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The Evolution of Male Parental Investment in Mammals

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1. Introduction

A variety of approaches have been used to understand the evolution of male parental care. General frameworks are provided by Trivers' theory of sexual selection (1972), the theory of life history strategies (see Horn, 1978; Stearns, 1976) and game theory (Grafen and Sibly, 1978; Maynard Smith, 1977). The factors invoked to explain male parental investment have varied with the level of analysis; intrinsic biological factors such as internal versus external fertilization (Dawkins and Carlisle, 1976; Ridley, 1978) or the capacity to invest (Orians, 1969) have been used to illuminate differences between large taxonomic units such as the vertebrate classes; ecological factors such as harshness (Wilson, 1975), richness (Jenni, 1974), and unpredictability (Pitelka *et al.,* 1974) have all been invoked to explain the presence of unusual levels of male investment in smaller taxonomic units.

In this paper, we will review the types of male parental investment seen in mammals and their taxonomic distribution. We will then consider the evolution of male parental investment and assess its role in molding the social and breeding systems of different species. We will try to determine if there are certain conditions when male care may place constraints on the breeding system, or particular ecological pressures which promote male parental investment. Unlike Spencer-Booth (1970), we will not be concerned with the motivation underlying male parental care or the stimuli eliciting this behavior.

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1.1. The Definition of Male Parental Investment

We conceive of male parental investment as *any increase in a prereproductive mammal's fitness attributable to the presence or action of a male.* This can include behavior directed at a pregnant female between conception and birth. It also includes behavior of the parental type by males other than the known (or presumed) father. Redican (1976) has used the term "paternalistic" in this context since in many species the actual father is unknown. We will not try to differentiate between parental behavior exhibited by fathers versus other males, since the same behavior patterns are usually shown with only quantitative differences in the behavior of fathers and nonfathers.

Our concept of parental investment is somewhat different than Trivers's (1972), i.e., "any investment by the parent in an individual that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring" (p. 139). First, there are many types of parental investment, especially protection and babysitting, where guarding of one individual does not necessarily reduce the fitness of another member of the same clutch or litter (or even other relatives). Second, in iteroparous species, and especially seasonal breeders, the extent to which investing in one set of offspring precludes future investment may be minimal. Whereas Trivers appears to view investment as a fixed quantity which is apportioned during an individual's lifetime, we tend to consider investment at different times as being at least partially independent. Third, as pointed out by Trivers and Hare (1976) and J. H. Ligon and S. H. Ligon (1978), some investment in young may increase an individual' s reproductive success by raising future helpers. Fourth, Trivers excludes investment by individuals other than the parents.

1.2. Categories of Male Parental Investment

We will later try to enumerate some of the myriad ways in which male mammals can and do help young of their species. First, however, we will define two major axes along which male parental investment can vary which aid both in organizing the data and in understanding how male parental investment can affect the social organizations of the species in which they occur.

The first distinction is between *direct* and *indirect* forms of male parental investment. *Direct* investment by a male includes those acts which a male performs towards young that have an immediate physical influence on them which increases survivorship. Feeding or carrying infants falls into this category as does sleeping with young, grooming young, or playing with young. References to male parental investment in the literature usually involve *direct* investment (we will occasionally use the term male parental care when referring to direct male investment).

Indirect male parental investment includes those acts a male may perform in the absence of the young which increase the latter's survivorship. These acts may

have delayed effects on survivorship of young and include such behaviors as the acquisition, maintenance, and defense of critical resources within a home range or territory by the elimination of competitors, the construction of shelters, and actions which improve the condition of pregnant or lactating females. Many forms of male parental investment that are indirect are also *incidental* to the species' breeding system, ecology, or social organization. These are activities which males would perform regardless of the presence of young. For example, breeding male zebras *(Equus burchelli)* or gorillas *(Gorilla gorilla)* defend harem females and offspring when the latter are threatened. Presumably, a male would display such protective behavior both in the presence and absence of young. Similarly, behaviors such as scent marking and long-distance vocalizations which aid in the spacing of individuals or groups, and thus may maintain critical resources for eventual use by young, should also be considered as indirect forms of male parental investment which appear to be an incidental consequence of social organization and ecology. There are suggestions in the literature that the frequencies of these behaviors alter in response to the existence of young, even when they are not performed in the direct presence of young. Thus, male behavior may be modified when young are born, even if direct male care is not seen.

Indirect and incidental forms of investment are often ignored, but may be important. Ewer (1973) suggested that in carnivores such as otters, where males hold territories that overlap the ranges of several females, the young may benefit considerably by the territorial male's exclusion of other males from the preferred feeding areas. In birds, Wittenberger (1978) has related the various breeding systems seen in grouse to differences in the advantages which a female can gain from male territoriality. He suggests that monogamy will evolve in those species where a female can increase her foraging efficiency by feeding on a male's territory.

The second axis which will be used to differentiate between patterns of male parental investment* relates to the degree to which investment in one individual or litter precludes investment in others, a parameter that has been recognized as important by other authors [e.g., Maynard Smith (1977) and Ridley (1978)]. Altmann *et al.* (1977) have coined the terms "depreciable" and "non-depreciable." They define depreciable as follows: "A depreciable contribution is like a nonrenewable or slowly renewable resource: it is reduced in availability to one individual to the extent that it is expended on or used by another" (p. 409). In this paper, *individual* will refer to a single female or her current litter. Although the distinction between depreciable and nondepreciable is clear in extreme cases, most patterns of male investment have both depreciable and nondepreciable components.

Crouching with or huddling over multiple offspring provides the commonest example of nondepreciable direct investment, while regurgitation or carrying of young is usually depreciable. However, if resources being devoted to the young,

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*It should be obvious that these axes can also be used to differentiate types of maternal care.

such as meat carried to a den, are in such abundance or renew so fast that assistance to one individual or litter has little or no effect on the contribution to others, then even acts of regurgitation may sometimes be considered as nondepreciable. It will be argued below that when depreciable investment is a sufficiently valuable resource for females to compete over it, the social system may be profoundly affected.

It should be emphasized that the same behavior pattern may be considered as depreciable under some conditions (or in some species) and nondepreciable in others. The categorization depends on the species' social organization and reproductive characteristics. For example, in a polygynous, but nongregarious species where females raise young separately, huddling by a male with young may be a depreciable investment since only a single young or litter can be nested with at a time, while in a polygynous social species where females rear young communally, the male may be able to huddle simultaneously with a number of litters. The behavior may be nondepreciable under the latter circumstances.

Most forms of indirect male parental investment are nondepreciable in that they benefit several young without differentiating among them. One exception is the activity of a male feeding a pregnant or lactating female. Only one litter can benefit from this behavior at a time.

1.3. Measuring Male Parental Investment

Real problems exist in measuring the costs to a male, in terms of energy and risks of injury, in parental behavior, and the benefits in terms of increased survivorship accruing to the young. A simple list of the presence or absence of each pattern of investment is clearly insufficient. Measuring the frequencies or durations of patterns of male parental investment is a better solution but still imperfect, since we cannot measure the real energetic costs and risks. For indirect and particularly incidental forms of investment, there is a problem in deciding if the male really incurs costs by his contribution.

One method would be to consider each behavior pattern separately and attempt to gauge the relative difference between the sexes in performance of the pattern. For example, one can measure the time in the nest with young for a mated male and female and determine which sex spends relatively more time with the young. This approach results in a different male : female ratio for each behavior pattern performed by a species. Although such ratios may be meaningful in comparisons among closely related species where the behavior patterns of parental care are similar, they will be less useful when comparing broad taxonomic groups. However, data on six muroid rodents presented by Hartung and Dewsbury (1979) suggest that in most cases the amount of parental care exhibited by the male and female of a species will be correlated, i.e., there will be species differences in overall parental investment which will be reflected in both male and female parental care. Thus, the use of ratios to compare even closely related species may still be inappropriate.

Also, some highly significant male behaviors, which may be crucial to development, can occur over a very limited time span. For example, male canids may exhibit little direct care to young prior to weaning but then contribute significantly to the weaning process by bringing solid foods to the young.

Measuring indirect investment, especially the role of males in securing and maintaining resources, is also difficult. When males and females hold partially, or totally, overlapping, long-term territories, the male may aid the female and young by excluding competitors and detecting predators. However, many forms of land tenure in mammals do not conform to this simple pattern. In the analysis of male parental investment in carnivores presented below, males were only recorded as aiding females by securing resources if females also defended the same resources from conspecifics. This criterion excludes many "lek-type" territories in males.

Even in those cases where females and males appear to defend a common area or resource, a decision has to be made on whether a resident male (or males) limits or exacerbates competition for resources. In some species, such as lions *(Panthera leo)* (Schaller, 1972), resident males may appropriate food acquired by females. In other species, resident males may not completely exclude other males (Rood and Waser, 1978) or may defend areas only temporarily (Leyhausen, 1965). Carnivore species where active intersexual competition for food or resources has been reported were not recorded as showing indirect male investment in the analysis that follows.

1.4. The Available Data on Male Parental Investment

The broad definition of male parental investment used here makes a comprehensive survey of the mammals impossible. A very large number of species probably show some form of incidental, indirect investment, such as antipredator and sentinel behavior or resource maintenance and defense.

Our vast ignorance of the social life of most species in the rodents and bats reduced the problem of attempting a comprehensive survey. In this review, we sought evidence for both direct and indirect forms of male investment in the carnivores and summarized the literature on direct male care in other mammals. For the summary of male parental investment in primates, we have relied extensively on reviews by Hrdy (1976), Mitchell and Brandt (1972), Mitchell (1969), and Redican (1976), and have not, for the most part, cited original sources. The summary of primate male parental investment is therefore not exhaustive, but the reader can find more recent references in the bibliography prepared by Williams (1978).

Many of the descriptions of male parental care are based on laboratory or zoo observations. Although the captive setting usually provides the opportunity for more quantitative data collection, the conditions of confinement may seriously distort natural behavior, especially when the social milieu is abnormal. The successful induction of parental care, including grooming, retrieving, and nest building in male rats *(Rattus norvegicus)* after a 6- to 7-day exposure to infants (Rosen-

blatt, 1967), exemplifies the manner in which caregiving behavior towards young can be elicited by manipulation of the social and physical setting.

A recent debate on male parental care in domestic gerbils *(Meriones unguiculatus)* highlights other problems with captive observations. While several authors (e.g., Elwood, 1975; Elwood and Broom, 1978; Gerling and Yahr, 1979) have shown that male parental care is common in gerbils and does not negatively affect pup survivorship, Ahroon and Fidura (1976) found that the presence of a male significantly increased pup mortality. More recently, several explanations have been proposed for these contradictory findings [Klippel (a.k.a. Ahroon), 1979], most of which relate to the transport and housing of the experimental animals in the Ahroon and Fidura (1976) study.

Descriptions of male parental care is captivity should be treated with caution, unless the persistence of male parental care in a variety of individuals under a variety of conditions indicates that such behavior could be occurring in nature or there is some corroborative evidence from the field.

Available data on male parental investment in mammals fall into three categories. Some sources refer to the existence of male parental investment without detailing the specific behavior patterns. A second category names the behavior pattern observed but provides no quantitative data to indicate how common the act is. Third, and most rarely, authors have presented the behavior patterns involved in male parental investment as well as quantitative supporting data. The information available from different descriptions is rarely comparable. Also, authors infrequently describe changes in or refer to indirect forms of male parental investment.

Another problem involves the evaluation of negative evidence. In some studies, male parental investment could not be seen or expressed due to housing or observation conditions. In some, it could have occurred, but was simply not mentioned. The most reliable negative sources are obviously those in which the conditions were adequate for the behavior to be performed and seen, and the author specifically indicates that no male parental care was observed. Such references are as rare as those in which an author not only describes but quantifies both direct and indirect male parental investment. Thus, the available literature is, for the most part, inadequate.

2. Results

2.1. What Can Male Mammals Do?

Male mammals can neither gestate young nor lactate; thus their intrinsic ability to aid offspring is more limited than the female's. However, if these sex differences are disregarded, it appears as though males have the potential to display the same parental care patterns as females and that their ability to aid offspring is constrained by the same factors limiting female parental care.

For example, herbivorous mammals of either sex could rarely increase their offspring's survival or fitness by attempting to carry or hoard grass and leaves. However, where food comes in large, energy-rich packets which can be either stored for later use or carried, the potential for parental investment by both male and female increases. Thus, beaver *(Castor fiber)* can create a food hoard for postweaning feeding of young, and some larger carnivores are able to kill and transport large prey to developing offspring.

In any species in which environmental manipulation (i.e., nest building, trail formation) may be a critical factor in increasing both individual and offspring fitness, the male's role could approximate the female's. Interestingly, this is one behavior category where the males of different taxonomic groups may vary most in their investment relative to the females. For example, few carnivore males are reported to take a major role in burrow and nest construction. However, in a recent comparison of male parental behavior in six muroid rodents, Hartung and Dewsbury (1979) provide data suggesting that males of some muroids exhibit as much manipulation of nesting materials as females or in some conditions more.

Similarly, the maintenance of the trail system by clearing debris off pathways in rufous elephant shrews *(Elephantulus rufescens)* is more common in the male than in the female (Rathbun, 1979). Those behaviors which are usually exhibited more by males than by females are typically indirect and also contribute to the fitness of the male.

Two other factors may increase an offspring's fitness, but are not typically considered as evidence for male parental investment. First, for a large segment of artiodactyls whose young are hiders, the pattern of "avoiding offspring" may increase offspring survivorship. Indeed, among hiders, females similarly avoid young as an antipredator device. Unfortunately, males which actively avoid young and males which ignore young are difficult to distinguish, even though the former may be an evolved characteristic.

Second, in some cases tolerance towards juveniles may be an evolved attribute which contributes to offspring fitness. The males of highly territorial species who attack intruder conspecifics, but who do not attack maturing young within the territory, may have evolved a differential response to conspecific young. Male aggression towards young may also be differentially inhibited or suppressed, depending on the relationship of the male to the young (Hrdy, 1976). That aggression towards young is usually inhibited in male mammals when it is known that the young could provide a nutritional food source for the males of some species through cannibalism (Sherman, 1979) further suggests an evolved response. Of course, genes promoting male aggression towards, and cannibalism of, young would not be easily spread in most species, since the young most immediately available to a male are more likely to be related than unrelated. Thus a male would be reducing his own fitness by regular cannibalism.

The tendency of males to harm young may be inhibited by counterstrategies evolved by the young. For example, there are several descriptions of male mammals treating conspecific young of both sexes as though they were females. Geist

(1971) provides quantitative evidence for this phenomenon in Stone sheep *(Ovis dalli)*, and Rood (1972) describes it for the caviid genera *Cavia* and *Microcavia*. Smythe (1978) and Kleiman (1971) similarly report that individual males of the dasyproctid genera *Dasyprocta* and *Myoprocta* court and urinate over infants as though they were females. In some species, young may bear odors which resemble the adult female (they may even be transferred from the mother during early ontogeny) or, at least, smell unlike a mature male. Clearly, it is to the advantage of the young to develop and maintain mechanisms for not provoking aggression from adult males.

2.2. What Do Male Mammals Do?

Since male and female mammals have the potential to be similar in parental investment patterns (disregarding gestation and lactation), a summary of male parental behavior will resemble a summary of female parental behavior. Figures 1–4 present categories of indirect and direct investment which may be observed. Resource acquisition, maintenance, and defense (Fig. 1) refers to those behaviors (scent marking, patrolling, vocalizing, food hoarding, expulsion of intruders) which contribute indirectly to ensuring that necessary resources are available for use by young. Figure 2 presents additional indirect forms of male parental invest-ment, including provisioning the female, shelter construction, and antipredator behaviors. Of all indirect forms of male parental investment, only investment in the female does not contribute to male as well as juvenile survivorship.

Figures 3 and 4 detail direct male parental care in mammals. Huddling encompasses all behaviors associated with resting or sleeping in contact with young; by increasing body temperatures of young such behavior increases growth rates of deer mice *Peromyscus californicus* (Dudley, 1974*a,b*). Retrieval refers to either carrying or leading young back to a shelter or secure site. The transport of young includes carrying young on a regular or irregular basis during ordinary movements through the home range. Groom and clean young includes licking, nibbling, and other cleaning movements as well as ingesting excreta of young. Providing food for young consists of regurgitation of food, carrying food to young, and permitting young to take food in the male's possession (through food sharing or food stealing). It may also include leading young to a rich food source. Baby-sitting refers to remaining with young during the absence of the mother. Playing and socializing with young is a broad category encompassing all social interactions with young that contribute to the social development and social integration of young. Behaviors such as mutual sniffing, greeting, wrestling, and scent marking young are included in this category. Active defense of young includes only those aggressive behaviors performed when young are being harassed and threatened by conspecific or nonconspecific intruders.

Table 1 is a summary of direct male parental care in mammals, exluding the

Resource acquisition

Resource maintenance

Resource defense

Figure 1. Categories of male parental behavior: Indirect male investment. I. Behavior associated with securing resources for female and young.

carnivores. Indirect male investment was included in the remarks section only if it was conspicuously mentioned in a reference. Table 2 presents all available data on both direct and indirect male parental investment in carnivores, as well as references which specifically indicate the absence of male investment.

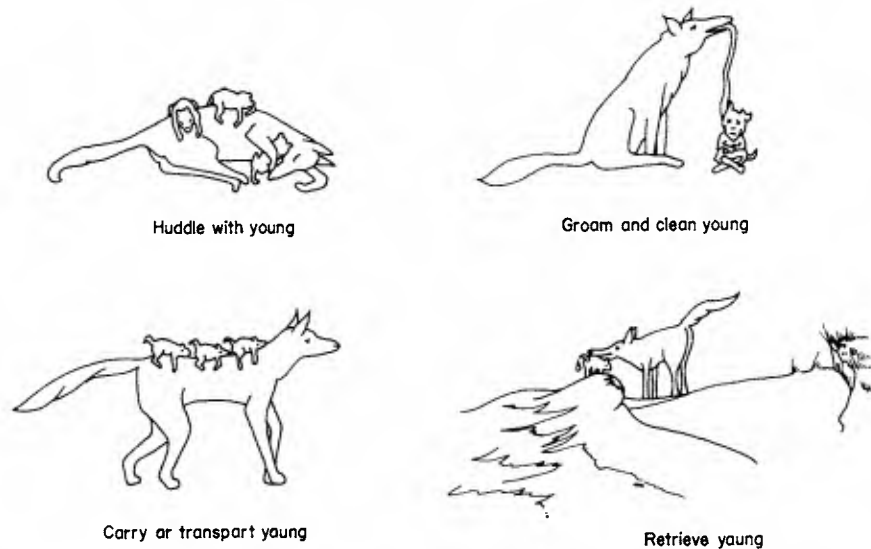Shelter construction and maintenance
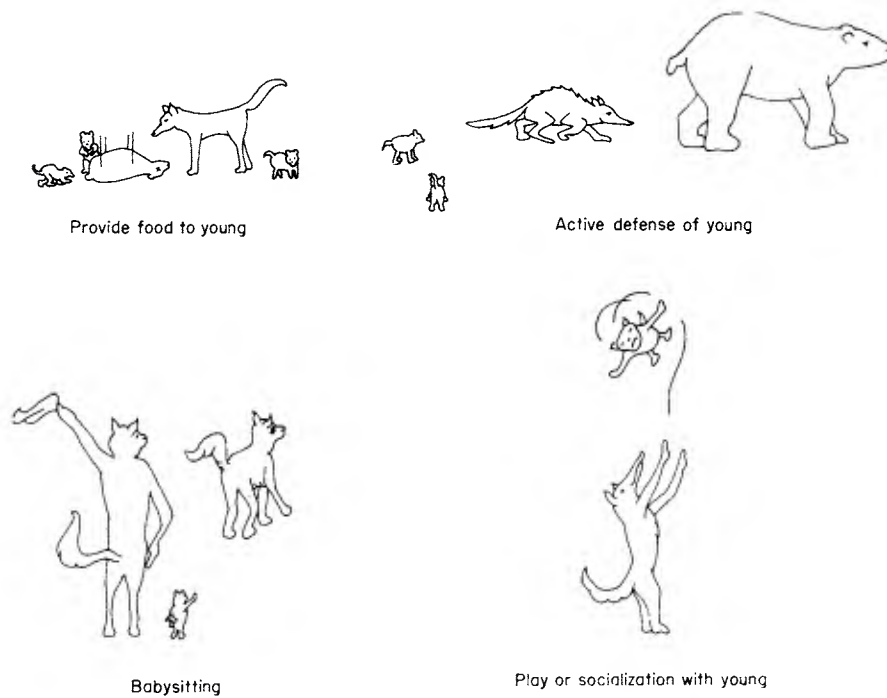
Sentinel and antipredator behavior

Care of female

Figure 2. Categories of male parental behavior: Indirect male investment. II. Other forms of indirect male parental investment.

Huddle with young   Groom and clean young

Carry or transport young   Retrieve young

Figure 3. Categories of male parental behavior: Direct male investment. I. Behavior often shown to young before they are weaned.

Figure 5 summarizes the data from Table 1 (and part of Table 2). The percent of genera within each mammalian order for which direct male parental care has been described is presented. Figure 6 presents the percent of genera in each order for which direct male parental care has been described relative to the total number of mammalian genera (from Walker, 1975). A comparison of the two figures reveals some interesting patterns. In several large orders direct male care has been recorded at low frequencies, regardless of how the data are presented; these include the marsupials, chiropterans, cetaceans, and artiodactyls. Several orders with few genera have a disproportionately large number of genera exhibiting direct male parental investment, especially the Perissodactyla, but the percent of genera are small relative to all mammalian genera. By contrast, although only a small percentage of rodent genera (6.4%) have been described as exhibiting direct male investment, the percentages for the rodents and primates are the same (2.2%), when all mammalian general are considered.

Nearly 40% of primate genera have been reported as exhibiting direct male parental care, the highest for any individual order. Yet, the carnivores show the greatest percentage of genera (Fig. 6), when all genera of mammals are considered.

Provide food to young   Active defense of young

Babysitting   Play or socialization with young

Figure 4.   Categories of male parental behavior: Direct male investment. II. Behavior often shown to young between weaning and independence.

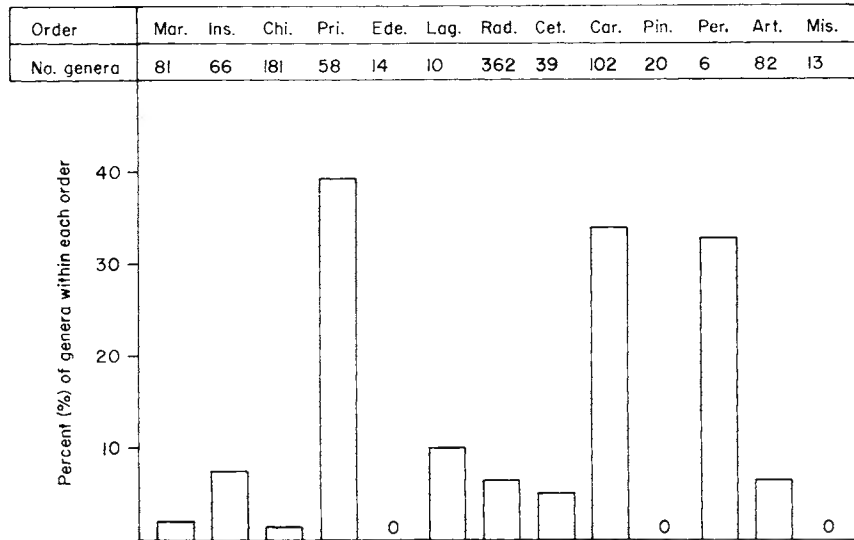Although the above figures are probably biased because our knowledge of different mammalian groups varies and the carnivores were researched more thoroughly than other orders, they may represent real trends. Thus, based on our current knowledge of the life histories and social systems of the marsupials, chiropterans, artiodactyls, and pinnipeds, it is unlikely that further research would reveal a much higher frequency of direct male parental care. A large percentage of the species within these orders tend to exhibit either or both of two characteristics; they are typically polygynous in their mating systems, and maternal care patterns are not very complex. By contrast the insectivores, once they are better known, might exhibit higher frequencies of direct male parental investment since maternal care patterns are complex and polygyny may be found to be less common than appears to be the case currently. Undoubtedly, once the rodents are better known, the genera of rodents in which direct male parental investment has been described will exceed the primate and carnivore genera, since the carnivores and primates are very well studied relative to the rodents.

Order	Mar.	Ins.	Chi.	Pri.	Ede.	Lag.	Rod.	Cet.	Car.	Pin.	Per.	Art.	Mis.
No. genera	81	66	181	58	14	10	362	39	102	20	6	82	13

Figure 5. The proportion of genera within each mammalian order in which direct male parental care has been recorded. Abbreviations: Mar., Marsupialia; Ins., Insectivora; Chi., Chiroptera; Pri., Primates; Ede., Edentata; Lag., Lagomorpha; Rod., Rodentia; Cet., Cetacea; Car., Carnivora; Pin., Pinnipedia; Per., Perissodactyla; Art., Artiodactyla; Mis. (miscellaneous) Monotremata, Dermoptera, Pholidota, Proboscoidea, Hyracoidea, and Sirenia.

Order	Mar.	Ins.	Chi.	Pri.	Ede.	Lag.	Rod.	Cet.	Car.	Pin.	Per.	Art.	Mis.
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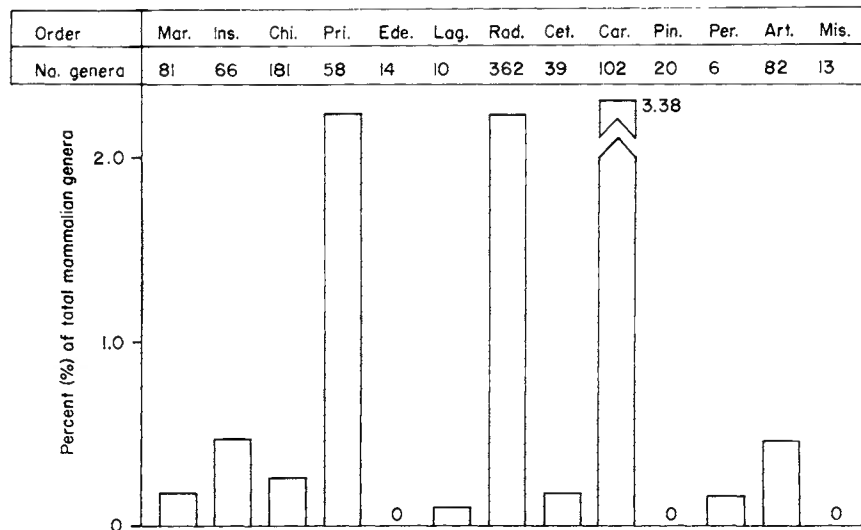
Figure 6. The genera of mammals in each order recorded as showing direct male parental care as a percentage of the total number of mammalian genera. Abbreviations as in Fig. 5.

Table 1. Direct Male Parental Investment in Mammals (Excluding Carnivora)[a,b]

Mammal	Depreciable	Nondepreciable	Source of observations	Modal mating system	Remarks	References
MARSUPIALIA						
Phalangeridae						
Petaurus breviceps Sugar glider	RT	DF, HD, BS	C	PGN		Schultze-Westrum (1965)
Dasyuridae						
Sarcophilus harrisii Tasmanian devil	CL		C	PGN		Turner (1970)
EUTHERIA						
Soricidae						
Suncus etruscus Etruscan shrew	RT	HD	C		SC	Fons (1974)
Cryptotis parva Least shrew	RT		C		SC	Conaway (1958)
Tenrecidae						
Hemicentetes semispinosus Streaked tenrec		HD	C		SC	Gould and Eisenberg (1966)
Tenrec ecaudatus Tenrec	PF		C		SC	Louwman (1973)
Macroscelididae						
Elephantulus rufescens Rufous elephant shrew	CL	HD, DF, PL	C, F	M	AP	Rathbun (1979) (personal communication)
Phyllostomatidae						
Phyllostomus discolor Spear-nosed bat	TR		F	PGN		Bradbury (1977)
Vampyrum spectrum False vampire	PF	HD	C, F	M		Greenhall (1968); Vehrencamp *et al.* (1977)
Pteropodidae						
Rousettus sp. Rousette bats	CL	HD	C	PBGM		Kulzer (1958)

Indridae					
Propithecus verreauxi	CL, TR, HD	HD	F	PGN	Mitchell (1969)
Sifaka					
Galagidae					
Galago senegalensis	PL, HD, DF	HD	C		Mitchell and Brandt
Senegal bush baby	CL, RT				(1972)
Tarsiidae					
Tarsius syrichta	TR, HD		C	M	Schreiber (1968)
Philippine tarsier					
Callitrichidae					
Callithrix jacchus	RT, TR, PF, HD		C	M	Mitchell (1969);
Common marmoset					Redican (1976)
Cebuella pygmaea	RT, TR, HD		C	M	Mitchell (1969);
Pygmy marmoset					Redican (1976)
Saguinus spp.	RT, TR, HD		C	M	Mitchell (1969);
Tamarins					Redican (1976)
Leontopithecus rosalia	RT, TR, HD		C	M	Mitchell (1969);
Lion tamarin					Redican (1976)
Cebidae					
Cebus albifrons	TR, PL	PL	C	PGN	Mitchell (1969)
Capuchin					
Saimiri sciureus	TR, PL, RT	PL	C	PBGM	Mitchell (1969);
Squirrel monkey					Hrdy (1976)
Alouatta palliata	TR, PL, RT	PL	F	PGN	Mitchell (1969)
Howler monkey					
Callicebus moloch	TR, RT, HD		F, C	M	Mitchell (1969)
Titi monkey					
Aotus trivirgatus	TR, RT, HD		F, C	M	Mitchell (1969)
Night monkey					

[a]Indirect male investment is indicated in "Remarks" only if it is very conspicuous. Definitions of mating systems are from Selander (1972).
[b]Key: Observation source: C, captive observations; F, field observations. Mating system: M, monogamy; PGN, polygyny; PBGM, polybrachygamy. Direct care: HD, huddle with young; CL, groom and clean; RT, retrieve; TR, carry and transport; PF, provide food to young; PL, play and socialize; DF, active defense; BS, babysitting. Indirect care: RA, resource acquisition; RM, resource maintenance; RD, resource defense; AP, antipredator, sentinel behavior; SC, shelter construction and maintenance; CF, care of female.

Table 1. *(Continued)*

Mammal	Depreciable	Nondepreciable	Source of observations	Modal mating system	Remarks	References
Cercopithecidae						
Macaca mulatta Rhesus monkey	PL, CL, HD, TR DF	PL, HD, DF	F, C	PBGM	Infrequent male care	Mitchell (1969); Redican (1976); Hrdy (1976)
Macaca fascicularis Crab-eating macaque	PL, DF	PL, HD, DF	C	PBGM		Mitchell (1969; Mitchell and Brandt (1972)
Macaca sylvana Barbary macaque	TR, RT, HD, CL BS, PL	BS, PL, HD	C, F	PBGM	Agonistic buffering	Mitchell (1969); Hrdy (1976); Redican (1976)
Macaca radiata Bonnet macaque	TR, RT, PL, DF	PL, DF	C	PBGM		Mitchell (1969); Mitchell and Brandt (1972)
Macaca fuscata Japanese macaque	TR, RT, PL, DF, CL, HD	PL, DF, HD	F	PBGM	Agonistic buffering, mainly with juveniles	Mitchell (1969); Hrdy (1976); Redican (1976)
Macaca nemestrina Pig-tailed macaque	DF	DF	C	PBGM		Mitchell (1969); Redican (1976)
Macaca arctoides Stump-tailed macaque	TR, RT, PL, CL, HD	PL, HD	C	PBGM		Estrada and Sandoval (1977)
Theropithecus gelada Gelada baboon	TR, PL	PL	F	PGN		Redican (1976)
Papio hamadryas Hamadryas baboon	TR, RT, DF, HD, BS	DF, HD, BS	F	PGN	Agonistic buffering adoption	Mitchell (1969); Hrdy (1976); Redican (1976); Mitchell and Brandt, (1972)
Papio anubis Anubis baboon	TR, RT, DF, BS	DF, BS	F	PBGM	Agonistic buffering adoption	Mitchell (1969); Hrdy (1976); Redican (1976)
Papio cynocephalus Yellow baboon	CL		F	PBGM		Mitchell and Brandt (1972)
Erythrocebus patas Patas monkey		DF	F	PGN	AP	Redican (1976)

Species						Reference
Presbytis entellus Grey langur	RT		F	PGN		Hrdy (1976)
Presbytis johnii Nilgiri langur	PL	PL	F	PGN		Hrdy (1976)
Pongidae						
Hylabates lar White-handed gibbon	TR, CL, PL		F	M		Mitchell (1969); Redican (1976)
Symphalangus syndactylus Siamang	TR, HD, BS, CL		F	M		Redican (1976)
Pan troglodytes Chimpanzee	RT, DF		F	PBGM	Adoption	Mitchell (1969); Hrdy (1976)
Gorilla gorilla Gorilla	TR, HD, CL	HD	F, C	PGN	Adoption	Mitchell (1969); Redican (1976); Tilford and Nadler (1978)
Pongo pygmaeus Orangutan	PL		C	PBGM		Zucker *et al.* (1978)
Leporidae						
Oryctolagus cuniculus Rabbit	CL		C	PGN	Scent mark young	Mykytowycz (1959, 1965)
Sciuridae						
Marmota caligata Hoary marmot	PL	HD	F	PGN	AP	Barash (1975)
Hystricidae						
Hystrix sp. Crested porcupine	CL, RT	HD	C	PGN		Mohr (1965)
Caviidae						
Dolichotis patagonum Mara		HD, DF	C	M	AP	Dubost and Genest (1974)
Dolichotis (Pediolagus) salincola Salt desert cavy		HD	C	M	AP	Kleiman (1974)
Dasyproctidae						
Cuniculus (Agouti) paca Paca	CL, HD		C	M	Scent mark young	Kleiman (1974)
Dasyprocta punctata Agouti			F, C	M	Scent mark and mount young	Smythe (1978)
Myoprocta pratti Acouchi	CL	HD, BS	C	M	SC, scent mark young	Kleiman (1969, 1972)

Table 1. *(Continued)*

Mammal	Depreciable	Nondepreciable	Source of observations	Modal mating system	Remarks	References
Chinchillidae						
Chinchilla lanigera		HD	C	PGN		Weir (personal communication)
Chinchilla						
Octodontidae						
Octodon degus	CL	HD, BS	C	PGN	Scent mark young, AP	Wilson and Kleiman (1974); Wilson (personal communication)
Degu						
Octodontomys gliroides	CL	PL, HD	C		Scent mark young	Wilson and Kleiman (1974); Wilson (personal communication)
Choz choz						
Capromyidae						
Capromys melanurus	CL	HD, DF	C	M		Bucher (1937)
Hutia						
Bathyergidae						
Heterocephalus glaber		HD	F, C	M	RA, RM, RD, SC	Jarvis (1978)
Naked mole rat						
Castoridae						
Castor fiber	CL, PF, TR	HD, BS	F, C	M	RA, RM, RD, SC, AP	Hodgdon and Larson (1973); Wilsson (1971)
Beaver						
Cricetidae						
Peromyscus melanocarpus	RT, CL	HD	F, C	M	SC, RD	Rickart (1977)
Peromyscus mexicanus	RT, CL	HD	F, C	M	SC, RD	Rickart (1977)
Mexican deer mouse						
Peromyscus californicus	RT, CL	HD, BS	C	M		Dudley (1974a,b)
California deer mouse						
Peromyscus maniculatus	RT, CL	HD, BS	C, F		SC	Howard (1949); Horner (1947); Hartung and Dewsbury (1979)
Deer mouse						
Peromyscus leucopus	RT, CL	HD	C			Horner (1947); McCarty and Southwick (1977); Hartung and Dewsbury (1979);
White-footed deer mouse						
Peromyscus polionotus	RT, CL	HD, BS, DF	C, F	M		Smith (1966)
Old-field mice						
Baiomys taylori	RT, CL	BS	C, F	M		Blair (1941)
Pygmy mouse						

Species						Reference
Reithrodontomys humulus Eastern harvest mouse	RT, CL	DF	C		SC	Layne (1959)
Onychomys leucogaster Northern grasshopper mouse	PF		C	M		Ruffer (1966)
Onychomys torridus Southern grasshopper mouse	RT, CL	HD	C	M	SC	Horner and Taylor (1968); Horner (1961); McCarty and Southwick (1977)
Meriones unguiculatus Clawed jird (gerbil)	RT, CL	HD	C		SC	Elwood (1975); Elwood and Broom (1978)
Meriones crassus Fat jird		DF	C		Prevent juvenile fighting	Fiedler (1973)
Meriones tamariscinus Tamarisk gerbil	RT, CL	DF, HD	C		Young lick and ingest female saliva; prevent juvenile fighting	Fiedler (1973)
Microtus ochrogaster Prairie vole	RT, CL	HD, BS	C	M	SC, RA	Thomas and Birney (1979); Wilson (in preparation); Hartung and Dewsbury (1979)
Microtus pennsylvanicus Meadow vole	RT, CL	HD, BS	C		SC	Hartung and Dewsbury (1979); Wilson (in preparation); Yardeni-Yaron (1952)
Microtus guentheri Levante vole		HD	C			
Microtus californicus California vole	RT, CL	HD	C		SC	Hartung and Dewsbury (1979)
Microtus montanus Montane vole	RT, CL	HD	C		SC	Hartung and Dewsbury (1979)
Muridae *Mus musculus* House mouse	RT, CL	HD	C	PGN	SC	Beniest-Noirot (1958)
Rattus fuscipes Rat	CL	HD	C	PBGM	SC	Horner and Taylor (1969)
Rattus (Myomys) daltoni Dalton's rat	RT	HD	C		SC	Anadu (1979)
Notomys alexis Hopping mice	RT, CL	HD	C	M		Stanley (1971); Happold (1976)

Table 1. *(Continued)*

Mammal	Depreciable	Nondepreciable	Source of observations	Modal mating system	Remarks	References
Pseudomys albocinereus Native mice	RT, CL	HD	C	PGN		Happold (1976)
Delphinidae						
Tursiops truncatus Bottle-nosed dolphin	BS		C	PBGM		M. C. Caldwell and D. K. Caldwell (1966)
Balaenopteridae						
Megaptera novaeangliae Humpback whale		DF	F			M. C. Caldwell and D. K. Caldwell (1966)
Equidae						
Equus caballus Horse	RT		F	PGN	AP	Feist and McCullough (1975)
Equus hemionus Kulan		DF	F	PGN	AP	Formozov (1966)
Equus burchelli Common Zebra		DF	C, F	PGN	AP	Wackernagel (1965); Klingel (1972)
Tapiridae						
Tapirus indicus Malay tapir	PL		C	PGN		Seitz (1970)
Rhinocerotidae						
Diceros bicornis Black rhinoceros	PL		C	PBGM		Dittrich (1967)
Suidae						
Phacochoerus aethiopicus Wart hog	HD		F	PGN		Geigy (1955)
Potamochoerus porcus Bush pig		BS	F			Skinner et al. (1976)
Bovidae						
Madoqua phillipsi Phillip's dik-dik	CL, DF		C, F	M	RA, RM	Simonetta (1966)
Oreotragus oreotragus Klipspringer	DF		C			Cuneo (1965)
Ovibos moschatus Musk-ox	RT	DF	F	PGN	AP	Tener (1965)

Table 2. The Presence and Absence of Male Parental Investment in the Order Carnivora[a,b]

Mammal	Direct										Indirect				References
	Males other than "father"	Any direct care	Huddle and sleep with	Groom and clean	Retrieve	Carry	Provide food	Active defense	Babysit	Play and socialize	Secure resources	Shelter construction	Antipredator sentinel	Care to female	
Canidae															
Canis lupus	+						+	+	+	+	+		+	+	Murie (1944); Haber (1977)
Canis latrans	+						+	+	+	+	+		+	+	Ryden (1974, 1975)
Canis aureus	+						+	+	+	+	+		+	+	van Lawick (1970); Moehlman (personal communication)
Canis mesomelas	+						+	+	+	+	+		+	+	Moehlman (1979) (personal communication)
Lycaon pictus	+		−	+	+	+	+	+	+	+	+	−	+	+	van Lawick (1974); Malcolm (personal observation)
Cuon alpinus	+						+	+						+	Davidar (1974)
Alopex lagopus							+			C				+	MacPherson (1969); Kleiman (1968)
Vulpes vulpes				C			+				+			+	Macdonald (personal communication); Tembrock (1957)
Vulpes corsac								C							Dathe (1966)
Vulpes velox							+								Egoscue (1962)
Fennecus zerda					C		+						C	C	Weiher (1976); Roberts, (personal communication); Koenig (1970)
Nyctreutes procyonoides					C		+							C	Stroganov (1962); Roberts (personal communication)
Otocyon megalotis							+		+	+			+	+	Lamprecht (1979)
Dusicyon culpaeus							+								Housse (1949)
Dusicyon griseus							+								Housse (1949)
Cerdocyon thous							C	C	C					C	Brady (1978)
Chrysocyon brachyurus								C							Brady (personal communication)
Speothos venaticus			C	C			C	C	C	C					Porton (personal communication); Drüwa (1977)
(17 spp.—no data)															

(continued)

[a]Care in captive animals is not recorded if it has also been seen in the field. Absence of care in captivity was not recorded, as many forms of care, such as resource defense, cannot be displayed in captive conditions. The distribution of species in genera follows Walker (1975).
[b]Key: +, recorded in field; −, recorded absent in field; ?, possible field record; C, recorded as present in captivity.

Table 2 (Continued)

Mammal	Males other than "Father"														References
		Direct									Indirect				
		Any direct care	Huddle and sleep with	Groom and clean	Retrieve	Carry	Provide food	Active defense	Babysit	Play and socialize	Secure resources	Shelter construction	Antipredator sentinel	Care to female	
Ursidae															
Ursus arctos		—									—				Stonorov and Stokes (1972)
Euarctos americanus		—									—				Rogers (1977)
Thalarctos maritimus		—									—				Perry (1966)
Melursus ursinus		—									—				Laurie and Seidensticker (1977)
(3 spp.—no data)															
Procyonidae															
Bassariscus astutus		—													Grinnell et al. (1937)
Potos flavus		—					C								Poglayen-Neuwall (1976)
Nasua narica		—								C	—				Kaufmann (1962)
Procyon lotor											—				Schneider et al. (1971)
Ailurus fulgens				C											Roberts (1975, personal communication)
(12 spp.—no data)															
Mustelidae															
Mustela erminea		?									+				Eringe (1977); Hamilton (1933); Powell (1978)
Mustela nivalis		?									+				Lockie (1966); King (1975)
Mustela rixosa		?													Hamilton (1933)
Mustela frenata		—													Quick (1944)
Mustela sibirica															Stroganov (1962)
Mustela putorius															Stroganov (1962)
Mustela lutreola															Gerell (1970); Novikov (1962)
Martes martes		—									+				Balharry (1978); Krott (1973)
Martes americana		?					+		+	+	+				Hawley and Newby (1957); Grinnell et al. (1937)
Martes flavigula		?									+				Stroganov (1962); Lekagul and McNeely (1977)
Gulo gulo		?													Kott (1959); Gipson (personal communication)

Species															Reference
Tayra barbara	−											C			Poglayen-Neuwall (1978)
Ictonyx striatus	−											+		+	Rowe Rowe (1978)
Meles meles												C			Middleton et al. (1974)
Arctonyx collaris															Parker (1979)
Mephitis mephitis												C			Verts (1967)
Lutra lutra	−						+					+	+	−	Erlinge (1968)
Lutra canadensis							+					C	+		Grinnell et al. (1937); Liers (1951)
Lutra maculicollis		C				+	+					C	−		Kingdon (1977)
Lutrogale perspicillata						+		+				+			Wayre (1978); Desai (1974)
Amblonyx cinerea			C	+		+		+				+	+	+	Wayre (1978); Leslie (1970)
Pteronura brasiliensis	+											+		+	Duplaix (1980)
Enhydra lutris												+	−		Kenyon (1969)
(45 spp.—no data)															
Viverridae															
Viverra zibetha	−	C										C			Lekagul and McNeely (1977)
Civettictis civetta	−											+	+	+	Rahm (1966); Kingdon (1977); Mallinson (1969)
Genetta genetta	−											+	−		Malcolm (personal observation)
Genetta tigrina	−											+	−		Carpenter (1970); Roberts (personal communication)
Nandinia binotata	−					C							−		Charles-Dominique (1978)
Arctictis binturong		C										C	+		Gensch (1962); Roberts (personal communication)
Fossa fossa												C	+	+	Albignac (1973)
Eupleres goudoti	−											+	+		Albignac (1973, 1974)
Galidia elegans												+	+	+	Albignac (1973)
Galidia fasciata												+	+	+	Albignac (1973)
Mungotictis decemlineata													+		Albignac (1973)
Salanoia concolor													−		Albignac (1973)
Herpestes pulverulentes	−											+	+	+	Rowe Rowe (1978)
Herpestes sanguineus	−											+	+	−	Rood and Waser (1978)
Mungos mungos	+		+	+	+	+	+					+	+	+	Rood (1974, personal communication)
Helogale parvula	+		C	+	+	+	+					+	+		Rood (1978); Kingdon (1977); Rasa (1972)
Ichneumia albicauda	−											C	−		Waser (personal communication)
Suricata suricatta	+			C		+							−		Ewer (1963, 1973); Roberts (personal communication)
Cryptoprocta ferox	−												−		Albignac (1973)
(53 spp.—no data)															

(continued)

Table 2 (Continued)

Mammal	Males other than "father"	Any direct care	Direct								Indirect				References
			Huddle and sleep with	Groom and clean	Retrieve	Carry	Provide food	Active defense	Babysit	Play and socialize	Secure resources	Shelter construction	Antipredator sentinel	Care to female	
Hyaenidae															
Hyaena hyaena							+			+	+				Mills (1978); Novikov (1962); Kruuk, (1976)
Hyaena brunnea															Mills (1978)
Crocuta crocuta							+			+ +	+ + +				Kruuk (1972)
Proteles cristatus		−													Kruuk and Sands (1972); Ketelhodt (1966)
Felidae															
Felis silvestris			C	C						C	+			C	Leuw (1957); Condé and Schauenberg (1969)
Felis libyca															Hemmer (1978)
Felis nigripes				C						C					Schürer (1978)
Felis serval		−	C				C			C	+				Geertsema (1976, personal communication)
Felis viverrina										C					Ulmer (1968)
Felis bengalensis							C			C					Dathe (1966); Roberts (personal communication)
Felis aurata										C					Tonkin and Kohler (1978)
Felis temmincki										C					Louwman and Van Oyen (1968)
Felis concolor															Seidensticker et al. (1973)
Felis geoffroyi										C	+				Scheffel and Hemmer (1975)
Felis yagouaroundi										C					Hulley (1976)
Lynx lynx										C					Berrie (1973); Dathe (1966)
Panthera leo		−	−	−	−	−	+	−	−	+	+ +	−	−	−	Schaller (1972); Bertram (1978)
Panthera tigris															Schaller (1972)
Panthera pardus							+			C	+ +				Bertram (1978)
Uncia uncia				C											Schaller (1972); Freeman and Hutchins (1980)
Neofelis nebulosa							C								Geidel and Gensch (1976)
Acinonyx jubatus		−						C			−				Schaller (1972); Bertram (1978)

In total, about 9–10% of mammalian genera have been described as exhibiting direct male parental investment. This percentage is quite high, considering that male mammals cannot lactate or aid during the early stages of development. The percentage is higher than the estimated 7.7% of genera in which monogamy occurs (Kleiman, 1977), suggesting that the potential for direct male parental investment in mammals is considerable and is not necessarily tied to a monogamous mating system. Indeed, many of the primates in which direct male parental care occurs neither are monogamous nor live in closed harems, the two social systems in which one would predict the greatest amount of male parental investment, based on certainty of paternity. Of course, the descriptions of direct male parental care we have used do not differentiate between species in which direct male parental care is commonly observed and those for which the behaviors are rarely seen. In many of the primates in which direct male parental care has been described, especially those species living in multimale groups, the behavior occurs erratically and idiosyncratically. Moreover, interactions with infants are often used to decrease aggression from more dominant males, a behavior which has been termed "agonistic buffering" (Deag and Crook, 1971) (see Table 1). Nevertheless, the capacity for demonstrating direct male parental investment appears to be common to a high percentage of primate genera.

Table 2 presents and Fig. 7 summarizes the distribution of both direct and indirect male parental investment in carnivores. References that stated that no male investment was seen in a field study were also included. Some data were found for 91 of the 232 species listed by Ewer (1973). Information is most sparse for the mustelids, viverrids, and procyonids. The data are biased towards large, diurnal species living in open habitats. Indirect investment, particularly male defense of a home range containing several females, will probably be recorded more frequently as more field studies are undertaken.

Male investment of some form has been reported, at least occasionally, in all four species of hyaenid, although it is not well developed in *Crocuta* and *Proteles*. Male investment has not been reported as absent from any canid, although there is considerable variation in the extent of male parental behavior within the family ranging from the almost solitary maned wolf *(Chrysocyon brachyurus)* to the highly social African wild dog *(Lycaon pictus)*. High levels of direct male care occur in tropical otters (Duplaix, 1980; Wayre, 1978) and in group foraging mongooses (Ewer, 1963; Rood, 1974, 1978). Direct male care in the form of playing with young and letting them take food items has been recorded in a number of felids in captivity. However, even in the species involved, not all males tolerate females and young. It is unclear whether these records are an artifact of captivity or whether some felids will show male parental care in nature under certain conditions.

Direct male care in mammals does not appear to be positively correlated with any particular diet type, although herbivores in general are underrepresented. It

is not restricted to any mode of life, being seen in terrestrial, aquatic, fossorial, and arboreal species. Male parental care has been recorded in more temperate than tropical rodents, but this probably reflects a sampling bias. Male parental investment may be more common in tropical than temperate ungulates. Male parental investment is not restricted to any particular mating system, although monogamous species are overrepresented. In particular, rodents reported as showing male parental behavior have usually been considered monogamous. This may reflect only the housing conditions of captivity.
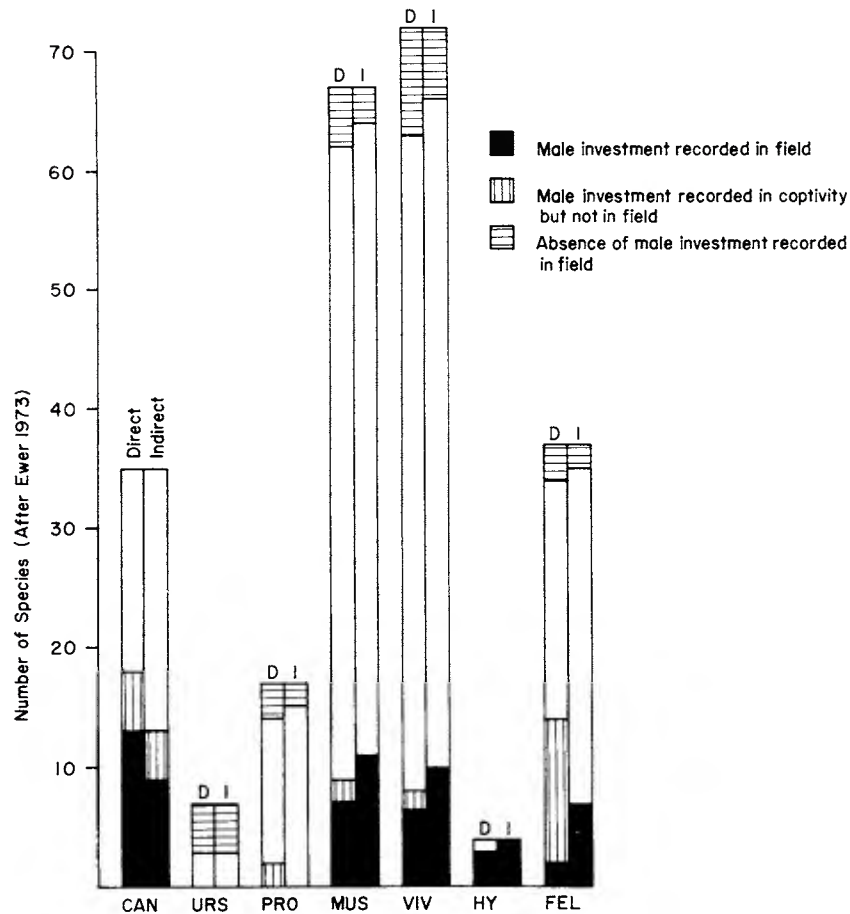
Figure 7. The presence and absence of recorded cases of male parental investment in all species of carnivores. Abbreviations: CAN., Canidae; URS., Ursidae; PRO., Procyonidae; MUS., Mustelidae; VIV., Viverridae; HY., Hyaenidae; FEL., Felidae.

In summary, high levels of direct male care appear to have evolved several times independently among the mammals. It is common in carnivores, perissodactyls, and primates and may be found to be more common among rodents and insectivores.

3. Discussion

3.1. Phylogenetic Considerations

Whether the mammals are considered to show a high or low incidence of species with male parental investment is largely subjective depending on how male parental investment is defined and with which other taxonomic groups the mammals are compared. Amongst the vertebrate classes, direct male investment in mammals is clearly less frequent than in the birds (Lack, 1968), probably more frequent than in the reptiles and amphibians (McDiarmid, 1978; Ridley, 1978), and comparable to or a little lower than in fishes (Breder and Rosen, 1966; Ridley, 1978).

In attempting to explain this pattern, Dawkins and Carlisle (1976) suggested that the evolution of internal fertilization and consequent susceptibility of the female to desertion might account for the low levels of male parental investment seen in mammals. However, this explanation does not help to elucidate the high levels of male parental care in birds.

A similar problem exists in the argument that internal fertilization lowers paternity certainty. Some of the most extreme forms of male parental care occur in birds such as the ratites and the American Jacana *(Jacana spinosa)* (Jenni, 1974) where the paternity certainty is lower than that in most monogamous species. However, differences in the internal development time between birds and mammals may affect certainty of paternity and thus have affected levels of male investment.

However, as Maynard Smith (1977) and Orians (1969) have noted, the evolution of lactation in addition to extended internal development does seem to have restricted the role that many male mammals can play. [Why male mammals do not lactate has been discussed by Daly (1979) and will not be considered here.] Male mammals cannot guard eggs, the most common form of male parental care in animals, and in many mammals the young are nearly independent at the time of weaning.

3.2. Factors That May Predispose Male Mammals to Care for Young

3.2.1. Intrinsic Ability to Aid Offspring

As has already been discussed, probably the most important factor explaining the distribution of male parental behavior relates to the male's ability to exhibit

parental care. Instances in which it appears males could provide care but do not have been mentioned above, e.g., in shelter construction, and will be further discussed below

3.2.2. Sociality

Permanent group living often seems to have fostered the evolution of male parental behavior. Incidental or indirect male investment, particularly alarm calls and the warding off of predators, is common in species living in large groups. More direct male care characterizes small "closed" groups often composed of genetically related individuals. Male primates constitute an exception, since male parental care is described for several species in which male immigration at puberty decreases the likelihood of males being related to all infants and juveniles.

The effects of sociality are very clear among the mongooses (Gorman, 1979). Species are divided into two distinct types; the diurnal, group foraging species such as *Mungos mungos, Helogale parvula,* and *Suricata suricatta* which show extensive direct male care including food provisioning, protection, and babysitting by males (Rasa, 1977; Rood, 1974, 1978), and a larger number of solitary, usually nocturnal forms where male investment seldom extends beyond mere tolerance of the young (e.g., Rood and Waser, 1978). Cooperative group foraging also seems important in the extreme case of communal breeding reported in naked mole rats *(Heterocephalus glaber)* (Jarvis, 1978), and in the wolf *(Canis lupus)* and other pack hunting canids. In the social species, males other than the father often provide care. In these cases the advantages of living in a group presumably outweigh the benefits of independent reproduction.

3.2.3. High Costs to Polygyny

As Maynard Smith (1977) and Trivers (1972) have stressed, the benefits to an offspring from male parental investment have to be counted by a male against his chances of mating again. Although in some cases a female would prefer a male who invests over one who deserts, there is also a point at which a female would prefer to mate with a successful polygynist who will give her effectively polygynous sons. ("Successful" and "effective" probably relate ultimately to the heritability of the traits leading to polygyny.) Except in cases of exceptional male investment (Grafen and Sibley, 1978), a male who mates with a number of females will outreproduce a monogamist.

Certain cases of direct male care in mammals may have evolved in situations in which a male could not consistently mate with more than one female, even if he deserted, because females are so widely dispersed and so irregularly in estrus. A number of small, dispersed, tropical forms such as dik-dik (*Madoqua* spp.) and other small ungulates, elephant shrews (Macroscelididae), and dasyproctids (*Agouti, Dasyprocta,* and *Myoprocta*) may fall into this category. In these cases

it does not appear that the habitat is "harsh" if measured in terms of the rate of adult mortality, but individuals would probably risk very high costs if they strayed beyond the limits of a territory which they know with great accuracy. In the case of the rufous elephant shrew, *E. rufescens,* the male devotes considerable time to maintaining a network of trails through the territory. In these species the intrinsic ability of a male to make a direct contribution to raising young seems limited. Indeed, maternal care is restricted by the precocial nature of the neonates and the absentee parental care system. However, the young may reap considerable indirect rewards by the use both of resources in the territory and of the system of escape trails (Rathbun, 1979).

3.2.4. Paternity Certainty

Few cases have been reported to date in which males invest in offspring to which they are distantly related or unrelated genetically. However, males other than the father certainly care for young both in those species with cooperative breeding ("helpers at the nest") and in some social species with a multimale group structure, e.g., baboons (*Papio* spp.) and capuchins *(Cebus nigrivittatus)* (Robinson, personal communication). In addition, there are species in which a male appears to be able to identify his offspring, e.g., species with male infanticide (Hrdy, 1977), but in which the male provides little or no care. Paternity certainty may represent a necessary but not sufficient condition for the evolution of male investment, and it is unsurprising that male parental care is commoner in species which are monogamous or live in one-male "closed"groups.

3.3. The Role of Male Parental Investment in Molding the Social Organization of Species

There are obvious correlations between a species social organization defined in terms of the mating and land tenure systems and the relative contribution of the sexes to raising young. Trivers (1972) suggested that the relative parental investment of the sexes was the factor "governing" or directing the operation of sexual selection. This may be useful when considering the operation of sexual selection at a single point in time. However, when the evolution of patterns of parental investment is considered, it is seldom clear if the relative parental investment of the sexes is a cause or a consequence of some antecedent pattern of sexual selection. In many cases the relative parental investment of the sexes seems to be constrained by some other aspect of the natural history of the species. Therefore, it is probably more useful to consider the correlations between mating system, variance in reproductive success, and differential parental investment as the result of co-evolution between the factors rather than attempt to erect one factor as directing the evolution of the other two.

For many indirect forms of male parental investment, it is unlikely that the behavior or distribution of females would be significantly altered if the males provided no investment. Klingel (1972) provides evidence that groups of female zebras *(E. burchelli)*, like many primate groups, retain their integrity even in the absence of males despite the fact that zebra males may actively defend their harems from predators. Similarly, the dispersion of females in many "solitary" species such as the mustelids and cats appears to be independent of male dispersion, although the males may provide important indirect benefits by excluding other males.

Even in some cases where a male direct its care to the offspring of a single female, it appears that the male's investment need not play an important role in the dispersion, rearing strategy, or intrasexual selection in the female. Rathbun (1979) reports that for a species of elephant shrew *(E. rufescens)* the male and the female rarely interact and most territorial defense is directed towards members of the same sex. It seems unlikely that the behavior of the female would differ if the males' ranges overlapped those of several females as is more usual in mammals generally.

For the species mentioned above, it appears that the mating systems have evolved in response to factors in the ecology or natural history of the species independent of the capacity of the males to invest in young. Even in species with monogamy, it is usually not the male parental investment which appears to restrict a male to mating with a single female. Male parental investment such as sentinel and antipredator behavior, and occasionally playing with young, which are seen in a number of group-living species especially, are probably displayed by males only to the extent that they do not interfere with a polygynous mating system. It is unlikely that a male in such species would ever give up an opportunity to consort or mate with a female in order to care for young.

The situation is different in species with high levels of depreciable male investment. Important components of the social organization and mating systems of these species can only be understood as consequences of the high levels of male parental care. These species, which include golden lion tamarins *(Leontopithecus rosalia)*, African wild dogs, and wolves *(Canis lupus)*, share a complex of behavioral characters which include more intense competition between females than males (Kleiman, 1979; Frame *et al.,* 1979), sex ratios tending towards males, disproportionate female emigration, and often care provided by adults in addition to the father. It appears that in these species females compete for access to male investment, which in tamarins involves carrying the young and also providing food (Hoage, 1977, 1978) and in canids involves providing food and protection for an extended period of dependence. The species involved are all classed as "obligate" monogamists by Kleiman (1977). The extent to which other obligate monogamous species show the same traits may depend on the extent to which the contribution of males to the young is depreciable.

4. Conclusions

Virtually no data exist for mammals which relate male parental investment to the fitness of offspring in a quantitative way. Some results (Malcolm, 1979; Moehlman, 1979), show that behavior of the parental type provided by animals in addition to the father increases the fitness of young born into the group, from which one presumes that parental behavior by the father also increases the fitness of the young. Mugford and Nowell (1972) have shown that male mice raised with the father are more aggressive during encounters (after a period of isolation) than mice raised alone with the mother. Such behavior might improve a male's fitness, although it is not known what behavior on the part of the father could cause this increased aggression.

Captive studies have produced confusing results with respect to the effects of male parental care on fitness. As already mentioned, in gerbils the male has been claimed to increase, decrease, or have no effect on the fitness of offspring (Ahroon and Fidura, 1976; Elwood and Broom, 1978; Gerling and Yahr, 1979; Klippel, 1979), but the different experimental conditions apparently greatly affected the results. In other experiments, huddling and retrieving by virgin mice housed with mothers (Sayler and Salmon, 1971) decreased the mean weaning weight of the young, suggesting that apparently caregiving behaviors may have deleterious effects.

For many species the reason why they do or do not show male parental care remains unclear. However, it is probably not useful to look for global explanations in terms such as richness or harshness of the habitat. In many cases there are probably two or more predisposing factors that act in concert. For instance, the advantages of cooperative hunting combined with the canid ability to regurgitate may have led to the high levels of male parental investment seen in the social canids. The absence of male parental behavior is often as surprising as its occurrence. Few male primates or bats share the prolonged burden of carrying the young, and large numbers of carnivores do not share food with their offspring.

To understand why certain species show male parental investment, it is necessary to know the alternative ways in which a male's reproductive effort could be channeled. Recent studies by Owen-Smith (1977) and Popp (1978) have related different male reproductive strategies in ungulates and baboons, respectively, to ecological factors. In particular, Owen-Smith argues that territoriality in ungulates represents a low-cost/low-benefit form of effort. These results suggest two ways in which the evolution of male parental investment in mammals could be investigated.

First, some modeling of the distribution of a male's reproductive effort into various channels, some of which include direct or indirect parental investment, would be useful. The usual models typically assume some unitary mode of reproductive effort which varies monotonically with fitness. However, as argued above,

some forms of male parental investment may not interfere with polygyny. The models would also have to include the role of heritability in the evolution of traits leading to polygyny (see Weatherhead and Robertson, 1979).

Second, field data could be collected on groups which show interesting patterns of variation in male parental behavior. Coyotes *(Canis latrans)* may show male parental care in parts of their range [e.g., Wyoming (Camenzind, 1978)] but not in others [e.g., Minnesota, (Berg and Chesness, 1978)]. The otters might also be a suitable group, as temperate forms are polygynous while most tropical species seem to live in monogamous groups, with one species *(Lutra maculicollis)* perhaps living in larger social groups (Kingdon, 1977; Proctor, 1962). The high levels of male tolerance and food sharing in captive small felids also suggest that they would be interesting to study, especially to compare a species at low and high population density where the ability to find mates might differ.

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