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Abstract: How coexisting carnivore species avoid interspecific competition is examined by consideration of their more prominent physical and behavioral characteristics. An attempt is made to explain coexistence to the 33 Transvaal carnivore species. The behavioral characteristics, which are considered here in various combinations, are daily activity regimen, food preference, habitat preference, geographical distribution, and social structure. The mean species body weight as an indicator of the size of prey on which a carnivore exists is also incorporated. Eighty-two % of the carnivores are shown to form a trend ranging from a nocturnal/solitary mode of life to an entirely diurnal/gregarious existence.

COEXISTENCE IN TRANSVAAL CARNIVORA

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ABSTRACT

How coexisting carnivore species avoid interspecific competition is examined by consideration of their more prominent physical and behavioral characteristics. An attempt is made to explain coexistence of the 33 Transvaal carnivore species. The behavioral characteristics, which are considered here in various combinations, are daily activity regimen, food preference, habitat preference, geographical distribution, and social structure. The mean species body weight as an indicator of the size of prey on which a carnivore exists is also incorporated. Eighty-two % of the carnivores are shown to form a trend ranging from a nocturnal/solitary mode of life to an entirely diurnal/gregarious existence.

INTRODUCTION

Some two decades ago this paper might well have been titled "Niche occupation by Transvaal carnivores." The concept that each species fulfills a unique functional role in a specific place dates back to Grinnell (1924) and Elton (1927), and has served a useful function in subjectively describing the niche of an animal. However, it never really explained in detail how each animal fills its particular niche. Modern study of the niche and niche theory flows from Hutchinson's (1957) landmark paper, and allows quantification of the role each animal plays, from measurements of the amounts of various resources (axes in a hypervolume) utilized. Prior to this, Gause's (1934) experiments led to the idea that competition serves to separate species, and therefore the niches they fill. Competition through evolutionary time therefore led to separation of resource utilization in coexisting species, and the niches species occupy are therefore as much an outcome of evolution as, for example, their physical characteristics. On the other hand, although the physical characteristics of a particular species may be fairly constant over much of its distributional range, the exact niche it occupies (not in the descriptive Eltonian sense but in the analytical Hutchinsonian one) usually varies, depending on the habitat it occupies and the nature of other species in the community.

The mammal fauna of the Transvaal has been intensively surveyed over the last five years (Rautenbach, in preparation). This Province possesses a particularly rich mammal fauna, consisting of 175 species of which 33 are carnivores. Adaptation and radiation has led to different parts of resources being utilized, especially food and activity periods by different members of this assemblage of carnivores. It is of interest to note how resources are shared and competition lessened, and coexistence enhanced.

Rather than work out niche occupation by the various carnivores, which to be meaningful would involve quantifying resource utilization in various axes by carnivores in specific communities, the approach here taken is to look at various attributes of co-occurring species, and then to see where and if competition may come into force. This is done by considering in combination average species mass, basic food preference, daily activity regimen, habitat selection, distribution patterns, and specific social characteristics. Trends in adaptations are also considered, especially the advantage of differential body size in coexisting carnivores preying on the same food types, as variation in body size could affect prey size taken (Rosenzweig, 1966). It was also necessary to categorize behavior, in the full realization that the behavioral scope of each species may well be wider than the particular category to which it is designated.

Table 1.—*The 33 species of carnivores occurring in the Transvaal. Average body weight expressed in kg, the log. value of the mean body weight in grams, as well as the daily activity, social structure, and basic feeding categories to which each species is assigned, are indicated. See text for further explanations. I = Insectivorous, P = Predatory, O = Omnivorous, and S = Scavenging.*

Species	Average weight (kg)	N	Log. weight (g)	Daily activity regimen	Social structure	Basic feeding adaptation
Otocyon megalotis	3.4	(7)	3.53	iii	3	I
Lycaon pictus	22.0	(12)	4.34	v	5	P
Vulpes chama	2.9	(22)	3.46	i	1	P
Canis adustus	10.0	(5)	4.00	ii	1	O
Canis mesomelas	7.8	(48)	3.89	ii	2	O
Aonyx capensis	12.1	(4)	4.08	iii	3	I
Lutra maculicollis	4.5	(1)	3.65	ii	3	I
Mellivora capensis	8.9	(5)	3.95	ii	2	I
Poecilogale albinucha	0.4	(4)	2.60	ii	3	P
Ictonyx striatus	1.1	(10)	3.04	i	2	I
Viverra civetta	12.4	(5)	4.09	i	1	O
Genetta genetta	1.9	(15)	3.28	i	2	P
Genetta tigrina	1.9	(24)	3.28	i	2	P
Suricata suricatta	0.7	(19)	2.85	v	5	I
Paracynictus selousi	1.6	(39)	3.20	i	2	I
Cynictis penicillata	0.8	(20)	2.90	iv	3	I
Herpestes ichneumon	3.1	(14)	3.49	v	3	P
Herpestes sanguineus	0.5	(25)	2.70	v	1	P
Rhynchogale melleri	2.8	(1)	3.45	ii	1	O
Ichneumia albicauda	3.6	(1)	3.56	i	2	P
Atilax paludinosus	4.3	(5)	3.63	i	1	I
Mungos mungo	1.3	(7)	3.11	v	5	I
Helogale parvula	0.2	(13)	2.30	v	5	I
Proteles cristatus	9.9	(14)	4.00	i	1	I
Hyaena brunnea	36.1	(7)	4.56	ii	2	S
Crocuta crocuta	69.7	(8)	4.84	ii	4	P
Acinonyx jubatus	35.1	(3)	4.55	iv	2	P
Panthera pardus	41.7	(4)	4.62	ii	1	P
Panthera leo	204.1	(4)	5.31	ii	4	P
Felis nigripes	1.5	(8)	3.18	ii	1	P
Felis serval	9.6	(5)	3.98	i	1	P
Felis caracal	10.5	(10)	4.02	ii	1	P
Felis libyca	4.7	(58)	3.67	ii	1	P

METHODS

Table 1 lists the 33 carnivore species occurring within the Transvaal, with average weight, expressed in kg of both sexes combined, indicated for each species. Weight data are based on Transvaal Museum records, supplemented by relevant information from Smithers (1971). Samples sizes (N) are indicated. The logarithmic values for the means of species weights as expressed in g were calculated and are also given.

Based upon personal observations and unpublished data (Rautenbach, in preparation; Nel, in preparation), as well as published information (see Smithers, 1971; Rowe-Rowe, 1977*a*, 1977*b*), an integral numerical value has been assigned to the daily activity regime of each species. These range from exclusively nocturnal with a Roman numerical value of i, to exclusively diurnal with a numerical value of v (Table 1). Categories ii and iv denote nocturnal species with some diurnal activity, and diurnal species with occasional nocturnal activities, respectively. Similarly, integral Arabic numerical values 1 through 5 have been designated for the solitary to gregarious behavioral range, ranked from very solitary with a numerical value of 1, through to very gregarious with a numerical value of 5. The various species were each assigned to one of these five social category values on the grounds of average social grouping, allowing for other situations mentioned in the literature.

The integral values assigned to these two behavioral patterns considered (activity and social groupings) are only arbitrary points spaced along a continuum, and each represents an average categorized value considered most typical for the species. Judgment herein was subjective. We could not use more than five subdivisions with any accuracy, but in spite of this the resulting divisions are found to be both convenient and meaningful.

Hunting behavior is adapted to basic food preference. Diet and the mode of acquiring nourishment are other important aspects of the adaptive behavioral makeup of a species' accompanying avoidance of competition. Also considered in this study, then, are the four basic feeding methods or food types of carnivores, that is scavenging, omnivorous, insectivorous (denoting a diet of any invertebrate), and predacious. In assigning each species listed in Table 1 to a feeding category, it must be stressed that carnivores are opportunistic with regard to food items taken, especially under low interspecific competitive conditions. Only what is considered to be the primary or optimum feeding trait of a species when under more intense interspecific competition is considered here.

In Fig. 1 the integral values of the activity regimen and the social structure are plotted against each other for each species. Intraspecific social interrelationships are presented on the horizontal axis, and the activity regimen on the vertical axis. In Fig. 2 the four basic feeding categories are presented by vertical columns, each of which is divided into diurnal and nocturnal subsections. The nocturnal subsections are stippled. Each species was assigned to its appropriate column with regard to its basic feeding behavior and characteristic daily activity cycle. Position against the vertical axis was assigned by the logarithmic value of the average adult body mass, expressed in g. The principle is that clustering of species indicates possible interspecific competition, and vice versa. This is based on the correlation between the size of the predator and the size of the prey it can effectively handle, or usually catches. It has been calculated that the maximum mass of prey that can be handled with efficiency by an individual true predator is 1.5 times that of the predator itself. Group cooperation accounts for a higher ratio between the individual predator and the prey. It conversely follows that a big carnivore could not exclusively hunt very small prey because the energy gain herein would not warrant the investment in such an energy expenditure.

RESULTS AND DISCUSSION

Those species falling within the limits of behavioral values 1i, 1ii, 2i, and 2ii in Fig. 1, are all nocturnal and solitary, and represent the majority (58%) of the Transvaal Carnivora. The lines in Fig. 1 connect the upper values for both variables of this nocturnal/solitary block, with the upper values of the very gregarious and exclusively diurnal group (value 5v). All species falling between these two lines are considered to represent a trend from a solitary and a nocturnal existence to an entirely gregarious and diurnal mode of life. No less than 82% of all carnivores in the Transvaal follow this trend. *L. maculicollis*, *P. albinucha*, *O. megalotis*, and especially *A. capensis* are behaviorally intermediate between the two extremes within this trend. It is within this trend that interspecific competition is potentially the highest, as will be elaborated below. Three of the four species at the extreme diurnal/gregarious end of the trend (Fig. 1) are small insectivores and thus potentially in direct competition.

Eighteen % of the carnivore species under consideration do not conform to this trend, and have adopted a strategy, which seems to minimize possible competition. However, where four species have radiated toward a diurnal/solitary mode of life (*H. sanguineus* very successfully), only two species radiated a short distance toward a nocturnal/gregarious existence.

There are no extremely nocturnal/gregarious species (value 5i), although the lion and the spotted hyena are approaching this condition. A possible explanation for the poor radiation toward an extreme nocturnal/gregarious behavioral range could be the difficulty of maintaining group structure in the dark. Smaller gregarious species are mostly insectivorous and diurnal and finding food in the dark may also present difficulties, apart from the difficulty in locating predators in time. Schaller and Lowther (1969) consider the lion, in contrast to the wild dog, as incompletely adapted to a social life because lions frequently quarrel over the proceeds of a hunt. If their interpretation is correct, the true position of the lion on the graph in Fig. 1 may be more toward the left, and consequently even closer to the general trend.

C. crocuta is basically a nocturnal animal, but may also be active during the day. According to Kruuk (1966, 1972) the species tends to scavenge by day, and to become efficient pack hunters and killers by night. The spotted hyena has a complex matriarchal social system, with the females physically bigger than the males and dominating them. *C. crocuta* thus has radiated successfully some distance away from the trend, toward a nocturnal/gregarious existence.

Otocyon, although regarded by most as a nocturnal species, has a diurnal mode of life in undisturbed areas during winter. In settled areas, however, it becomes exclusively nocturnal. In discussing the eastward range extension of the species in the Transvaal, Pienaar (1970) mentions that it is exclusively nocturnal in the Kruger National Park, and ascribes this to a form of protective behavior of colonists in a new territory. In the Transvaal as a whole the species is almost entirely nocturnal, but on the other hand it occurs for the most part in this Province only in settled areas. Studies elsewhere (Nel, 1978) show that activity is perhaps correlated to the need to thermoregulate efficiently. Most observations on the bat-eared fox in the Transvaal are

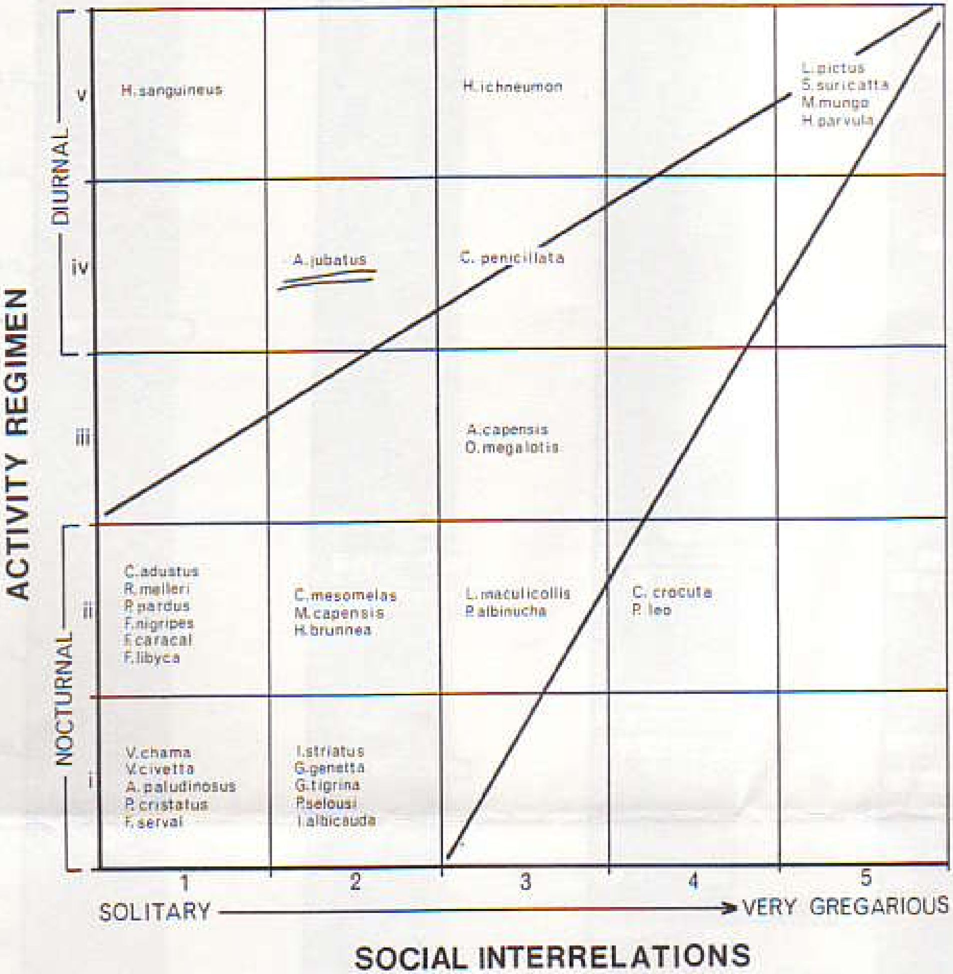

Fig. 1.—Graphical presentation of species separation by plotting the categoric values assigned to intraspecific social relations against the categoric values of daily activity cycles. See text for further explanations.

of solitary or small groups of animals, but again this would depend on the time of year of observations (Nel, 1978). This species is thus plotted in the position 3iii within the trend, although it could be argued that the Transvaal population should be plotted together with the lion just outside the trend.

It thus would appear that a vacuum exists at the nocturnal/gregarious end of the behavioral range, but that carnivores in the Transvaal do not utilize it, for reasons at present not fully understood.

H. sanguineus is the most predacious of the Herpestinae in the Transvaal, being an efficient killer of vertebrate prey. It is furthermore solitary and diurnal, in contrast to the general tendency for the more predatory small carnivores to be solitary and nocturnal (see Ewer, 1973:277). This seeming anomaly could result from an adaptive radiation to utilizing resources (especially habitat and food) with a low utilization pressure.

H. ichneumon and *C. penicillata* are only partly social species. When hunting for food both species are solitary and in this respect they are reminiscent of *H. sanguineus*. *H. ichneumon* is predatory, whereas *C. penicillata* is insectivorous. The distributional ranges of these two species furthermore do not overlap at all. *C. pencillata* is unique in the sense that when actively seeking food it is a solitary insectivore, in contrast to the other diurnal insectivores, which are social species.

The cheetah displays the three basic felid hunting techniques—stalking, utilization of the forepaws to fell its prey, and an oriented neck or choking throat bite according to the size of the prey. However, the cheetah atypically (for a felid) outruns its quarry

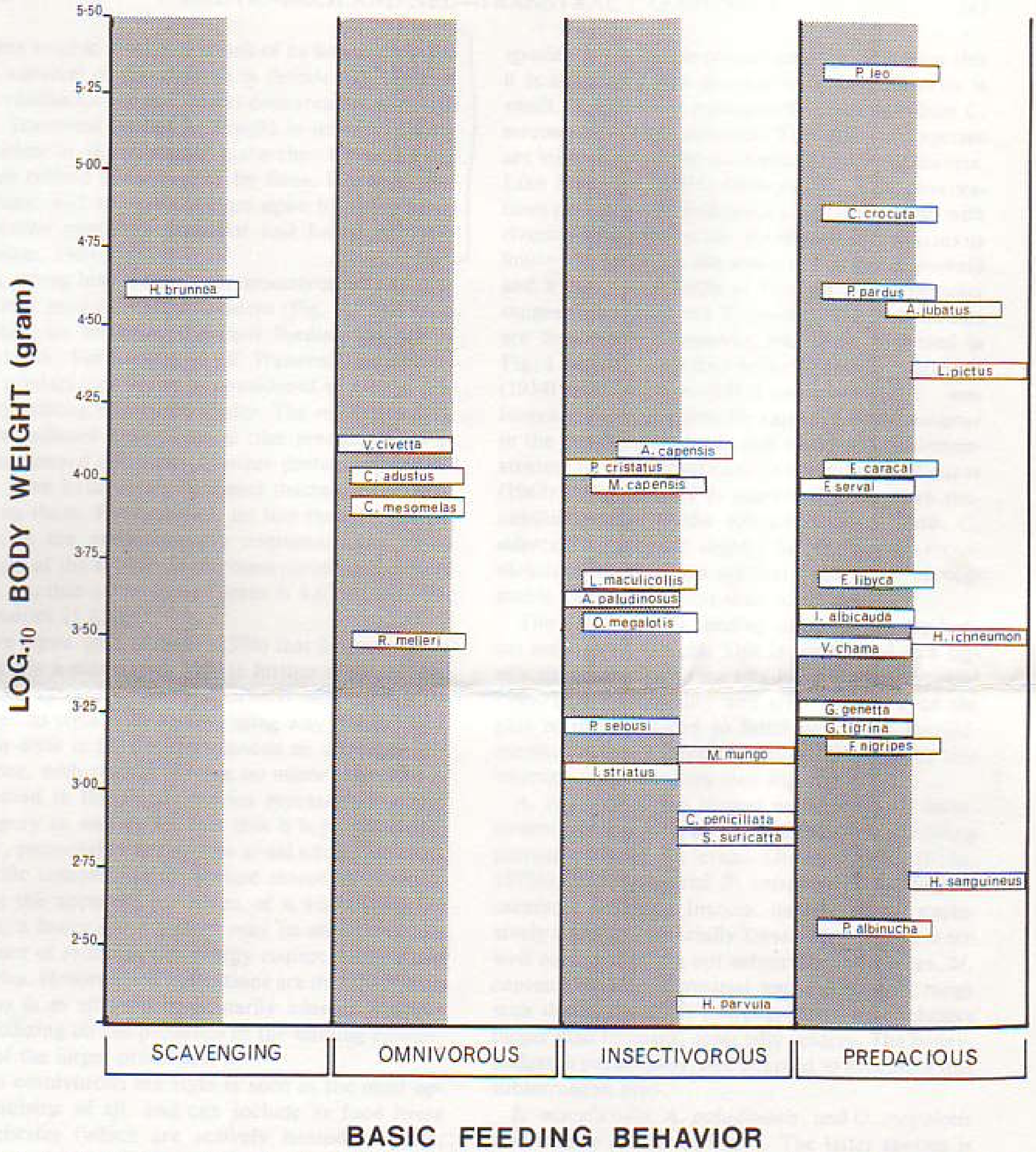

Fig. 2.—Graphical presentation of niche occupation. The four basic feeding categories are presented as vertical columns, each subdivided by a stippled column denoting nocturnal activity and an unstippled column denoting daylight activity. Species are assigned to their appropriate columns and are vertically spaced against the X-axis representing the log. value of the mean body weight in grams.

and possesses distinctive anatomical adaptations for this particular way of hunting, which can best be performed in daylight. There appears to be very little need for group participation. The cheetah thus clearly acquired behavioral and physical adaptations to enable it to radiate adaptively into a less competitive area. Of the four carnivores above the trend illustrated in Fig. 1, the cheetah utilizes a different trophic level as a result of its larger size. Yet the survival of the cheetah is threatened. Perhaps the reason for its precarious conservation status in the Transvaal should be sought in its low ranking position in the predator hierarchy. Cheetahs are often robbed of their prey by lions, leopards, and hyenas, and are even preyed upon by these more powerful predators (Schaller and Lowther, 1969; Pienaar, 1969).

A strong bias towards the insectivorous and predacious modes of life is evident (Fig. 2). The ratio of species between the four feeding classes is 1:4:12:16. Forty-eight % of Transvaal carnivores are predacious, which is considered to be the primary feeding trait of the Order. The remaining 52% have radiated away from a true predacious existence toward utilization of other protein resources, and have behaviorally adapted themselves to procuring them. Furthermore, no less than 75% of all species are predominantly nocturnal. The mean weight of the species in the omnivorous category is 8.25 kg, that of the insectivores is 4.07 kg, and the predators 25.82 kg.

We agree with Skinner (1976) that *H. brunnea* is basically a scavenger. This is further substantiated by the special dental and cranial adaptations acquired to cope with a scavenging way of life. Such a life style is for several reasons an uncertain existence, with chance playing no minor role. This is reflected in the single species represented in this category as well as the fact that it is primarily solitary, presumably in order to avoid excessive intraspecific competition for limited resources. Considering the apparent hardships of a scavenging life style, a lower mean weight may be an appropriate manner of reducing the energy requirements of the species. However, all indications are that the brown hyena is in all aspects primarily adapted towards capitalizing on the proceeds of the hunting endeavors of the larger predators.

An omnivorous life style is seen as the most opportunisitic of all, and can include as food items vertebrates (which are actively hunted), insects, carrion, and vegetable matter, especially fruit. The concept of a smaller body size as a means of reducing the energy requirements of the species with such a precarious existence can be illustrated by the fact that the mean species weight in the omnivorous category is only 8.3 kg, as opposed to the mean of 25.8 kg of the predatory category and mean of 36.1 kg of *H. brunnea* in the scavenging category.

R. melleri is much smaller than the other three species in the omnivorous category, and from this it is concluded that overlap in feeding interests is small. *V. civetta* is ecologically separated from *C. mesomelas* and *C. adustus*. The latter two species are inhabitants of the open plains and avoid forests. Like Smithers' (1971) findings, our own observations on *V. civetta* indicate a close association with riverine and subriverine woodlands. *C. adustus* is limited in range to the eastern Transvaal lowveld and a small area north of Pretoria. *C. mesomelas* ranges throughout the Transvaal. The two species are thus partly sympatric, and as is suggested in Fig. 1 may be in conflict here. Although Shortridge (1934) and Smithers (1971) speculate that *C. mesomelas* is being gradually replaced by *C. adustus* in the overlapping zone, this could not be demonstrated in the Transvaal. According to Pienaar (1963) *C. mesomelas* is numerically the more successful species in the Kruger National Park. *C. adustus* is however slightly larger than *C. mesomelas*, and indications are that it relies less on vegetable matter as a food source.

The insectivorous feeding category has the lowest mean body weight. This is considered as a significant adaptation to the small size of the individual prey, and the quantity and effort required on the part of the carnivore to fulfill its energy requirements. There are three clusters in this category that warrant closer scrutiny (see Fig. 1).

A. capensis is the biggest member of the insectivorous group. It is an aquatic mammal subsisting almost entirely on crabs (Rowe-Rowe, 1977*a*, 1977*b*). The terrestrial *P. cristatus* is the biggest carnivore living on Insecta, namely almost exclusively termites (especially *Triner vitermes*). It is not well equipped to dig out subterranean termites. *M. capensis* is also terrestrial and overlaps in range with the aardwolf. It however hunts invertebrates bigger than termites, especially spiders. The honeybadger is particularly well adapted to procuring this subterranean prey.

L. maculicollis, *A. paludinosis*, and *O. megalotis* also form a cluster in Fig. 1. The latter species is however a terrestrial inhabitant of the open plains, whereas the former two are to varying degrees semiaquatic. The spotted-necked otter and the marsh mongoose appear to be in conflict as they both rely heavily on crustaceans in their respective diets, and furthermore overlap in geographic range and habitat requirements. *A. paludinosus* is however a more versatile animal because it is more mobile on land. It wanders greater distances away from water and utilizes a wider spectrum of food resources. It is furthermore believed to hunt for aquatic prey only in the shallows, as opposed to *L. maculicollis*.

C. penicillata and *S. suricatta* also overlap in distributional range. Where the suricate is very gregarious and almost exclusively insectivorous, the yellow mongoose is a solitary hunter, which takes vertebrate prey as well as invertebrates.

The predatory category is the true domain of the Felidae, and no felid has radiated away from it. They are specialist killers, the only group capable of handling prey larger than themselves singlehanded. This is achieved mostly by means of a lethal well-directed single neckbite, or derivations thereof. Felidae are, in general, also expert stalkers.

Of the nonfelids in this feeding category, the mustelid *P. albinucha* is an exception, in that it behaves very similarly to the Felidae with regard to killing efficiency and the size of prey that it can handle. The remainder, that is the viverrids, canids, and *Crocuta*, all belong conditionally to the predatory category. *C. crocuta* and *L. pictus* rely on group cooperation to kill, and are relatively inefficient predators when alone. The remainder of the nonfelids rely on the other food sources already discussed, and when they kill, it is mostly prey much smaller than themselves (excluding domestic stock).

Very little is known of the serval, but from the information that is available, it would appear not to be in conflict with the caracal, as is indicated in Fig. 1. The serval appears to be restricted to areas with permanent surface water and its associated forests, and preys mostly on rodents. The caracal, on the other hand, does not prefer forests and is a true predator of prey more equal in size to itself.

The geographic ranges of *V. chama* and *I. albicauda* overlap only peripherally in the Transvaal. *F. libyca*, on the other hand, is widely distributed and overlaps with the ranges of both the former species. *F. libyca* and *V. chama* are separated in size to the extent that they presumably avoid conflict by means of differential choice in prey size. *I. albicauda* is restricted to riverine forests, whereas *F. libyca* has a wide habitat tolerance. The latter species therefore appears to be a universalist, the former a specialist extremely well adapted to its particular narrow niche. In the zone of contact between these two species, it can be postulated that *I. albicauda* has the edge in a competitive situation.

The two species of genets are partly sympatric. Our own experience agrees with that of Smithers (1971) in that these two species are ecologically separated. *G. tigrina* prefers a habitat close to water, whereas *G. genetta* exists away from it. The range of *F. nigripes* overlaps partially with that of *G. genetta*, and not at all with *G. tigrina*. However, so little is known about the general biology of the black-footed cat, that no suggestions can be offered as to how it avoids conflict with the small-spotted genet.

CONCLUSIONS

A behavioral trend is indicated in carnivores, which ranges from a direct correlation between a nocturnal/solitary mode of life, to an entirely diurnal/gregarious existence. We conclude that 82% of the Transvaal carnivores fall within this trend. Presumed adaptive radiation away from this trend is restricted to six species. Carnivores are considered incapable of adapting to an entirely nocturnal/gregarious life style.

In the majority of coexisting species interspecific competition is avoided, primarily through different food sources, differences in size of food items (correlated to different body size of the carnivores), or differential use of habitat types. However, in the instances of the two jackal species, *L. maculicollis* and *A. paludinosus*, as well as *F. nigripes* and *G. genetta*, at least partial interspecific competition is suspected. A more intimate knowledge of the general biology of these six species may in time show more subtle mechanisms of avoiding conflict.

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