

On the Ecological Separation between Tigers and Leopards

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ABSTRACT

In the Royal Chitawan National Park, Nepal, the tiger (*Panthera tigris*) and the leopard (*Panthera pardus*) coexist in the riverine forest/tall grass vegetation types. These two big cats differ in the size of prey killed, use of vegetation types, and in activity periods. Although the tiger's weight is four times that of the leopard, coexistence is reportedly not the general rule. A comparison of the results from Chitawan with Kanha National Park (India), where resident tigers occur but leopards are only transients, and Wilpattu National Park (Sri Lanka), where there are leopards but no tigers, indicates that coexistence in Chitawan is facilitated by a large prey biomass, a larger proportion of the ungulate biomass in the small size classes, and by the dense vegetation structure. Some consequences of predator size and the role of interspecific dominance are discussed.

THE *Panthera* RADIATION was mainly accomplished by minor morphological changes which included changes in body size. These big or so-called "roaring" cats are the predators of large mammals, primarily ungulates. They are specialized for capture through stealth and for killing, alone in dense cover, prey which are frequently as large as or larger than themselves. In the lion, *P. leo*, the only social felid, hunting efficiency is increased through cooperative stalks, an adaptive response to open savanna conditions (Schaller 1972, Kleiman and Eisenberg, 1973).

Leopards and tigers inhabit thick vegetation and are sympatric over much of Asia. Leopards are one-fourth as heavy as tigers, yet it is not clear how these solitary-living large felids achieve ecological separation. Locally, they are frequently allopatric. "Where tigers are numerous, leopards are few" is an oft-repeated statement (Schaller 1967, 1972; Ranjitsinh, pers. comm.).

We frequently encountered both leopards and tigers in the Royal Chitawan National Park, Nepal (Seidensticker and Tamang 1974). What particular factors are present and facilitating sympatry of these congeners in Chitawan that are not present in other areas of range overlap? Intensive radiotracking of two resident (reproducing) females, a tiger and a leopard, has provided data which are useful in understanding their ecology and evolutionary history.

METHODS AND ENVIRONMENTAL CONDITIONS

His Majesty's Government of Nepal gave the Smithsonian Institution permission to immobilize selected tigers and leopards and use radiolocation equipment

in the Chitawan Valley, and I was able to capture and radio-track tiger and leopard from December 1973 to mid-April 1974 when my work terminated. Details of capture are described in Seidensticker *et al.* (1974) and equipment and radiotracking procedures in Seidensticker *et al.* (1970, 1973).

The Chitawan Valley is located at the base of the outermost Himalayan range, the Mahabharat Lekh, and is bounded on the south by the low-lying Churia and Someswar Hills (Siwaliks). The Royal Chitawan National Park covers an area of 544 km², extending eastward from the Narayani River and southwest from the Rapti River over the Churia and Someswar Hills to the international border with India. The forests are composed predominantly of deciduous and semi-deciduous species. *Shorea robusta* dominates over the Churia Hills, but the low-lying areas along the river within the Park are a mosaic of riverine forests dominated by *Bombax malabari-cum* and *Trewia nudiflora* and tall grass areas (to 5 m, see fig. 1) which include *Saccharum* sp. and *Phragmites karka*. Except for strips of forest along the river, the low-lying areas outside the National Park are primarily under cultivation. The climate is monsoonal with 230 cm of annual rainfall.

On 9 and 17 December 1973, respectively, a female leopard and tiger were captured and radiotagged; over the ensuing four months their movements and activities were closely monitored. During this period they used essentially overlapping home ranges within the riverine forest/tall grass vegetation type in the northeast corner of the Park near the village of Sauraha. The tiger was accompanied by 2 cubs approximately 6 months of age when first captured; the leopard gave birth to 3 cubs on 26 or 27 January 1974.



FIGURE 1. A domestic elephant in the riverine forest/tall grass habitat in the Sauraha Area, Royal Chitawan National Park, Nepal. The Himalayan snow peaks (7864 m) rise 100 km in the distance. November 1973.

HOME RANGE AND DAILY MOVEMENTS

Home range areas were determined in the classical manner, by plotting all locations and connecting the outermost points. The areas used by both tiger and leopard are shown in figure 2 and total 9.3 and 8.0 km² respectively. However, actual areas used by both cats were slightly smaller; neither ventured into the cultivated area adjacent to the Park, nor did the leopard roam the open banks along the Rapti River.

From tracks and direct observations at least 2 male and possibly 2 female tigers and 1 female and possibly 2 male leopards moved over the area utilized by the two radiotagged cats (fig. 2) at least part of the time. None of the other females, however, were accompanied by young.

Muckenhirn and Eisenberg (1973) estimated leopard home ranges in Wilpattu National Park, Sri

Lanka (Ceylon), to be 8-10 km², similar to that which I found for the radiotagged leopard. The area used by the tiger is considerably smaller than the range estimated for a female tiger in Kanha National Park, India, by Schaller (1967) where he estimated home range for a female with 4 cubs to be 65 km². Female tigers with cubs at the western end of Chitawan also used larger areas (C. McDougal, unpublished data). The difference in available prey biomass between the Sauraha area and western Chitawan or Kanha is an important proximate factor.

The tiger was fairly consistent in the total area she used each month (5.0-6.9 km², fig. 3). The leopard showed a great deal of fluctuation, with area used each month ranging from 2.8 to 6.3 km². This was in response to the birth of young and to the restricted mobility of the young during the first months of life. Both females continued to show an upward

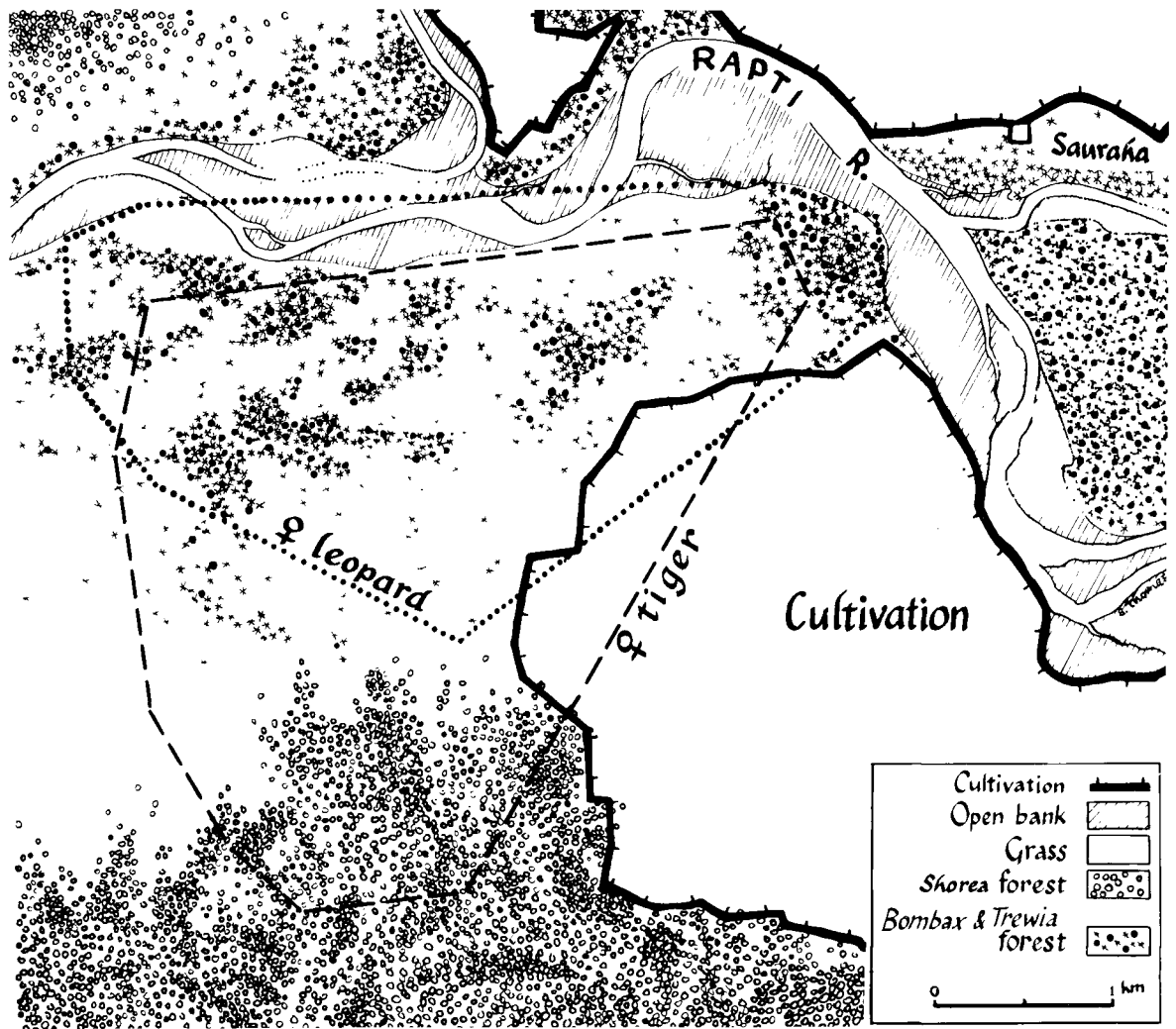


FIGURE 2. The home ranges of a female tiger and female leopard determined by radiotelemetry from mid-December 1973 to mid-April 1974, Royal Chitawan National Park, Nepal. The edge of the cultivation is the Park boundary.

trend in the cumulative area used indicating that during the 4 months they had not yet utilized all their home range areas.

Intensive radiotracking studies of the puma (*Felis concolor*), slightly larger in size than the leopard, revealed that females were most restricted in their use of space during their young's first year of life and least restricted during the interval after independence of the young and before a new litter was born (Seidensticker *et al.* 1973). I followed the movements of the female leopard for 7 weeks before the birth of her cubs and she did not use a maximum home area during this period.

The puma young's transition to independence is abrupt; after independence, the young dispersed from

the natal area within a few weeks. This dispersal does not occur with tigers. Young tigers, especially males, tend to move about independently of the female within the same area for an extended period of time during their second year (Schaller 1967; McDougal and Seidensticker 1976) and there is evidence that this dispersion also occurs in the leopard (Schaller 1972). It appears that newly independent tigers and leopards will remain for some time in the home area of the female, a pattern similar to that of the black bear, *Ursus americanus* (Rogers, in Wilson 1975). There is no hard evidence available yet on just when and how young tigers and leopards do disperse or the mechanisms involved.

The differences in the way female *Panthera* and

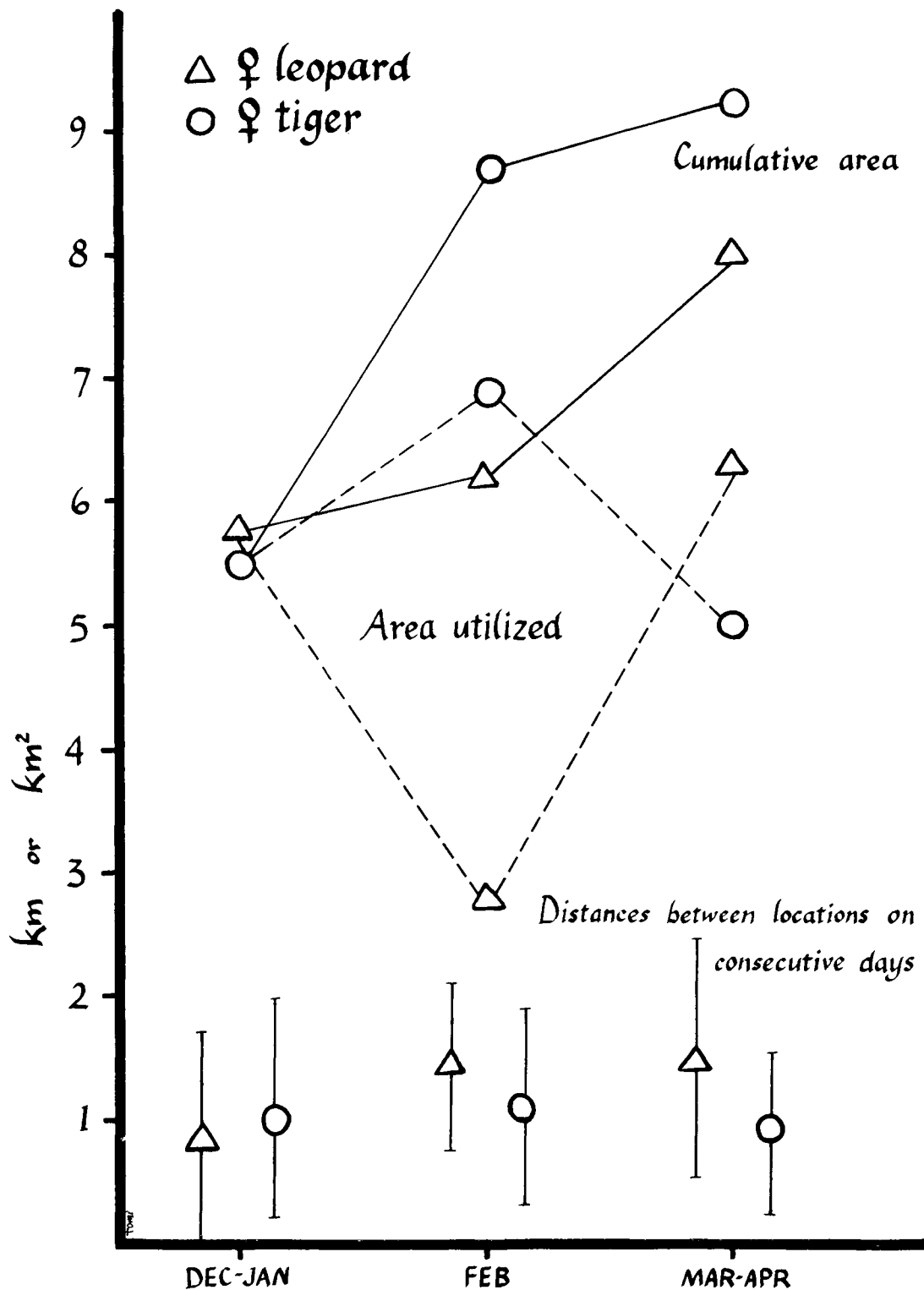


FIGURE 3. A summary of areas utilized, cumulative area occupied and linear distance between locations on consecutive days for a female tiger and female leopard, Royal Chitawan National Park, Nepal. Total radiolocation days are 84 and 92 for the tiger and leopard respectively.

puma utilize their home areas during pregnancy may be related to the dispersal pattern of the young. It seems related to habitat structure and environmental stability, as Geist (1974) has reported for certain north temperate ungulates, and the mechanisms used in the location of suitable areas for establishing themselves as breeding adults (Seidensticker *et al.* 1973). This issue is a critical one in the conservation of solitary predators, especially in small sanctuaries.

An index of movement was derived by measuring the straight-line distances from the first location on consecutive days. These are shown for both species over the 4-month tracking period in figure 3. The mean distances moved by the tiger were fairly consistent over the period, during which time her cubs were from 6 to 10 months of age. The leopard showed considerable variation, related to the birth of her young in late January. After the birth, her average straight-line distance markedly increased (from 0.84 to 1.41 and 1.49 km respectively), although the area she utilized decreased from 5.5 and 2.8 km² in February but again increased during March and April to 6.3 km².

These day-to-day movements are only a rough index of the actual distances moved by either cat; the actual route taken between these two points could be, and frequently was, many times longer. However, both species would make direct movements from one location to another, then would slowly move back and forth. They were apparently moving directly to a hunting area before beginning deliberate hunting movements.

HABITAT SEPARATION

As shown in figure 2, the tiger and leopard used extensively overlapping areas in the riverine forest/tall grass type. The exception to this practice was during February and March when the tiger occasionally used the edge of the *Shorea* forest to the south. Considering just the riverine forest/tall grass type where there was complete overlap, the tiger was located in the tall grass more frequently than the leopard in December and January; February showed a reversal, with the tiger more frequently using the forested area; in March and April, there was again a shift, with the tiger once again more frequently found in the tall grass (fig. 4).

In 1973-74 grass-burning began fairly early in the eastern region of the Park. The first fires were in late December, but the majority of the riverine type was burned in February. These fires, started by local people and park personnel, are slow moving and relatively cool. Only small areas burn at one time,

and a fire did not usually continue through the night. This kind of burning results in a patchy distribution of burned and unburned areas, but the burned areas, though much more open than before, remain a tangle of grass stalks.

These burns were used more frequently by the leopard than the tiger. The leopard appeared to make direct movements to burned areas immediately after the fire; the tiger only infrequently displayed this behavior. Overnight a fire changed an area of dense cover to one of marginal cover. This change altered the utilization patterns of these areas by axis deer (*Axis axis*), sambar (*Cervus unicolor*) and wild swine (*Sus scrofa*); the tiger more often frequented the forest where they concentrated. The leopard hunted among the tall burnt stalks of grass where the hog deer (*Axis porcinus*) remained.

In Chitawan the grass began to grow soon after the fire. In a month's time the new growth was a meter in height. The tiger responded to this growth and again more frequently utilized these areas. The leopard shifted her movements back to the forests. Thus, we see a higher tolerance for a more open habitat by the leopard than by the tiger. This is borne out by other observations of leopards crossing open and cultivated areas where tigers were not seen.

In addition to these responses to habitat fluctuations, there were many fine-grained differences in area used which are difficult to measure quantitatively. Tigers frequently walked along roads; leopards did so only infrequently, and the tiger seemed to use different trails and crossings than the leopard. The tiger is a terrestrial predator. Potentially the leopard could expand her niche through arboreality, but I did not observe this; I only observed her in trees with kills.

ACTIVITY PERIODS

Body movements produce changes in transmitter signal patterns which are detected as slight variation in beats per minute, and this pattern was used to determine whether or not an instrumented cat was active. Actual movement was determined by monitoring changes in location. These determinations were made while some distance from the cat's location, frequently over a kilometer away, and thus data were not biased by investigator influence. While the analysis of movements and home range utilization are based on once-a-day sampling, frequently these cats were located repeatedly during a single day. These data are included in table 1 and together provide a crude index of diel activity and change in activity periods over the season. Though reported in the old

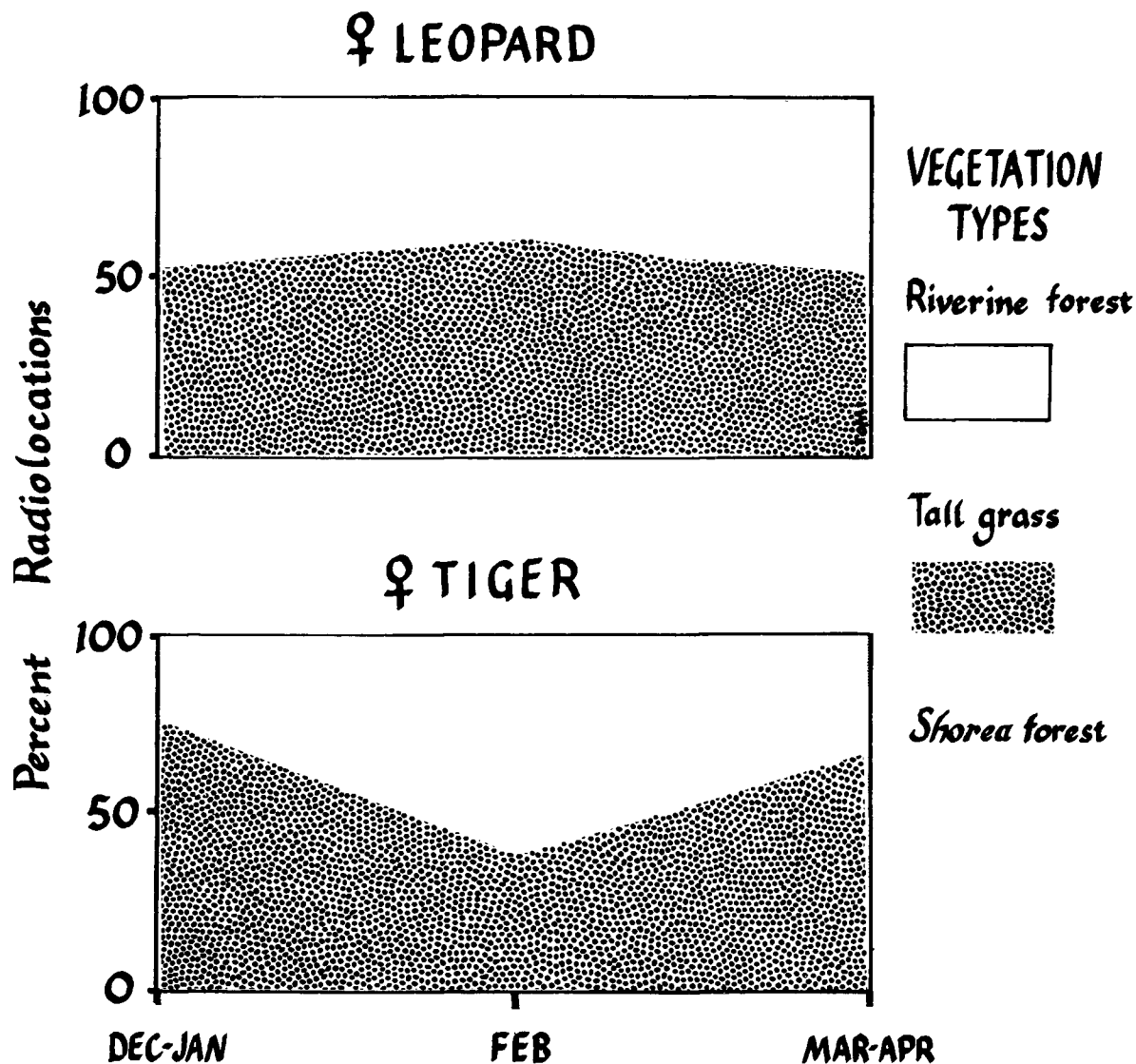


FIGURE 4. The use of vegetation types by a female tiger and female leopard, Royal Chitawan National Park, Nepal. Total radiolocation days are 84 and 92 for the tiger and leopard respectively.

literature as primarily nocturnal or crepuscular in their activity, I found both the tiger and leopard active and moving about throughout the diel cycle (table 1). Both cats moved less during the midday period than in the morning or evening, but during all periods 75 percent of the receptions indicated activity. The tiger moved about more frequently at midday during February and March-April when the weather was much warmer. But in February, the leopard increased her midday and late evening movements; she was most frequently encountered moving in the evening during the March-April period.

The reasons for these movements were not immediately clear, but could be related to differential search patterns employed in hunting in the burned tall grass areas in February and in March-April after the new growth had begun. These movements could also be related to different thermo-regulatory strategies. The big tiger seemed much more susceptible to the stifling heat than the smaller leopard and was more inclined to remain inactive during the day and hot evenings and become active in the cool early morning period (table 1). The leopard, which may be less susceptible to heat, was active more often dur-

ing the day and early evening.

This supports Kleiman and Eisenberg's (1973: 638) observation that the "... evolutionary sequence in *Panthera* has been an initial adaptation away from moist, warm biotopes and a gradual successive invasion of cool, moist biotopes by the tiger and dry tropical areas by the leopard. An ultimate adaptation of the lion occurred in response to dry, open savanna conditions."

FOOD SEPARATION

The ungulate fauna occurring within the home ranges of these two females included Indian one-horned rhinoceros (*Rhinoceros unicornis*), axis deer, hog deer, sambar, muntjac (*Muntiacus muntjak*) and wild swine. Also occurring in the Park were domestic water buffalo and cattle. Both females were known to have killed individuals of these species, with the exception of rhinoceros, muntjac and wild swine (table 2). Only the tiger was known to have killed a rhinoceros calf and wild swine and I found only the remains of a leopard-killed muntjac. However, I observed the leopard hunting young swine (stripers) on two occasions. I believe she killed them and consumed them on the spot, leaving no trace. We have records of tigers killing muntjac from the eastern end of the Park (McDougal and Seidensticker 1976).

Thus, there is a substantial overlap of species taken, but my data are too few to make a quantitative statement of diet separation in terms of species alone.

There is considerable variation in prey taken when size class of prey is considered (table 2), indicating size is an important factor in prey selection. The leopard killed prey ranging from less than 25 to 100 kg in weight with most kills in the 25-50 kg range. In Africa, Schaller (1972) found that the leopard usually killed in the 20-70 kg size class with an upper limit of 150 kg. The tiger's wild prey was primarily in the 50-100 kg range but ranged up to the size of male sambar and adult domestic buffalo and cattle. Arranging kills in relation to body weight of the predator shows a greater diversity of size classes taken by the tiger (table 2).

The duration of time spent with ungulate kills, measured as the number of nights, ranged from 1 to 4 (mode = 2-3; n = 17) for the tiger, and 1 to 2 (mode = 2; n = 8) for the leopard. The average number of nights after leaving one kill and before making another was 3.7 (n = 7; 1-7) for the leopard and was 3 (n = 10; 1-6) for the tiger. The size of prey was directly correlated with the length of stay. On average the leopard's kill rate was once every 6 days or less and the tiger's about once every 5 or 6 days.

TABLE 1. Activity patterns of a female tiger and female leopard, Royal Chitawan National Park, Nepal.

	Number of radiolocations: % of locations indicating activity (movement)					
	05.00 - 10.00 hrs.		10.00 - 16.00 hrs		16.00 - 21.00 hrs.	
	Leopard	Tiger	Leopard	Tiger	Leopard	Tiger
Dec. - Jan.	16: 81 (31)	24:96 (29)	17:76 (18)	14:93 (39)	13:100 (15)	12:92 (42)
Feb.	18: 76 (22)	15:87 (20)	18:89 (29)	13:85 (15)	9: 78 (11)	12:75 (17)
Mar. - April	22:100 (27)	16:87 (38)	11:82 (55)	8:50 (25)	10: 90 (60)	—

TABLE 2. Kills made by tigers and leopards near Sauraha, Royal Chitawan National Park, Nepal.

	<25	25-50	50-100	100-200	200-400	<0.25	0.25-	0.50-	1.0-	2.0-
							0.50	1.0	2.0	4.0
	Size classes of kills (kg)					Kill weight/predator body weight				
Tiger: Wild species ^a	—	3	5	1	3	3	5	—	4	—
Domestic livestock ^b	—	—	1	—	13	—	1	—	2	11
Leopard: Wild species ^c	1	9	2	—	—	1	2	5	4	—
Domestic livestock ^d	—	—	2	—	—	—	—	2	—	—

^a Species killed (No.): *Rhinoceros unicornis* (1), *Cervus unicornis* (4), *Sus scrofa* (2), *Axis axis* (2), *Axis porcinus* (3).

^b Species killed (No.): Domestic cattle (2), domestic water buffalo (12).

^c Species killed (No.): *Sus scrofa* (+), *Cervus unicornis* (3), *Axis axis* (4), *Axis porcinus* (4), *Muntiacus muntjak* (1).

^d Species killed (No.): Domestic cattle (2).

INTERACTIONS AND AVOIDANCE

In the Serengeti National Park, Tanzania, where the large carnivores have been well studied, the lion occupies mainly the woodlands and plains and the leopard the thickets and riverine forests. Both are primarily nocturnal hunters. Schaller (1972) suggested that for a leopard a riverine forest may not be the preferred habitat, but a refuge from lions; interspecific intolerance was particularly striking and he noted that the lion pursued leopards with the same facial expressions and vocalizations used in intraspecific strife.

Lions and leopards, but not tigers, inhabit the same forest areas in the Gir Sanctuary in India and they frequently prey upon the same species. cursory observations indicate they are taking different size classes of prey and are active at different times. However, there are no quantitative data available to clarify interspecific relations (Berwick 1974, pers. comm.).

In Chitawan, leopards pulled about half of their kills into trees. This habit seems to be primarily a response to scavengers (Eisenberg and Lockhart 1972). I have only one record where a tiger may have appropriated a kill from a leopard, but the record was not certain.

I have no other observations on overt interactions. C. McDougal (pers. comm.), working with baiting sites for both tigers and leopards at the western end of the Park, told me of instances where a tiger killed a leopard at these sites. Usually when a tiger began to kill baits at sites formerly frequented by leopards, the latter would no longer come and kill there. At one forest baiting site in February, March, and April, 1975, McDougal (pers. comm.) reported 5 instances where a male leopard killed a bait (a goat or small buffalo) that was later appropriated by tigers, twice by a male cub about its own size. In two instances the male leopard came back and fed later. A female leopard which was known to have killed at the site when the male leopard was in the vicinity did not remain in the area when the tigers were present.

I think it is clear that social dominance (Morse 1974) is a central factor in tiger-leopard coactions. I have outlined some of the means whereby coexistence is achieved in Chitawan; I now consider patterns of avoidance.

In the field it appeared that even beyond differences in habitat utilization, the leopard and tiger tended not to frequent the same areas. To test this hypothesis I examined the distribution of all locations for both females 0.25-km² quadrats. Of a total of 94 quadrats, 40 contained only the tiger's, 32 contained

only the leopard's, 13 quadrats had both, and 9 contained neither ($\chi^2 = 8.89$; $p < .05$). The implication is that something other than random variation is causing the leopard not to use the same areas as the tiger and this was occurring in an area with a considerable degree of vegetational heterogeneity.

The straight-line distance between the tiger and leopard was measured on 66 occasions when I knew the locations of both simultaneously or within a short period of time. The distance between them averaged $1.54 \pm .95$ km. Fourteen percent of the locations were from 0.1 to 0.5 km; 23 percent were 0.5 to 1.0; and the remaining were all over 1 km. Thus from a temporal-spatial point of view, 37 percent of the time, these cats were within 1.0 km of each other; 11 percent of the time within 0.25 km, but they were never found closer than 150 m.

More work must be done before we can fully understand the mechanisms by which avoidance is achieved. These results indicate that the leopard was probably moving primarily independently of the tiger and not keying her movements through some interspecific scent-oriented mechanism, such as has been described by Leyhausen and Wolff (1959) for feral house cats (*Felis catus*). The leopard was using areas not frequented by the tiger, thus greatly minimizing their chance of meeting. This was further facilitated by differences in habitat preference and activity periods. Of course, olfactory and visual channels can come into play at close range, allowing the leopard to detect and avoid the tiger.

DISCUSSION

While there is a wealth of anecdotal literature available (see Perry 1964 and Turnbull-Kemp 1967), only Schaller's (1967) observations on the tiger and leopard in central India, and Eisenberg and Lockhart (1972) and Muckenhirn and Eisenberg's (1973) investigation of the leopard in Sri Lanka (where the tiger does not occur) provide quantitative details which can be used for comparative purposes in clarifying the ecological relationships between these large felids.

In Kanha National Park, Schaller found that leopards were not permanent residents in areas in the center of the Park where tigers were most numerous, but were commonly found around the villages at the periphery or outside. Axis deer, sambar, gaur (*Bos gaurus*), and barasingha (*Cervus duvauceli*) comprised the majority of the wild ungulate biomass, estimated to be 600-700 kg/km². Including domestic livestock, the biomass density estimate was 2400-2500 kg/km². These are all large animals; adult

weights exceed 45 kg. The biomass density estimate for mammalian herbivores in Wilpattu National Park, Sri Lanka, where leopard are numerous, was estimated to be 766 kg/km². The major species included elephant (*Elephas maximus*), water buffalo (*Bubalus bubalis*), axis deer, sambar, and wild swine. The smaller species, muntjac, mouse deer (*Tragulus meminna*), porcupine (*Hystrix indica*), hare (*Lepus nigricollis*), and langur (*Presbytis entellus*) comprised about 6 percent of the total. In Wilpattu leopards most frequently killed axis deer and wild swine.

In the absence of the tiger in Wilpattu, the leopard can exist on a prey resource which is similar in structure and less abundant than that which supports the tiger in Kanha. In the presence of the tiger in Kanha, the leopard shifts its use to areas where the tiger does not occur frequently. This is the classic response of a shift in niche breadth as a function of interspecific social dominance (Morse 1974).

What conditions are present in Chitawan which allow these two large predators to coexist? I think there are at least 3 factors: a large prey biomass, a large proportion of the ungulate biomass in the smaller size classes, and the dense vegetation structure.

Not considering the rhinoceros, which is not preyed upon by the leopard and whose young are only rarely killed by the tiger, the ungulate biomass in the riverine forest/tall grass habitat where this study was conducted was estimated to be 2798 kg/km² (Seidensticker 1976). This figure is greater than Wilpattu and slightly higher than the wild and domestic biomass in Kanha.

Absolute abundance of prey is a factor, but of great importance for these similar but different sized predators is the availability of prey in both the larger and smaller size classes (MacArthur 1972, D. Wilson 1975). In the riverine habitat in Chitawan, 42 percent of the ungulate biomass is comprised of hog deer and muntjac (adult weight < 40 kg) and the remainder of axis deer, sambar and wild swine (adult weight > 45 kg). Hog deer, the most abundant species, is a small deer which is especially adapted for living in tall grass environs (Schaller 1967, Seidensticker 1976). In Kanha, the majority of prey are larger sized animals.

The heterogeneous tall grass/riverine forest mosaic contrasts strongly with the rather open short grass meadow/*Shorea* forest habitat of Kanha. This feature can be expected to affect both the biomass of prey available and the size of the species which occur there (Geist 1974, Eisenberg and McKay 1974). It also affects defendability of the area for the tiger. In Kanha where the structure of the vegetation is

simple, I hypothesize the expulsion rate (Schoener 1971) of leopards by tigers is potentially greater in Kanha than it is in Chitawan. The expulsion rate facilitates the co-existence of leopards in Chitawan and time-sharing and within-habitat segregation of both vegetation type and area used.

From these observations, the general form of the ecological relationship between these two species can be outlined. For this outline I have drawn heavily from Morse (1974) and D. Wilson (1975).

The leopard and the tiger are similar in morphology, differing mainly in size by a factor of about 1 to four. Rosenzweig (1966: 602) accumulated data which indicated that ". . . size differences provide a potent means of permitting similar species of carnivores to coexist." It is clear, however, that large differences in body size alone are not sufficient to permit these congeners to coexist.

Both the mean and the range of food size can increase with an increase in predator size (D. Wilson 1975). In Chitawan, the average weight of a wild prey species was 97 kg and 28 kg for the tiger and leopard respectively and the tiger took a wider range of prey sizes. This fact means that the larger tiger can kill prey that are unavailable to the leopard but the reverse is much less true. However, differences in body size facilitate specialization and increase efficiency in hunting certain sizes of prey (MacArthur 1972). D. Wilson (1975: fig. 2) has developed a general success-of-capture curve for a wide range of taxa that shows as predators proceed from the smallest to the larger prey, it very soon reaches peak efficiency, followed by a plateau, and then a gradual decline. Success-of-capture curves for different sized prey by tigers and leopards have not yet been determined. Judging from the frequency of kills in different size classes (table 2), there is a broad overlap in the size of prey these two cats frequently kill and, thus, the potential for considerable competition.

Interspecific social dominance can confer the right of first choice in food and space. The tiger, through interspecific interactions, can reduce the abundance of leopards and in effect substitute ability in combat for ability in utilization of resources (MacArthur 1972), and thereby secure a wider potential resource base (Kanha observations). The leopard, as subordinate, can derive no benefit from interspecific interactions with the tiger. For the leopard to coexist with the larger cat in many areas of range overlap, it must have the ability to exist within a decreased niche breadth or else shift to areas where the tiger is absent. Selection pressure on the leopard is directed both toward specialization by reducing

overlap with the tiger in use of resources and toward expansion of the fundamental niche in terms of areas and habitats it occupies. That both factors are involved can be seen from the comparisons of the Chitawan data with those from Sri Lanka and Kanha: in Sri Lanka, the leopard showed greater diversity in its diet than in Chitawan; in Kanha, leopards were resident only in areas where the tiger was absent.

One consequence of this is that social subordinates tend to show greater plasticity or ability to change behavior as conditions change (Morse 1974). The leopard has the widest geographical distribution of the *Panthera*; it is found in a wide range of habitats; and, in the face of expanding human pressure, it is much more resilient than the tiger or the lion (Meyers 1974).

The structure of the habitat can restrict the opportunity of the tiger to interact with the leopard and thus restrain the advantage of dominance. The Chitawan observations show that the leopard can re-

spond to this factor and coexist with the tiger through specialization in feeding, shifts in activity patterns and within-habitat differences in vegetation type and space utilization. Through exploitation competition the leopard can interfere with the tiger's access to prey at the lower end of the scale in prey size and thus exert selective pressure on the tiger if resources are in short supply (D. Wilson 1975).

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