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Life History Patterns and the Comparative Social Ecology of Carnivores

Marc Bekoff
University of Colorado

Thomas J. Daniels
University of Colorado

John L. Gittleman
Smithsonian Institution

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Marc Bekoff[1], Thomas J. Daniels[1], John L. Gittleman[2]

[1] University of Colorado
[2] Smithsonian Institution

INTRODUCTION

The mammalian order Carnivora is characterized by a great range of behavior- al, ecological, and morphological adaptations, as well as substantial intraspecific variability (i.e. behavioral scaling; see 324). For example, in wolves (see Table 1 for scientific names), body size ranges from 31 to 78 kg, litter size varies from 1 to 11, home-range size differs 50-100 fold, populations are found in every vegetational zone except tropical forests and arid deserts, and individuals may live alone, in pairs, or in large packs (124, 204, 332).

Despite such widespread variation, comparative analyses indicate that there also is remarkable consistency (86, 105) in the ways many diverse carnivores adapt to their habitats. Therefore, it is possible to highlight trends in the phylogeny of behavior and life history characteristics by drawing on data from numerous disciplines, including anatomy, physiology, taxonomy, behavior, and ecology (16, 54, 83, 84, 92, 93, 97, 128, 191, 196, 199, 242, 243, 313, 331).

Due to space limitations, we will primarily review field studies focusing on the variation in behavior, body size, and life histories and emphasize data collected on identified individuals that have been observed directly (sometimes supplemented by radio-tracking) over long periods of time. Such studies are limited in number and comparative breadth, so information from shorter field studies and data on captive animals will also be used as a supplement. Comparisons of artificially and nonartificially fed groups must be treated carefully, however, since food resources have strong direct effects on social behavior (263). In addition, comparisons of exploited and (relatively) unexploited populations must take the food source into account (156). Finally, we will briefly discuss some practical aspects of data collection and analysis.

Our approach is pluralistic in two respects. First, rather than focusing on either intraspecific or interspecific variation, we emphasize the reciprocal exchange of information between both levels of analysis. Comparative studies generate hypotheses that often can only be verified in single-species studies, and the generality of functional explanations of a species' trait rests with comparative analyses among related taxa. Second, because confounding variables involving size constraints and phylogenetic effects are frequently associated with behavioral and ecological diversity (62, 64, 112, 113a), we include allometric and phylogenetic trends in our discussion of carnivore behavioral ecology.

Both descriptive studies and field experiments are still sorely needed for most carnivores. Textbooks, reviews, and popular articles frequently exaggerate our knowledge of certain phenomena (71). As Dunbar (75) stressed, long-term field studies must be performed if we are ever to learn about the evolution of the behavior and social ecology of long-lived "higher" species, in which intraspecific variation is so obvious.

Table 1. Scientific and common names of Carnivores referred to in the text.

Family Genus and species	Common name	Family Genus and species	Common name
Canidae		Viverridae	
Dusicyon culpaeus	South American fox (culpeo)	*Helogale parvula*	Dwarf mongoose
Dusicyon griseus	Chico gray fox	*Suricata suricatta*	Meerkat
Fennecus zerda	Fennec fox	*Hemigalus derbyanus*	Banded palm civet
Lycaon pictus	African wild dog	*Ichneumia albicauda*	White-tailed mongoose
Otocyon megalotis	Bat-eared fox	*Mungos mungo*	Banded mongoose
Alopex lagopus	Arctic fox	*Nandinia binotata*	Palm civet
Canis lupus	Wolf	*Osbornictus piscivorous*	Fishing genet
Canis latrans	Coyote	*Genetta genetta*	Common genet
Canis aureus	Golden jackal	*Fossa fossa*	Fanaloka
Canis mesomelas	Black-backed (silverbacked) jackal		
Nyctereutes procvonoides	Raccoon dog	Hyaenidae	
Vulpes vulpes	Red fox	*Hyaena hyaena*	Striped hyena
Cuon alpinus	Dhole or red dog	*Hyaena brunnea*	Brown hyena
Cerdocyon thous	Crab-eating fox	*Crocuta crocuta*	Spotted hyena
Speolhos venaticus	Bush dog	*Proteles cristatus*	Aardwolf
Chrysocyon brachyurus	Maned wolf		
		Felidae	
Procyonidae		*Herpailurus jagouaroundi*	Jaguarondi
Procyon lotor	Raccoon	*Leopardus geoffroyi*	Geoffroy's cat
Nasua narica	Coati	*Puma concolor*	Mountain lion or cougar
		Felis margarita	Sand cat
Ursidae		*Prionailurus bengalensis*	Bengal cat
Ursus americanus	Black bear	*Panthera leo*	African lion
Thalarctos maritimus	Polar bear	*Panthera tigris*	Tiger
Helarctos malavanus	Malayan sun bear	*Panthera pardus*	Leopard
		Panthera onca	Jaguar
Ailuridae		*Acinonyx jubatus*	Cheetah
Ailurus fulgens	Red panda	*Leopardus pardalis*	Ocelot
		Lynx canadensis	Lynx
Ailuropodidae		*Lynx rufus*	Bobcat
Ailuropoda melanoleuca	Giant panda	*Caracal caracal*	Caracal
Mustelidae			
Mustela nivalis	Least weasel		
Mustela erminea	Stoat or ermine		
Mustela vison	American mink		
Mustela frenata	Long-tailed weasel		
Metes metes	European badger		
Lutra lutra	European otter		
Enhydra lutris	Sea otter		
Martes americana	American marten		
Martes pennanti	Fisher		
Gulo gulo	Wolverine		
Mephitis mephitis	Striped skunk		

GENERAL CHARACTERISTICS OF CARNIVORA

Broadly speaking, members of the order Carnivora are distinguished from other mammals by their carnassial dentition and the high proportion of vertebrates their diets (Carnivora is derived from the Latin *caro: carnis* meaning "flesh" and *voro*, "to devour"). As in other mammalian orders, however, there are many interesting exceptions to these general characteristics. For example, the white-tailed mongoose and the bat-eared fox are insectivorous; the red panda and the giant panda feed primarily on bamboo; and the black bear maintains itself on a catholic herbivorous/frugivorous diet. Besides their dentition and diet, carnivores' other pronounced traits (93, 140, 242, 243, 271) include: (a) a jaw joint that is a transverse hinge, which facilitates biting and cutting but does not permit grinding action by the teeth; (b) a vertebral column that is strong and flexible and a long tail; (c) a brain that is relatively large, particularly in comparison to herbivores and insectivores; (d) anal and forehead scent glands that are well-developed and are used in marking, social recognition, and defense; (e) a walking gait that ranges from plantigrade to digitigrade; and (f) in most species, soft fur covered by longer guard hairs.

The order Carnivora is divided into two superfamilies, Canoidea and Feloidea, and seven polytypic families-Canidae, Ursidae, Procyonidae, Mustelidae, Viverridae, Hyaenidae, and Felidae. Although there is continuing controversy, growing evidence suggests that the red panda and giant panda belong in two monotypic families, Ailuridae and Ailuropodidae, respectively, rather than in the Procyonidae or Ursidae, as was previously thought (83, 251).

CANIDAE The Canidae, with 36 species divided among 16 genera, is composed of small- to medium-sized carnivores (1-60 kg) distinguished by their cursorial mobility and strong jaws and cheek muscles (60, 226, 227, 285). Canids live in a wide variety of habitats. More behavioral and ecological information is available for Canidae than for any other carnivore family because they are typically diurnal and include an unusually large number of group-living species (4, 16, 24, 97, 105, 124, 157, 159, 191, 204, 331, 332). In many of these species, both parents provision and protect their young (158). Much of our discussion below centers on patterns in the Canidae.

PROCYONIDAE Closely related to Canidae is Procyonidae, which includes 18 species in 6 genera. Procyonids are comparatively small carnivores (0.8-12 kg) confined to the New World, and all are semiarboreal, prefer temperate and tropical vegetational zones (144), and have a plantigrade gait. Most of them are solitary, although raccoons are frequently seen in extended family groups (102; Seidensticker, personal communication) and coatis live in female-banded groups with as many as 10 adults (143, 266, 267).

AILURIDAE AND AILUROPODIDAE Both red pandas and giant pandas (placed in Ailuridae and Ailuropodidae, respectively) are from central Chinese provinces; red pandas also occur in Nepal, Sikkim, and northern Burma. These two species feed primarily on bamboo and are solitary except during the breeding season (155, 251).

URSIDAE The family Ursidae (bears) consists of 7 species divided among 6 genera, which (with the exception of the Malayan sun bear) inhabit the Northern Hemisphere and northern South America. Their dentition reflects a shift away from carnivory toward herbivory: The anterior premolars are small and the carnassials are nonsectorial and have lost most of their shearing character. Ursids' walking gait is plantigrade. They are relatively solitary; adults only remain together during breeding or when food is abundant in patches. Maternal care may last for an extended length of time during harsh seasons (93, 129, 130), which, combined with small litter sizes and long interbirth intervals, results in comparatively low reproductive rates.

MUSTELIDAE The last family included in the superfamily Canoidea is Mustelidae. It is divided into the following subfamilies: Mustelinae (weasels, polecats, fisher, martens, wolverine, tayra), Mellivorinae (badgers), Mephitinae (skunks), and Lutrinae (otters). Mustelidae consists of 67 species in all, distributed among 27 genera, and they are found everywhere except Australia, Antarctica, and Madagascar. Mustelids are small- to medium-sized carnivores (.025--45 kg) with long bodies, short legs, and usually medium to long tails. The aquatic Lutrinae and the omnivorous Mephitinae and Mellivorinae are recent radiations that diverged from the basic carnivorous characteristics of the family. Most species are solitary and live in forest habitats (89, 90, 296), although group living is found in European badgers (164, 165) and sea otters (147). Most species in this large family have only been studied in captivity.

VIVERRIDAE The oldest lineage within the superfamily Feloidea is Viverridae. This family has retained many of the features thought to be representative of ancestral carnivores (Miacidae). The Viverridae is the largest carnivore family, is comprised of 70 species distributed among 39 genera, and is confined to the Old World tropics and subtropics. It has six subfamilies: Viverrinae (civets, genets, linsangs), Paradoxurinae (palm civets, binturong), Hemigalinae (fanaloka, banded palm civet), Galadinae (Madagascar mongooses), Herpestinae (mongooses, suricate), and Cryptoprocinae (fossa). Viverrids are small carnivores (0.45-14 kg) and generally have long tails and relatively short limbs that are semiplantigrade or digitigrade (the claws are partly retractile in digitigrade species). The family is a somewhat heterogeneous assemblage and is more ecologically diverse than any other carnivore group, ranging from solitary, forest-living species (common genet) to open savannah, group-living animals (banded and dwarf mongooses). Their dietetic affinities vary from insectivorous (banded palm civets) to frugivorous (palm civet) to piscivorous (fishing genet). Viverridae have not been studied in as much detail as other families (2, 110, 135, 152, 316).

HYAENIDAE The family Hyaenidae contains three species of hyenas (in two genera) and the aardwolf. Hyenas are found in Africa, the Middle East, and central and south Asia; aardwolves live in southern Africa. Hyenas are fairly large animals (8-70 kg) with particularly large heads and powerful jaw and neck muscles. Their teeth are large and the carnassials are well developed. Their forequarters are heavier than their hindquarters, their legs are thick, and they have a digitigrade gait. Behaviorally and ecologically, the hyenas are diverse (212, 213, 216, 230). The striped hyena is omnivorous, foraging on fruits, insects, and small mammals (as well as scavenging); it lives in acacia savannah and open grassland habitats (163, 250). Brown hyenas are also omnivorous and live in small family groups of 4 to 14 individuals in open shrub or woodland savannah habitats (213-216, 229, 232). The spotted hyena is strictly carnivorous, with larger carnassials than the other hyenas, and it lives in "clans" of up to 80 individuals in Ngorongoro Crater or in temporary associations in the Serengeti (161, 162). The aardwolf is different from the hyenas, though it is sometimes confused with the striped hyena because of its similar appearance. It has a reduced dentition and a small head and shoulders, feeds mainly on termites, and is solitary (166).

FELIDAE The last carnivore family, Felidae (cats, caracal, puma, ocelot, jaguarondi, lynx, leopard, jaguar, lion, cheetah), contains 37 species and 21 genera. The classification of Felidae remains somewhat uncertain, particularly with regard to the genera *Felis* and *Panthera* (227). We have adopted Ewer's taxonomic scheme (93). Felidae are found on all continents except Australia. They are small- to large-sized carnivores (1.5-300 kg), short faced, with highly sectorial carnassials and sharp retractile claws (except for cheetahs). The tongue is covered with curved, backwardly directed, horny papillae. Felids are highly carnivorous, and although they are found in every type of habitat, they most often reside in woodland and fringe-woodland terrain. All felids are solitary (157), except for lions, which live in prides of 2 to 18 adult females (usually related to one another) and 1 to 7 adult males (32, 33, 37, 50, 87, 157, 182, 273). In the central Kalahari, female pride mates are frequently unrelated; prides periodically disband and some females join "foreign" prides, especially when prey densities are low (M. J. Owens, personal

communication). Male breeding coalitions appear to contain nonrelatives more frequently than was previously thought (234); males are typically unrelated to pride females. [Comparative data can be found in Eaton (77-80).]

LIFE HISTORY PATTERNS

Interspecific Comparisons

Cross-species comparisons of life history traits in Carnivora reveal extensive differences in rates and modes of reproduction. Undoubtedly, much of this variation may be accounted for by body size differences (83, 319), and such allometric effects must be incorporated into comparative studies. Even taxonomically related and similarly sized species differ markedly, however. In the Viverridae, the fanaloka and common genet both weigh an average of 1.7 kg, but their life histories are quite different. The fanaloka's gestation period is about 85 days, it usually has a litter size of one, and it weans its young about 52 days after birth (1, 2, 316), whereas the common genet's gestation period is about 72 days, its litter size is 3-4, and it weans its young around 175 days after birth (93, 253, 308, 316).

Because of the great variation within the order, carnivores are an excellent group for studying the adaptive patterns of life history traits. Furthermore, although some variables are difficult to measure (e.g. weaning age) and certain taxa are overrepresented in the available data (e.g. Canidae), the following variables have been consistently measured in both captive and natural populations: gestation length, birth weight, litter size, age at weaning, age at sexual maturity (i.e. at first reproduction), age of independence (i.e. at dispersal from natal territory or establishment of foraging independence), interbirth interval, and longevity. In the following sections, we discuss the variation in these life histories in relation to size constraints, taxonomy, food habits, and ecological characteristics. [Discussions of sexual dimorphism can be found in Ralls (245, 246), Eisenberg (83), and Gittleman (105)].

Body and Brain Size

A close relationship between adult body or brain size and life histories is widely found in eutherian mammals (83, 210, 211, 319). All of the above life history variables correlate significantly with carnivore's adult body weight and brain weight (Table 2), and a common slope can be drawn for the whole order (see 105). Many of the slopes of life history traits are similar to those found in other mammalian groups, supporting the hypothesis that the same physiological and energetic factors produce constants in scaling throughout the Mammalia class (51, 202, 319).

Because some error and uncertainty of dependence occurs among these variables, the slopes in Table 2 were calculated using major axis analysis, rather than standard regression techniques (126). The slope for gestation length on body weight for 93 carnivore genera is 0.10, which is similar to Western's (319) figures for artiodactyls (0.16), primates (0.14), and carnivores (0.12), and to Kihlstrom's (148) calculations for 208 species of eutherian mammals (0.17).

Birth weight also scales similarly across diverse mammalian taxa. Using regression analysis, Leitch et al (179), Leutenegger (180), and Millar (210) independently calculated exponents between 0.63 and 0.83 for a wide array of bats and other small mammals, carnivores, and primates. The exponent for 62 genera of Carnivora, the largest representative sample thus far assembled, is 0.81, similar to other exponential values.

Litter weight; ages at weaning, independence, and sexual maturity; and longevity also scale to both body and brain size (105). Although physical models cannot explain the precise functional causes of such

allometric scaling (51, 203, 319), comparative evidence on carnivore life histories warrants the inclusion of size factors in analyses of both inter- and intraspecific variation among these traits.

Table 2 Statistical relationships between 8 life history traits and adult body and brain weight across the order Carnivora (from 105)

Life history trait	Compared to body/brain weight	No. of genera	No. of families	Correlation coefficient (r)	Coefficient of determination (r^2)	Slope of major axis line across order	Heterogeneity across families F(df)
Gestation length	Body	93	7	0.85	0.73	0.10	2.8 (6, 86)[b]
	Brain	93	7	0.82	0.68	0.15	1.4 (6, 86)[e]
Birth weight	Body	62	6	0.87	0.75	0.81	5.7 (6, 54)[d]
	Brain	62	6	0.91	0.83	1.35	10.45 (6, 54)[d]
Litter weight	Body	59	6	0.84	0.71	0.86	6.1 (6, 52)[d]
	Brain	59	6	0.88	0.78	1.63	6.3 (6, 52)[d]
Weaning age	Body	62	6	0.62	0.38	0.23	2.5 (6, 55)[a]
	Brain	62	6	0.58	0.34	0.37	2.4 (6, 55)[a]
Age at independence	Body	26	4	0.84	0.71	0.41	4.6 (4, 23)[c]
	Brain	26	4	0.88	0.77	0.76	6.7 (4, 23)[d]
Age at sexual maturity	Body	54	7	0.81	0.65	0.37	5.8 (6, 47)[d]
	Brain	54	7	0.77	0.60	0.58	9.4 (6, 47)[d]
Interbirth interval	Body	54	5	0.67	0.45	0.10	4.9 (5, 49)[b]
	Brain	54	5	0.64	0.41	0.13	5.2 (5, 49)[d]
Longevity	Body	48	7	0.75	0.57	0.12	2.4 (6, 41)[a]
	Brain	48	7	0.76	0.58	0.22	2.2 (6, 41)[e]

[a] $p < 0.05$

[b] $p < 0.025$

[c] $p < 0.01$

[d] $p < 0.001$

[e] $p > 0.05$

Although life history patterns across Carnivora reveal constant scaling, differences among families are evident if one compares deviations from a line of best fit for each life-history trait plotted against either body or brain weight (14 out of 16, or 88%, are statistically significant; see 105). Particularly marked familial differences are observed for relative birth weight, litter weight, age at independence and at sexual maturity, and interbirth interval (Table 2).

Thus, in comparing carnivores with other mammalian orders (210, 319), it is essential to recognize that variation within the order is significant among families for a number of life history traits; researchers need to account for this variation before suggesting functional explanations. Therefore, in the following discussion we focus on behavioral and ecological relationships with life histories *within* families.

Life History Patterns and Feeding Ecology

Carnivores are well-known for their dietetic preferences, and thus, it is not surprising that variation in carnivore life histories is associated with food habits. In the following comparisons (summarized from 105), relationships among different species have been scaled to maternal body size (indicated by our use

of the term *relatively).* We divided carnivores into two groups: (a) omnivores, species in which meat constitutes less than 60% of the diet (as determined from the available literature) and (b) carnivores, species in which meat accounts for over 60% of the diet (105).

Among Canidae, omnivorous species such as black-backed jackals, fennec foxes, and crab-eating foxes have relatively heavier offspring, longer gestation periods, and lengthier periods of dependence prior to weaning, as compared to more exclusively carnivorous species such as wolves, coyotes, African wild dogs, arctic foxes, and red foxes. There is weaker evidence indicating that omnivorous canids reach sexual maturity earlier than carnivorous canids.

The differences between omnivorous and carnivorous canids may be explained in two ways. First, omnivores can choose from a wider variety of foods, and in terms of nutritional requirements, reproduction in omnivores is probably less risky. When the food supply fluctuates, a species such as the black-backed jackal, which feeds on beetles, termites, fallen fruits, berries, snakes, and various birds and mammals (40, 259, 260, 284), can maintain itself more easily than a strict carnivore. Thus, an omnivorous canid may have the energetic capacity to endure an extended period of gestation, followed by a long lactation period for relatively larger offspring.

Carnivorous species, in contrast, tend to have shorter gestation periods and give birth to lighter young, perhaps to minimize vulnerability to prey fluctuations and, consequently, to reduce maternal energetic cost of feeding offspring. Population changes seem congruent with these comparative trends. For example, during a five-year decline in coyotes' major source of prey-the snowshoe hare, *Lepus americanus-in* Alberta, Canada, the pregnancy rate declined over 25% and the mean litter size fell from an average of 4.9 ± 1.1 to 3.6 ± 1.0 (301, 302). A similar decline in reproductive rates was observed in lynx inhabiting the same area (43).

Postweaning experiences are also markedly different in carnivores and omnivores. Carnivores progress towards the age of independence more slowly than do omnivores. Among the larger canids (wolves and coyotes) and felids (African lions, tigers, leopards, and cheetahs), which generally feed on larger-sized prey, "teaching" the young how to hunt is probably more critical in strict carnivores than in omnivores. At 12 to 15 months of age, juvenile lions, tigers, and leopards begin to make foraging excursions with their mothers, and they gradually become more successful hunters (182, 272, 273). Mothers may also bring their young maimed prey so they can learn stalking methods and killing techniques. Lionesses may even distinguish between serious hunts, with only adults participating, and training hunts, with juveniles following and watching adults in pursuit (276).

Carnivores' relatively slow progress toward independence may therefore be related to their need for more hunting experience prior to dispersal. Except for hyenas, however, this trend only seems to apply to larger Carnivora. Smaller felids, Mustelidae, and Yiverridae--all strict carnivores that feed on small rodents-rely more on rushing and/or ambushing prey, rapidly clasping them with the forepaws, and delivering a swift killing bite (85, 182), rather than on the elaborate stalking procedures observed in larger species.

BODY SIZE AND DIET Haldane (117) wrote, "The most obvious differences between different animals are differences in size, but for some reason the zoologists have paid singularly little attention to them." Although this situation has improved in recent years (51, 63, 237, 287a, 288, 322), few authors of single- or cross-species studies on carnivores have analyzed behavioral and ecological differences in relation to size. Not only is size important in all species, however, but the range of body sizes found in the Carnivora is unparalleled in any other mammalian order (105, 270) (see Figure 1a). Such broad differences may be due to ecological effects, phylogenetic history, or both. Phylogenetic effects are frequently difficult to

detect, and with a less than complete fossil record, they are almost impossible to explain, at least at the family level.

Available fossil specimens suggest that diet may have influenced carnivore body size (287). Fossils indicate that the first ursids, dating back to the early Miocene, were probably small forest dwellers like their miacid ancestors (130, 168). The Ursidae may have increased in body size as they entered more open habitats and expanded the proportion of fruits and vegetation in their diets (83).

Figure 1a **Distribution of body weight (kg) across families within Carnivora (from 105). Number of species shown on ordinate. Arrow indicates median value for each family.**

Figure 1b **Distribution of body weight (kg) across categories of prey size (from 105). Number of species shown on ordinate. Arrow indicates median value for each prey size category.**

Figure 1c **Number of prey (see text for definition) plotted against body weight (kg) for different carnivore species (105).**

The Canidae are cursorial predators, adapted to either running down prey over considerable distances or pinning it down with large forepaws and delivering a killing bite. Selection for increased size in Canidae, as in Hyaenidae and some felids, probably occurred with the exploitation of large prey in open country habitats (83, 93, 198). In Mustelidae and Yiverridae. smaller individuals were adapted for exploiting small

rodent prey and invertebrates, as well as to make the predator less conspicuous in open vegetation (93). Small size in felids may also have been selected to promote arboreality (157).

Dietetic factors were probably especially important in the phylogeny of size among predatory species, where body size limits the range of available prey. Comparative data on extant species support this idea. The recent accumulation of measurements on diet and body size in carnivores permits a more comprehensive examination of this relationship (105). Prey are categorized into four size classes depending on the weight of prey that compose at least 50% of the diet: (a) very small (less than 1 kg, e.g. the brush vole, *Lagurus curtatus):* (b) small (1-10 kg, e.g. the snowshoe hare, *Lepus americanus);* (c) medium (10--100 kg, e.g. the white-tailed deer, *Odocoileus virginianus);* (d) large (more than 100 kg, e.g. the wildebeest, *Connochaetes taurinus).* A direct relationship between carnivore body weight and prey size is observed across 62 species (105; Figure 1b). In some respects, this trend is hardly surprising. A stoat or genet would not have the strength or energetic capacity to track, pull down, and consume a large ungulate; similarly, an African lion may not move swiftly enough to follow and pounce on a vole, nor would it be energetically efficient for it to do so habitually. Yet, small mammals may be important in the diet of large carnivores-as studies of lions living in the Kalahari suggest (M. J. Owens, personal communication).

Nevertheless, the empirical association between carnivore weight and prey weight suggests that the margin of variance in the relationship is rather slight. Aside from marked differences in prey size for extremely large or small carnivores, species such as the South American fox or bobcat are restricted, *on the average,* to prey of a certain size. Nonetheless, morphological characters such as long canines and claws (93) and social hunting patterns (53, 228) may extend the limits of prey size in some cases (e.g. mountain lion, spotted hyena, wolves, African wild dog, coyotes, African lion).

Prey diversity and body size As theoretical models would lead us to expect (278, 322), diversity of prey may also be related to differences in body size. Prey diversity can be measured in a number of ways. In carnivores, however, detailed, species-by-species descriptions of dietary contents are only available for the well-studied canids, felids, hyaenids, and mustelids, and comparative studies are therefore restricted to a crude index of diversity based on measurement of size classes. Carnivores may be classified according to the size of both "typical" (i.e. composing at least 50% of the diet) and less common prey.

By categorizing species in this fashion (Figure 1c), we find that the number of prey size classes in the diet increases with body weight ($r_{69} = 0.64$, $p < 0.01$). There are many possible causal factors involved. Larger carnivores tend to have greater home-range areas (107), and therefore the absolute chance of coming across a variety of preys is greater. Also, larger species probably have stronger forelimbs and wider jaws, enabling them to eat both small and large prey easily. Conversely, small species are morphologically limited to a smaller range of food and live in smaller home ranges.

The availability and abundance of prey also varies across different size classes. Smaller carnivores (e.g. gray fox, stoat, European wild cat) can specialize on small rodents such as *Peromyscus* or *Microtus* that reach high population densities and remain fairly common. In contrast, it would be difficult, if not impossible, for species like the African lion, mountain lion, or spotted hyena to specialize on large ungulates the size of water buffalo *(Syncerrus caffer)* or elk *(Cervus canadensis),* which have lower population densities and turnover rates. Larger carnivores must maintain t1exible dietetic preferences in order to increase the absolute number of potential foods.

The advantages of increased prey diversity for large carnivores have been poorly studied. At southern latitudes in mainland Chile where the South American fox and the Chico gray fox are sympatric and differ in size, the former is larger and feeds on a greater variety of rodent species than the latter, independent of prey distribution (103). Thus, in some instances, diversity may be just as salient a factor as prey size in

the selection of carnivore body size. A causal relationship has not been established, however, and diversity may be the result of increased body size, not the factor selecting for it.

Life History Patterns and Habitat

Interspecific differences in carnivore life histories are also associated with vegetation or habitat types. In Canidae, open grassland species (African wild dogs, arctic foxes) have relatively lighter birth weights than open grassland or woodland species (South American foxes, crab-eating foxes) or forest dwellers (dholes, red foxes). In Felidae, species living in sparse woodlands (mountain lions, Geoffrey's cats, leopards) have lighter total litter weights (litter size times birth weight) than do forest-living species (bengal cats, ocelots, lynx, tigers, jaguars). In explaining absolute differences in litter size between Canidae and Felidae, Kleiman & Eisenberg (157) argued that carnivores living in more forested habitats have a diversified food base, including both arboreal and terrestrial prey, that is not available in open grassland or sparse woodland terrain.

Spatial heterogeneity is also reflected in contrasting environments: Forest habitats may present more perceptual and ranging complexity than open grassland or savannah areas (83). In a study of a relatively small sample of Mustelidae, Gittleman (105) found that females of forest-living species (stoats, American minks, American martens, fishers) and aquatic forms (European otters, sea otters) reach sexual maturity later than open grassland/woodland species (long-tailed weasels, European badgers) and open grassland/forest species (wolverines, striped skunks).

Few detailed data are available on postnatal development, maternal care, natal dispersal, or establishment of territory in species of *Mustela* or *Martes* (291, 292, 296) because of their solitary existence. Behavioral observations on the aquatic European otters and sea otters, however, indicate that in addition to maternal care, both species have unusually long and attentive periods of adult care (269). Sea otter pups are usually born in the water and are supported on the mother's chest as she swims on her back (146, 147). The demands of foraging for scarce foods in oceanic waters and of locating areas protected from heavy seas may select for delayed sexual maturity to ensure familiarity and effective utilization of the environment so that young may be reared successfully (146, 277).

Life History Patterns and Social Organization

As important as ecological effects on life history patterns is the social environment in which life histories evolve (19, 20, 24, 106, 193). In many carnivores (wolves, coyotes, dwarf mongoose, lion), subadults and adults assist in provisioning, guarding, and socializing young born into the social group. Helping (alloparental) behavior or communal rearing may select for life history patterns that diverge from the traits found in species in which maternal or even biparental care is prevalent. Across Canidae--after controlling for size—birth weight, litter weight, age at which females first breed, and age at independence all increase with the degree of sociality, which is defined as the average number of individuals associating during the rearing of young (24). Moreover, across all Carnivora, species in which communal rearing is common reach sexual maturity later and have heavier litters than species in which maternal or biparental care is the modal pattern (106).

The causal mechanisms underlying these comparative trends are difficult to pinpoint. However, recent detailed field studies on the effects of helping (see below) may further our understanding of the relationship between intra- and interspecific variation in the association between life history traits and patterns of care-giving. In various canids, for example, individuals other than parents sometimes contribute directly to feeding young or parents and to guarding the den site. In black-backed and golden jackals, helpers-usually nonbreeding adults 11-20 months old-spend about 55% of their time at dens

protecting pups, regularly contribute food to the young and to the lactating mother by regurgitation, and defend carcasses for utilization by the entire pack (222; for comparative data see 27, 29, 123, 195, 214, 217, 229, 231).

In some species, food provisioning does not appear to be a major part of helping (29, 171, 254--257), which primarily involves den sitting. Either food provisioning or den sitting may provide the necessary energetic requirements to select for differences in birth weight, litter size, or natal dispersal (29, 106). How helping actually affects life history patterns is unknown, however, and deserves careful attention in future research programs.

SOCIAL ECOLOGY AND SOCIAL ORGANIZATION

Methods of Study and Data Analysis: Observation and Radio-Tracking

The first step in obtaining detailed information about patterns of social organization is the compilation of ethograms, or behavioral repertoires, based on direct observation. This process involves describing basic motor patterns unambiguously, so that observers can reliably record the repeated occurrence of a particular behavior and other people can know exactly what was observed. Comparative analyses of social interaction patterns and the behavior involved rely on these basic descriptive data, especially when frequencies or rates of occurrence are used to differentiate closely related species (for data on carnivores, see 13, 15, 17, 25, 38, 156, 157).

Although many carnivores are difficult to study under field conditions, social interaction patterns and spatial relationships among individuals must be rigorously analyzed and quantitatively assessed (65, 115, 127, 178, 188, 201, 236, 304). For example, quantitative measures of association patterns (178, 188, 236), dominance relationships (14, 57), and territorial behavior (on the defense function, see 208; on the index of defendability, see 219; see also 145) have been used successfully for other animals, but they are just as applicable to analyses of carnivore social patterns.

Multivariate statistical procedures can also provide detailed information about social organization and basic behavioral patterns (14, 17, 18, 29, 65, 127, 136, 314, 315). As Hilborn & Stearns (132) pointed out, evolutionary biologists must look for multiple causes; single factor studies may delay progress when multicausal factors are actually operating-as they usually are (see 83). Statistical analyses at any level, however, cannot substitute for inadequate investigation and description of the "deep structure" of the problem at hand (109).

It is clearly important to gather observational data in any study of social organization. Most carnivores are difficult to observe or even to locate on command, however; many species are nocturnal and/or very secretive, and they move about rapidly. In these cases, observation must be supplemented by radio-tracking (for reviews of this technique, see 7, 59, 207). Radiotelemetry allows us to track individual animals over long distances and often for long periods of time. Biological attraction points (74) that influence movement patterns can also be detected. In addition, radio-tracking permits researchers to locate animals that cannot be seen and to assess spatial relationships among individuals with some degree of accuracy. As Macdonald (191) stressed, though, accurately and reliably interpreting the social significance of movements of radio-tagged animals (in his case, red foxes) poses many problems. In addition to not knowing what the interacting animals are doing to one another, it is difficult to assess whether their movements are independent or correlated (76).

One important methodological problem with radio-tracking free-ranging animals is that for many species, home range (territory) estimates are positively correlated with the number of radio locations gathered (for a review, see 26). Simulations relating area estimates to sample size (Figure 2) and analyses of the

available literature (175) indicate that in many instances, the samples used to estimate space use have been too small. The number of locations that constitute an adequate sample may vary with a species' size, the season (e.g. presence of snow), habitat, sex, age, social status (resident, transient, or group member), reproductive condition, food resources, and the presence or absence of conspecifics or other species; what is sufficient for one individual may be inadequate for another. Field workers relying heavily on telemetry need to show that sample size is not a confounding variable. Radio-tracking can be a valuable tool in the study of social ecology and social organization when the effects of sample size and the accuracy with which signals can be located are taken into account.

Figure 2 **The relationship between estimated mean home range size (indicated by solid line) and variability (indicated by slashed line) (coefficient of variation) and number of locations. "0.50N polygon" and "0.95N polygon" refer to the convex polygons that encompass 50o/c and 95% of the total number of locations** *(N).* **The results of the present simulation indicate that, on average, field workers should obtain between 100 and 200 locations in order to estimate the home range area (***N* **within which mean area and variability level off) reliably. Sampling differences for small species occupying relatively small home ranges indicate that fewer locations may be sufficient, and variability in social status, age, sex, and reproductive condition also have to be considered, as do food resources, habitat (terrain, plains, forests) and differences in sampling and analytical methods (see 26 and 30).**
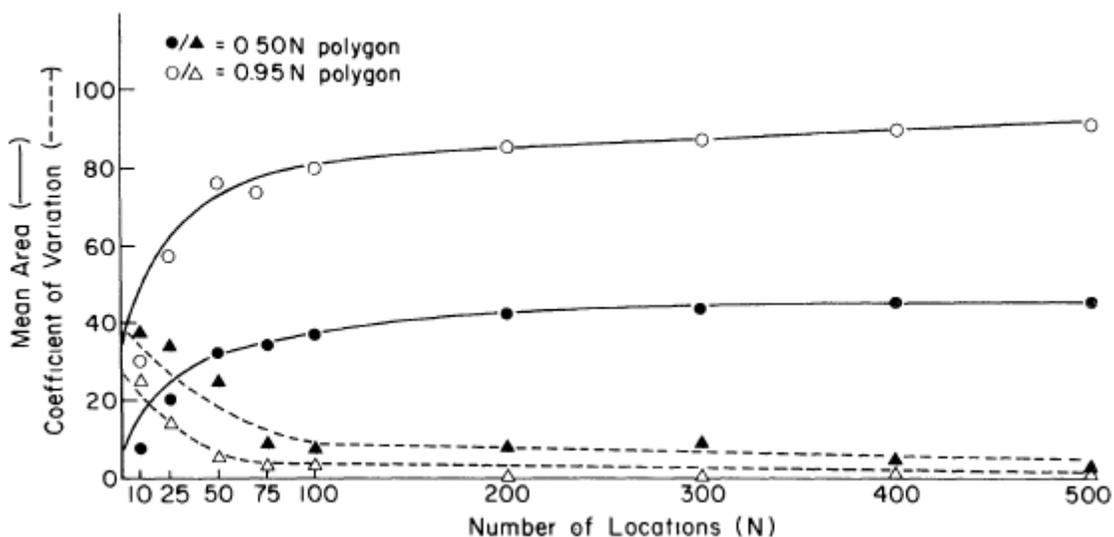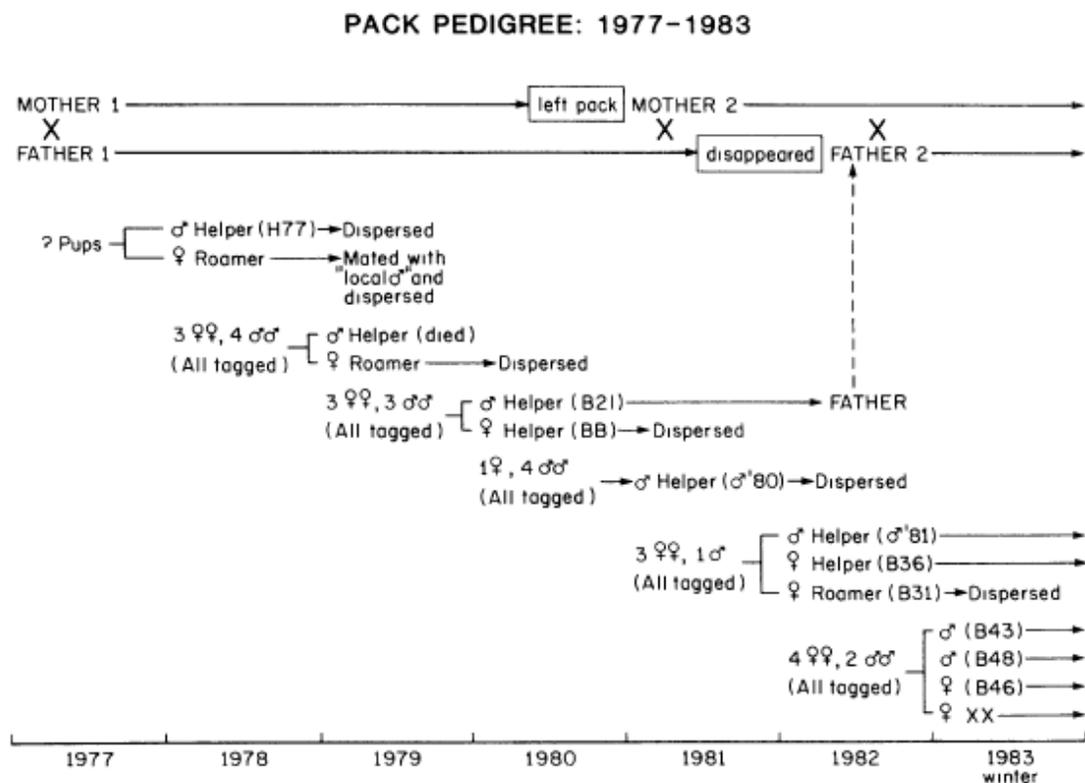

Assessing Kin Relationships

In order to conduct detailed analyses of carnivore social organization genetic (kin) relationships (Figure 3) must also be determined whenever possible in order to assess the relative roles of kin selection (39, 118, 119, 321, 324) and other possible pathways--e.g. reciprocity, mutualism, and indirect effects (323)--in the evolution of different forms of social behavior (9, 19, 20, 29, 39, 45, 46, 49, 58, 83, 96, 194, 234, 248, 257, 279, 306). For some carnivores exhibiting complex patterns of social organization, kin selection alone may be inadequate to account for observed behavioral interactions [e.g. dwarf mongooses (257), African wild dogs (248), coyotes (29), lions (234), and brown hyenas (231)]. The relative importance of different mechanisms may vary among individuals as well.

Kin relationships within social groups-as measured by the coefficient of genetic relationship, r-vary among species of social carnivores *(r* equals 0.125-0.5 in African wild dogs, 0.38 in red foxes, 0.5 in Arctic foxes and in jackals, 0.15-0.22 in lions, and 0.03 in spotted hyenas; data from 194). These coefficients may

differ with age and sex (34, 37) as well, as a result of differences in patterns of dispersal and philopatry. In many instances, the kin relationships are not actually known, and they are inferred from social interaction patterns with varying degrees of accuracy. The importance of determining kin relationships is demonstrated by an often cited example of kin selection from an excellent field study of wild turkeys (*Meleagris gallapavo;* 312) that may be flawed because relationships among the birds were not known (11).

Figure 3 Social groups of carnivores often are comprised mostly of genetically related individuals (extended families). This figure presents a pedigree for a pack of coyotes observed in the Grand Teton National Park, outside of Jackson, Wyoming, from 1977 to 1983 (28, 29, 314, 315). Young of each year that are accounted for either dispersed or died before they were about 9 months of age. After the original pack mother (Mother 1) left the group in late 1980, a new and unrelated female (Mother 2) joined the pack and mated with the original pack father (Father 1) in 1981. Then, after he left the pack in spring 1981, his son, male helper B21, mated with the new female in 1982 and 1983. In 1982, the help that B21 provided to male '81 and female B36 was reciprocated when B21 and the new female's pups were born. The new pack mother was the only unrelated coyote to join the pack in 6 years (see 29 for details).

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PACK PEDIGREE: 1977-1983

CARNIVORE SOCIAL GROUPS

In addition to the widespread but predictable differences in relative life history patterns among carnivores, there is considerable variation in social organization. Groups vary in size from lone individuals to packs of over 10 animals, age and sex ratios differ greatly, and group members may or may not be closely related. Although some species are typically considered to be "solitary" outside of the breeding season and care-giving period (e.g. felids other than lions and most mustelids and viverrids), Leyhausen (182, p. 257) has correctly stated that "the only mammal one could conceivably speak of as being socially indifferent is a dead one." Field data clearly show that members of solitary species communicate with one another using olfactory, auditory, and even visual signals, and through this exchange of information, they are able to avoid contact and maintain nonoverlapping home ranges or territories (whose boundaries are actively defended).

In some cases, intraspecific variation in social organization, due primarily to differences in food resources and habitat, is at least as pronounced as interspecific differences [coyotes (29), wolves (124), Kalahari lions (M. J. Owens, personal communication), brown hyenas (232), golden jackals (190), striped hyenas (163, 189), red foxes (186, 187, 191, 192, 331), raccoons (102), spotted hyenas (161), and African wild dogs (100, 248)]. Although extreme intraspecific variation appears to be rare among carnivores in general, it may be misleading to characterize some species' social organization as having a modal group size (solitary or social), a typical group composition, or active defense of territorial boundaries.

Nonetheless, Altmann & Altmann (6) pointed out that animals' behavior and social organization often exhibit a range of species-specific stereotypy that is much narrower than one would expect based on experimentally demonstrated capacities for plasticity. Stressing that behavior is an important aspect of the environment, they argue that consistency in social interaction patterns among group members is made possible by the heritable component in some life history patterns. Although there is intraspecific variation in social organization among conspecifics living in different areas within a given habitat, where food resources do not drastically change, successive generations do adopt similar social organizations [coyotes (27, 29), African wild dog (100), and lion (32, 34-36, 120, 273)] with respect to most or all of the following variables: group size, group composition, patterns of emigration and space use, and mating and care-giving habits.

How Social Groups are Formed and Maintained

Understanding the many interrelated behavioral processes involved in social group formation and maintenance requires at least: (a) analyzing the development and maintenance of social bonds and relationships among offspring and between younger and older individuals (15, 20, 23, 134); *(b)* studying social interaction patterns between older group members and "outsiders"; (c) determining movement patterns for individuals identified by sex and age; and, in the best of all possible worlds, *(d)* learning enough about the behavioral patterns of dispersers and nondispersers to make educated guesses about how individual movement patterns influence reproductive fitness--e.g. Do resident animals help rear offspring born into the group? Do nondispersing individuals eventually inherit a portion of their natal area? Do dispersers breed at an earlier age than individuals remaining in their natal territory? Do dispersers suffer higher mortality rates than nondispersers? (see 20, 100, 120, 194, 311 for detailed discussions).

DEVELOPMENTAL ANALYSES OF SOCIAL BEHAVIOR Comprehensive studies of behavior must consider at least four major topics: evolution, adaptation, causation, and development (299, 300). While it may be beyond the ability of any one researcher to provide substantive answers to questions in all four areas, a complete analysis ultimately rests on the generation of data in all of them. Because every

population is age structured (56), developmental questions are important to consider in evolutionary and ecological research in social biology (23).

Ontogenetic trajectories A general concept applicable to both carnivores and other taxa is Wiley's (320) model of ontogenetic trajectories, in which movements of individuals through different social positions are described. This analysis can be used to trace longitudinally how individuals become incorporated into social groups (Figure 3) and to determine if variations in the natal environment affect development and later behavior (122). Wiley (320) related the evolution of different mating and social systems to ontogenetic profiles that differed in the age at sexual maturity, and he stressed that delayed reproduction is not a secondary consequence of social organization.

Wiley also pointed out that the evolution of complex social organizations is inextricably linked to the evolution of an optimal allocation of effort among reproduction, growth, and maintenance throughout an individual's lifetime. His model of ontogenetic trajectories highlights the complex trade-offs among demographic variables such as age at sexual maturity, fecundity, mortality, and developmental pathways (see also 56, 298). Clearly, life history and demographic analyses are important in studying the relationship between behavioral development and the evolution of sociality (8, 24, 94).

Development and social organization A major difficulty in relating patterns of behavioral development to social organization is that developmental data are extremely difficult to gather under field conditions. Nonetheless, limited field data and information from captive animals concerning the ontogeny of social relationships indicate that even among closely related species (15, 17, 20, 38), interspecific differences in social organization may be associated with variations in behavioral development. Similar results have been reported for rodents (121, 325) and Bighorn sheep [*Ovis canadensis* (31)].

Apart from the problems of gathering developmental field data, intraspecific variability in social organization is highly pronounced in some taxa, making interspecific comparisons difficult. It is not known whether these intraspecific differences are reflected in variations in early social development in carnivores, as they are in Bighorn sheep (31) and lemurs [*Lemur* spp. (295)]. Field observations of coyote pups born in different habitats and into different types of social groups do not reveal any major variations in development during early life (M. Bekoff, unpublished data). But it is entirely possible that observed differences in social interaction patterns and spatial relationships among older siblings and between parents and offspring in coyote populations displaying different organizational patterns (solitary individuals, mated pairs, packs) are associated with varying developmental profiles, as perhaps are interspecific differences in social organization among some canids (20, 38). In polar bears, for example, population density influences association patterns among age and sex classes, and as a result, social organization varies (173).

To the best of our knowledge, there are no longitudinal field data for carnivores that can be used to support or refute with any degree of certainty hypotheses about the relationship between development and intraspecific variations in social organization. While there may be differences in a single species' behavioral repertoire that are dependent on habitat and parallel observed interspecific variations, this pattern apparently is not found in canids, at least. A fruitful area for further comparative study would be the analysis of differences in the frequency (or rate) of occurrence of shared behavioral patterns among carnivores (156, 157), similar to the studies done among different species of can ids (see 15, 17, 25 and references therein).

Social play behavior Variations in early social play experience may influence the development and maintenance of social bonds within a group of animals and consequently affect social interaction patterns among all group members, individual movement patterns, and the social organization in general (15, 21,

22, 88, 94, 174, 332). Detailed field data relating individual patterns of social play to later behavior are lacking and are needed to verify what appear to be robust findings based on captive animals. Information also needs to be collected on age and sex differences, variations related to social rank (15, 21, 192), and the distribution of different types of social play according to the sex, age, rank, and genetic relatedness of the participants.

SOCIAL INTERACTION PATTERNS BETWEEN OLDER GROUP MEMBERS AND OUTSIDERS
Another perspective on group formation and maintenance can be gained by studying how resident group members interact with outsiders that may be incorporated into the group. Limited comparative data indicate that some organized carnivore groups (i.e. not temporary aggregations) are relatively closed to outsiders (e.g. coyotes, jackals, and wolves); new members are rarely accepted into what are essentially extended family groups (29, 204; see also 303). In a six-year study of coyotes (29), a strange adult female was the only individual incorporated into a stable coyote pack. She was accepted after the breeding female left the group and subsequently mated with the only breeding male in the group. After he departed, she successfully bred two times with his son, who had previously been a helper (male B-21 in 29; see Figure 3). In dwarf mongooses (257) and Kalahari lions (M. J. Owens & D. D. Owens, personal communication), however, males and females commonly transfer between groups.

The permeability of relatively closed societies, as well as the openness of other types of social groups, may be influenced by age and sex differences in the degree of aggression toward outsiders or by the loss of social cohesion due to environmental stresses (M. J. Owens & D. D. Owens, personal communication). Individuals of different social rank may also vary in their attitude toward admitting new group members (48, 98). Young animals are usually more accepting of new group members than older, high-ranking individuals. The heightened level of aggression among members of the same sex also appears to influence group composition in diverse carnivores (32, 87, 100, 218, 222, 230, 240, 248, 294, 328).

SOCIAL ECOLOGY, DISPERSAL, AND PHILOPATRY Dispersal (i.e. the movement of individuals away from their place of birth) and natal philopatry (i.e. the continued residence of animals at their birthplace. past the age of independence; see 311) directly influence social organization and breeding patterns (6, 15, 20, 27, 29, 100, 104, 114, 120, 194, 222, 223a, 311). The dispersal patterns of both young and older individuals--primary and secondary emigration, respectively (100)--need to be studied further; they may vary with age, sex, and social rank. The benefits and risks associated with remaining in the natal area (possibly inheriting part or all of the natal home range or territory, providing help in rearing individuals born into the group, delaying breeding in groups where only one male and female typically breed) and dispersing (leaving a group in which breeding is unlikely or in which an individual is socially incompatible with other group members, the possibility of pairing and breeding, the possibility of increased mortality) must be considered in each specific instance.

Among wide-ranging carnivores, the difficulty of analyzing movement patterns is obvious. Radio-tracking combined with direct observation is essential, and individuals must be marked as early in life as possible. In many instances, young animals leave their natal groups and change morphologically (size, coat characteristics) between sightings. Individuals may also leave their natal area and return at a later date (29, 194), or they may leave alone and then be seen with other animals with which they may not have been previously associated. The fates of littermates that disperse together and of different-aged siblings that depart at different times also needs to be documented (100).

Many interrelated factors such as population density, food resources, and the cumulative effects of social interactions undoubtedly influence an individual's own "decisions" about whether or not to leave its natal area. These same factors probably result in involuntary dispersal by some individuals that might otherwise have remained; departure can be caused by aggression between littermates, siblings, older

group members, parents and offspring, and/or adults and unrelated younger animals (15, 32, 142, 151, 154, 204, 330).

In lions, Elliott & McTaggart Cowan (87) reported a positive relationship between population density and the age at which subadults are expelled from the pride (265, 273). Bertram (32) concluded that pride size in lions is regulated by density-dependent recruitment or expulsion of subadult females. Although lion population density is influenced by food availability and social behavior, expulsion of females often occurred when food did not appear to be in short supply. He stressed the behavioral regulation of lion pride size (which may also apply to wolves), suggesting that this type of regulatory mechanism may be influenced by a pride's experience of past food shortages or its assessment of probable future shortages (see 286 for a discussion of prospective assessments of food resources). Pride size did not change in response to short-term changes in food availability. Kalahari lion pride members, however, do disband and disperse during periodic, severe droughts when large antelope prey become scarce (M. J. Owens & D. D. Owens, personal communication).

Food resources seem to have a major influence on dispersal in other carnivores (29, 88, 102, 123, 153, 185, 191, 192, 225, 232, 309, 311, 330), and differences in food availability-in quality, quantity, and distribution-are primarily responsible for intraspecific variation in social organization. When food is in short supply, dispersal is usually more pronounced. Animals may leave because they are hungry (309), or they may be driven out by more dominant individuals.

Age, social rank, and differential dispersal Age and social rank are positively related in many carnivores. Consequently, youngsters may be unable to compete for necessary resources, including mates, and may be more disposed than older animals to leave their natal group (32, 87, 101, 185, 192, 309).

In African wild dogs living on the Serengeti Plains in northern Tanzania, individuals (usually females) commonly leave their natal pack when there is a dominant breeder of the same sex (usually a parent) present (100). Reich (247, 248) described a unique situation in which a female wild dog supplanted her mother and then mated with her father and older brother in two successive years.

In wolves, young socially subordinate individuals may get smaller rations from each kill (also observed in lions; 32), and hunger may increase subordinates' tendency to split off from their natal pack and form small hunting groups (309 and references therein). Wolves may also leave large packs, however, when there is no indication that food is in short supply. Therefore, as in lions, leopards (294), and probably most other carnivores, social and ecological factors need to be considered together (204-206, 233, 309, 330). Fritts & Mech (101) also noted that subordinate wolves tend to occupy the edge of their pack's territory or travel outside the territorial boundaries, perhaps obtaining information on the potential for colonization outside or at the edge of their natal pack's territory. Furthermore, wolves approaching breeding age often disperse early and attempt to form new social units, rather than trying to breed within their natal packs.

In addition to studying the association between social rank and age, the development of dominance relationships among littermates must be considered in a discussion of dispersal and philopatry (15, 20, 222, 330). Differential dispersal among littermates is common and may be related to relative dominance status. Because dispersal is risky (29, 32, 87, 120, 185, 192, 222, 289, 330), dominant individuals should be likely to exercise their prerogative and drive out subordinate littermates. Aggression between siblings of the same sex may be heightened further (222).

Both dominant and subordinate individuals may be predisposed to leave their natal groups because of an inability to develop strong social bonds, though for different reasons (15, 20). Based on data on captive coyotes, it has been postulated that dominant animals may disperse because other littermates avoid or

constantly challenge them, whereas subordinate animals may disperse because they are scapegoats and actively avoid their siblings (15).

Golightly's (108) data on the relationship between social rank and energetics in juvenile coyotes indicate that high- and low-ranking coyotes have substantially higher daily metabolic rates than middle-ranking individuals, probably due to the regular challenges to which dominant individuals are subjected and to continued harassment of the subordinate coyote by other group members; the subordinate individual spends considerable effort avoiding interactions. Unfortunately, there are no field data on the comparative dispersal patterns of individuals with different social ranks or on rank-related energetics. But, as Golightly pointed out, the possible energetic advantages to dispersing must be considered along with other potential benefits (also see 48).

Sex differences in dispersal Some researchers argue that among mammals, males tend to disperse more and further than females do (114), which appears to be related to a polygamous mating system (the predominant mammalian pattern). While this sex bias may hold true for some carnivores and other mammals, there are notable exceptions in at least mountain lions (280), brown hyenas (214), dwarf mongooses (257), and African wild dogs (99, 100; but see 248). In brown hyenas, both males and females disperse, apparently in order to increase their chances of breeding. Males leave their natal group and become nomadic (males living in groups were not observed to mate), while females disperse to seek a vacated territory [see Mills (214); his data were collected in the southern Kalahari]. In the central Kalahari, dispersal by female brown hyenas is less common than male emigration (231). In dwarf mongooses, males and females commonly transfer between groups (257). Female dispersal appears to predominate in African wild dogs (99, 100), but the pattern may vary from one habitat to another (248). In lions, new prides may be formed when subadult females leave their parent pride and settle in an adjacent area (120; M. J. Owens & D. D. Owens, personal communication). For most other carnivores, sufficient data are not available for any categorical generalizations to be made.

The complex relationships among behavioral, ecological, genetic, and possibly energetic factors are extremely difficult to tease apart under field conditions, and intraspecific and interspecific differences should be anticipated. Whether or not specific dispersal patterns have evolved because they favor outbreeding (i.e. reduce potential inbreeding depression) (100, 223a, 280) is not clear, because data for inbreeding depression in wild populations of carnivores are, at best, scanty and inconclusive (248, 281, 282, 329). Wolves, for example, may be highly inbred (204, 238, 329) and still not suffer from inbreeding depression. Eisenberg (82) noted that the structure of many natural populations may be a mosaic of highly inbred subpopulations.

WHY DO SOME CARNIVORES LIVE IN GROUPS?

Although animals that live in groups have attracted a disproportionate amount of attention, group living has evolved in only 10% to 15% of carnivore species (105). Comparative information on typically solitary species such as felids (37, 182, 274, 280, 293, 294) and a canid [the maned wolf (73)] has also increased our understanding of the evolution of social groups in other taxa, and it has become clear that solitary does not mean asocial (181).

Our discussion will concentrate on the possible benefits of grouping, but there may also be costs associated with living in a group. These costs include an increased probability of detection by potential competitors and predators, decreased food availability per individual, increased transmission of ectoparasites and diseases (55, 191), and increased probability of aggression (and injury) among group members. The costs and benefits of group living are not necessarily additive (200) and may differ for

each individual. (General comparative reviews of the evolution of sociality and group living can be found in the following references: 3, 36, 37, 42, 48, 69, 70, 81, 83, 105, 157,209, 264, 317, 318, 322, 326.)

A Classification of Carnivore Groups

Gittleman (105) has classified carnivore groups into four major types: (a) population groups-individuals sharing a common home range; (b) feeding groups-individuals utilizing the same food resources at a given time; (c) foraging groups-individuals banding together while searching for food or hunting; and (d) breeding groups-individuals forming a reproductive unit. Population, feeding, and foraging groups are identical for most carnivores that have been studied. In some species, population group size is related to feeding group size but not to foraging group size (wolves, spotted hyenas, brown hyenas, lions, coyotes); populations may break up into smaller hunting groups and then regroup when feeding.

OPTIMAL GROUP SIZE Group size varies both inter- and intraspecifically, but there appears to be an optimal range within which individual group members benefit the most (37, 48, 53, 70, 91, 111, 157, 161, 169, 170, 172, 228, 252, 273), especially with respect to the exploitation of food resources and individual energy budgets. Caraco & Wolf (53) determined that lions achieve highest individual efficiency (capture success, food availability/lion, food intake/lion) in groups of two, regardless of prey size, whereas Nudds's (228) analysis showed that optimal pack size for wolves is a function of prey size.

For both lions and wolves, groups often exceed the size calculated as optimal for hunting efficiency. For wolves at least, the addition of individuals to an optimally sized pack appears to be less costly in terms of individuals' energy returns than a reduction below the optimum (228). Rodman (252) pointed out that the genetic gain through relatedness (i.e. increases in inclusive fitness) may offset the disadvantage to individual group members when surplus members are kin. Thus, despite possible costs to individual fitness, groups may evolve because of the increase in total relatedness. Competition may also promote large groups among predators that defend their kills against scavengers (37, 91, 169).

Despite possible genetic gains and the increased ability to catch prey and defend kills in larger than optimally sized groups, an upper limit on group size is imposed by: (a) decreased hunting success (70, 273), (b) reduced food intake per individual because of increased within-group competition, and (c) the need for small- to medium-sized predators to reduce competitive pressure by hunting and feeding inconspicuously (169), among other factors. Foraging groups that are smaller or larger than expected may form, however, when prey loss needs to be minimized (169).

Group size may also be limited by small carnivores' need to decrease the likelihood of detection by potential predators (110, 256, 257). Suffice it to say, what is optimal in one setting may not be in another, even for conspecifics. Furthermore, in determining the optimal group size for a given species, researchers must take into account all possible variables, not just food exploitation (169, 252).

INFLUENCE OF HABITAT ON CARNIVORE SOCIAL GROUPS Comparisons of closely related species living in similar and different habitats provide additional information on the evolution of carnivore social groups (105, 110, 157, 228, 248, 256, 272-274, 280, 293). In general, species living in open grassland or in both open grassland and woodland habitats have larger population groups than forest dwellers (105), but the nature of food resources (73, 141, 204) and competition can alter group sizes on the local level.

For predators, an open environment usually increases the chance of being detected by prey, and some form of group hunting is required for successful predation, especially on prey larger than the individual hunters. For smaller carnivores, such as mongooses, the risk of predation is greater in open habitats, and larger groups afford more protection and increased vigilance (79, 256); increased detection by predators could impose an upper limit on group size in the absence of behavioral regulation. Food resources are

usually readily available to the many small carnivores for which anti predatory defense is the major force behind sociality (105, 310). Most smaller carnivores displaying group defense are insectivores, and Waser's (310) model indicated that a mongoose excluding a single competitor from its foraging range would only gain about l% in prey density. Thus, prey distribution and abundance may be a precondition for the evolution of grouping in response to the need for group vigilance (105).

A comparison of lions-the only highly social felid-with a closely related, morphologically similar solitary species such as the tiger illustrates nicely the role of habitat in the evolution of felid sociality (293). In Nepal, tigers live in dense, broken terrain, where small-sized prey are scattered and difficult to locate. Successful predation requires stalking and ambushing techniques. The necessity for crypticity along with the maintenance of an almost exclusively meat diet appears to have favored a solitary existence among tigers and other felids occupying similar habitats, such as mountain lions (280), jaguars, and leopards (274). Sociality in lions, on the other hand, seems related to increased hunting and feeding efficiency and the necessity of defending large kills in open savannah habitats (36, 53, 273). Similar selective pressures (open habitat and ungulates that were rapidly evolving into large-bodied, long-legged, fast-moving prey) also appear to have favored the evolution of sociality in wolves (157, 228).

COMPARATIVE SOCIAL ECOLOGY: THE PERVASIVE INFLUENCE OF FOOD

As we have repeatedly stressed above, the way in which food resources are exploited (located, hunted, scavenged, defended) and the nature of the available food (quality, quantity, spatial distribution) strongly influence interspecific relationships and result in marked intraspecific variations in social organization.

Interspecific Relationships

Radinsky's (242-244) studies of the evolution of skull shape in carnivores provide a paleoethological perspective on interspecific competition suggesting that the partitioning of prey resources by size--due to anatomical differences may have been a factor in the initial radiation of carnivores. This finding is consistent with Rosenzweig's (258) suggestion that sympatric carnivores can coexist in "hunting sets" because they specialize on prey of different sizes. There are comparative data on differential prey size selection by sympatric carnivores for viverrids [white-tailed mongooses, large spotted genets, and African civets (137)], hyaenids (12), and canids and felids (37, 167, 172, 239).

Even if different species share the same prey, variations in hunting methods, prey selection, activity patterns (time-sharing), and mutual avoidance can foster coexistence (12, 37, 137, 139, 172, 224, 297). Bertram (37) has reviewed patterns of coexistence among five carnivores that inhabit the Serengeti Plains (cheetah, leopard, lion, spotted hyena, and wild dog), all of which feed on ungulates. Differences in hunting methods (stalking or pursuing), preferred prey, activity patterns, and prey selection (in terms of age/sex and health) all interact to reduce competition and promote coexistence. Social hunters (lions, wild dogs, spotted hyenas), which use various methods to pursue prey, tend to live in long-lasting social groups, whereas cheetahs and leopards, which predominantly hunt alone, live in groups containing only one adult. Cheetahs, which suffer extreme competition from spotted hyenas (224) and lions (172), actively avoid these and other competitors and eat fast at kills. They are too light and fragile to defend kills successfully, and they can be displaced from food by any animal larger than a jackal (172).

Intraspecific Variation in Social Organization

With few exceptions, intraspecific variation in carnivore social organization as a response to local food resources is the rule among species in which group living is associated with the exploitation of food resources by group members (canids: 28, 29, 41, 72, 88, 95, 100, 101, 123, 131, 160, 190, 192, 193, 204-206, 222, 248, 261, 262, 309, 330, 332; felids: 32, 35, 36, 120, 138, 183, 235, 273; brown hyenas:

215, 230, 232; striped hyenas: 163, 189; spotted hyenas: 161, 162, 184). It is also prevalent in species in which the availability of ample food permits aggregations to form, but in which exploitation of food is not typically a group affair (mustclids: 149, 164, 165; procyonids: 102; ursids: 10, 66, 67, 177, 225; brown and striped hyenas may also fit into this category, see 163, 214, 232). For example, when abundant food is clumped and economically defendable (44, 111), coyotes (29, 41, 52, and Figures 3 & 4), golden jackals (190), Kalahari desert lions (M. J. Owens & D. D. Owens, personal communication), domestic cats (138), and striped hyenas (189) show increases in population and feeding group size and decreases in territorial area. They may also defend food resources and territorial boundaries if intruder pressure increases.

Figure 4 **This figure shows locations at which 4 members of a coyote pack were observed around Blacktail Butte in the Grand Teton National Park, outside of Jackson, Wyoming [see Figure 3 and (29)]. The existence of abundant food that was clumped and economically defendable favored the formation of a stable pack in this area of the park for at least 7 years, during which there was significant overlap by pack members in the use of their group-defended territory (29). The 4 polygons shown encompass 25%, 50%, 75% and 95% of all locations. Area is measured in km^2. Only pack members defended territorial boundaries, and the size of their territory was much smaller than the home ranges of coyotes living either as mated pairs or alone. The ⚔ was the common observation point.**
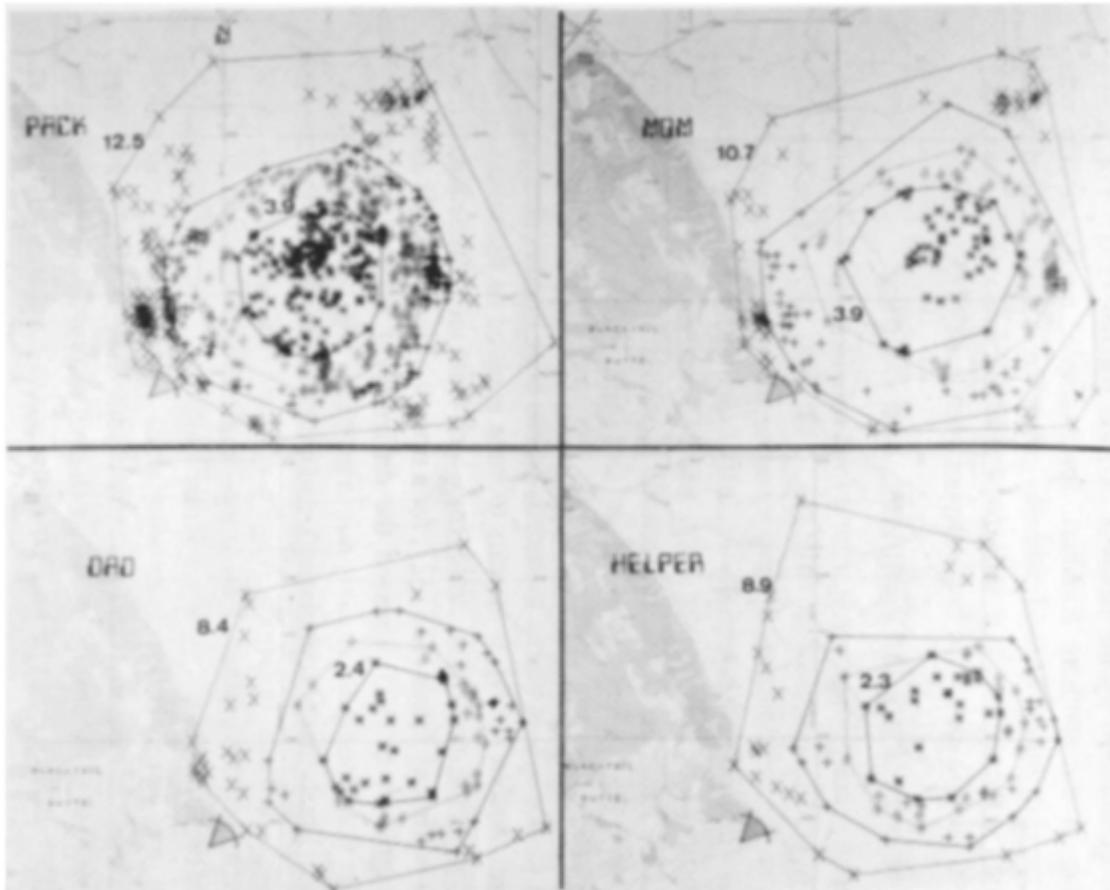
Group and territorial sizes can also vary independently. Range size and configuration may be determined by the pattern of dispersion of food resources (and the influence of topography on the economics of defense), while group size may be determined by the richness of food patches (131). For brown hyenas

living in the southern Kalahari, for example, territorial size was affected by the distribution of food, whereas group size was influenced by the quality of food in the territory (i.e. the size of available carcasses). Thus, both territorial and group size varied but were not correlated (215).

Mating Patterns, Parental Behavior, and Helping

Mating patterns, care-giving behavior, and food resources are, not surprisingly, closely related to one another (61, 153, 249, 268, 327). Here we look specifically at the relationships among resource availability, monogamy (a prolonged association and essentially exclusive mating relationship between one male and a single female; see 327), and helping behavior [alloparental behavior (324), i.e. care (food, protection) provided to young animals by individuals other than parents; (for reviews and comparative data see 29, 46, 47, 49, 123, 194, 195, 222, 229, 231, 249, 255, 257, 311)].

Although monogamy is rare in mammals [it has been documented in about 3% of species studied (153)], it appears to have evolved as the predominant mating strategy in the majority of canids for which there are sufficient data (but see 125) but not in any felids (153, 327; for a review of the available data, see 105). Harrington et al (125) stressed the difficulty of determining mating patterns under field conditions (mainly due to problems with actually observing identified individuals that are copulating), and their cautious approach deserves close attention. In many instances, researchers base their conclusions about mating patterns on circumstantial evidence--e.g. close association of a pair outside of the breeding season, absence of other adults in the pair's home range.

In general, monogamy is associated with increased male parental care (153, 158). In addition, monogamy (and possibly helping; see 105, 229, 249) has apparently evolved in environments in which food resources are energetically costly to collect and in species in which the litter size is comparatively large, as in canids (61, 153).

Kleiman (153) differentiated between two general types of monogamy facultative and obligate. Facultative monogamy occurs when the necessary resources are thinly and patchily distributed and when only a single member of the opposite sex is available for mating. Paternal care and helping may be lacking. The only carnivore for which facultative monogamy has been described under field conditions is the maned wolf (73).

Obligate monogamy occurs when a single female cannot rear a litter without aid from conspecifics, perhaps because the carrying capacity of the habitat is insufficient to allow more than one female to breed within the same home range at a given time. [Wittenberger & Tilson (327) de-emphasize the importance of carrying capacity in the development of monogamy.] Although canids (with the possible exception of maned wolves) would be classified as obligately monogamous, the *need* for care from the father or helpers is probably not *essential* for successful rearing of young (327). The presence of helpers, and in some cases paternal care, is positively correlated with pup survival in a variety of canids, however, though the relationship is not always statistically significant (29, 194, 195, 220-222; see also 223). But, as a result of prey scarcity, pairs may produce more surviving young than do groups with one or more potential helpers; this phenomenon has been observed in wolves (123). In red foxes, if food is scarce, the presence of helpers may temporarily reduce the reproductive success of breeding individuals (305).

A detailed review of helping behavior is beyond the scope of this paper. (Recent summaries can be found in 29, 105, 106, 123, 194, 195, 222, 249, and 255). Kin selection and reciprocity, often working together, account for most instances of helping in carnivores (29, 194, 195, 222, 231, 255, 257). Among canids, helpers frequently are nonbreeding and nondispersing older siblings of the young for which they care, and an individual that previously helped his younger siblings (or half siblings) may be reciprocated in kind if he

or she later breeds and if the recipients of his or her help have not dispersed (29, 231; see also Figure 3). Helpers and other nondispersing individuals may also inherit part or all of their natal area and subsequently breed there.

CONCLUSIONS

The diversity of extant carnivores makes them an exemplary group for studying the evolution of life history patterns and social behavior and ecology from a comparative perspective. Although some general explanations of carnivore social ecology appear to have broad applicability, most species have not even been considered in these syntheses. We need to know more about the *how's* before we flood the market with grandiose theories about the *why's* (113). Methods of collecting and analyzing data must be carefully considered in interpreting the results of a given study, and comparisons of two or more research projects should be undertaken with caution. Long-term field projects on unexploited populations are needed; researchers and funding agencies need to make the necessary commitments, despite the obvious risks (75), which are far outweighed by the potential rewards.

From a practical point of view, comparative data on social ecology may be as useful for the development of nature reserves (197) as they are in management programs. Furthermore, the study of social carnivores may shed some light on the evolution of human behavior (150, 161, 275).

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