispinosus*), it is generally tolerance of a female for her daughter rather than a male for his son that leads to the formation of nuclear family groupings. Such family groups consist of several females related by descent with their progeny and a dominant, single male utilizing roughly the same home range. Thus a so-called solitary species can exhibit a "family" structure which demonstrates a minimum of direct social contact; this can be taken as the simplest type of inbreeding population unit in the sense of Anderson (1970).

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