Tiger predatory behaviour, ecology and conservation

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Synopsis

The tiger (*Panthera tigris*) is the largest obligate predator in the Asian temperate and tropical forest ecosystems in which it occurs. The plasticity and constraints in tiger resource acquisition are examined in the context of abrupt and pervasive environmental change throughout the tiger's range—changes that threaten its survival. Prey capture in tigers is plastic, allowing tigers to capture prey of a wide range of sizes and types. In Nepal's Chitwan National Park, tigers selected large cervids, thereby gaining access to a substantial proportion of the ungulate biomass which is not available to smaller felids. In mainland environments where primary prey are larger ungulates, tigers are larger, as much as twice the size of the Sunda Island tigers. Large body size may increase the efficiency of preying on big ungulates, but decreases the efficiency of living on smaller prey types. The smaller body size of the Sunda Island tigers may increase the efficiency of capturing the smaller prey that are relatively abundant in rainforest environments, feeding primarily on plant reproductive parts, but does not preclude the capture of large prey, such as *Bos* (800 kg).

Understanding tiger resource acquisition is important to tiger conservation. The integrity of tiger ecotypes should be recognized in the management of captive and wild tigers as a metapopulation or metapopulations. The loss of larger prey types from habitat fragments can be expected to severely affect the survival of tigers in those habitats; larger tigers should be more severely affected than smaller tigers because of their different success-of-capture curves. The extirpation of tigers from an area can result in changes in the relative abundance of large ungulates and may result in an increase in the number of smaller predators, thus altering community structure in these ecological systems.

Tigers do not kill human beings in numbers proportionate to their availability and their potential vulnerability. Killing of humans becomes a problem when individual tigers are excluded from normal prey populations through social processes and/or

when tigers become habituated to humans and learn how to capture them, when humans and tigers frequently use the same areas.

Introduction

The landscape in the Asian geographic range of the tiger has changed dramatically over the last century, and this change has accelerated in the two decades we have been watching tigers. Tiger habitat is shrinking and fragmenting. The fragments are more and more isolated—surrounded, and even occupied, by people with very real needs. We have seen the extinction of the tiger in some habitat fragments and we can predict its eventual extinction in many others (Seidensticker 1986). Increased protection is needed, but the conservation of the tiger also requires that we know about its ability to respond, behaviourally and numerically, to abrupt environmental change and to significantly altered environments.

While all the primary behavioural systems of tigers—mating, rearing, dispersal, foraging and refuging (e.g., Eisenberg 1981)—can be expected to be affected by environmental change, we examine here some aspects of tiger morphology and predatory behaviour in order to explore plasticity and constraints in resource acquisition. After teasing apart this key portion of the tigers's ethogram and describing predatory behaviour and its flexibility, we relate this to resource acquisition, especially the tiger's access to a substantial portion of available ungulate biomass, and explore the consequences this may have for the structure of Asian habitats where tigers occur. We also briefly discuss the killing of humans by tigers. All of this is essential in developing a comprehensive understanding of the tiger's behavioural flexibility and ecological needs and thus of its conservation needs, so that we can take appropriate action to maintain this endangered species, our largest cat.

Prey capture

Predatory behaviour in general is a three-part series of events including prey detection, capture and consumption. Success is obviously achieved when the tiger consumes a kill, but the risks to a tiger's own survival come while seizing and killing large prey. Plasticity in prey capture is a key component in flexible acquisition of resources.

Observing tigers kill

Our observations of tiger killing behaviour were made primarily in the riverine forests and tall grass of the Chitwan National Park, Nepal, in 1973 and 1974. The habitats and landscape of the Chitwan Valley have been described by Seidensticker (1976a), McDougal (1977) and Sunquist (1981).

Because natural acts of tiger predation were rarely seen we watched tigers killing domestic water buffalo (*Bubalus bubalis*). These water buffalo had been set out and tethered by a forefoot to facilitate tourist viewing of tigers (McDougal 1980) or to facilitate their capture (Seidensticker, Tamang & Gray 1974), a technique devised during the Raj to bring tigers into positions from which they could be killed by hunters. (The practice of 'baiting' for tigers and other big cats to facilitate tourist viewing has now been discontinued in the national parks and tiger reserves in India and Nepal.) In addition, we examined many wild ungulates that had been killed by tigers. Tigers were individually identified by their distinctive facial markings (McDougal 1977).

Placing prey in a position to be killed

Schaller (1967, 1972) separated the process of tigers and lions (*P. leo*) killing large mammals into two parts: bringing the prey animal down, and actually killing it. Bringing the prey animal down corresponds to seizing it· (Eisenberg & Leyhausen 1972) or placing it in a position to kill it.

Initial contact

In 26 buffalo kills, we saw all stages of the attack and killing sequence. Initial contact was a bite to the throat or the nape ($n = 12$), seizure with the teeth and with one or both forepaws almost simultaneously ($n = 4$), or seizure with the forepaws before seizure with the teeth ($n = 10$). All bites were directed toward the neck region, but reports and photographs scattered in the literature show tigers first biting other parts such as the prey's leg or shoulder (Schaller 1967).

Movements used to bring prey down

The sequences of behaviours we saw tigers use to bring down prey, the orientation of the prey and the age of the tiger are shown diagrammatically in Fig. 1 and briefly described here:

Seizing the throat. After seizing the prey by the throat, the tiger retains its grip and both animals stand until the prey collapses.

Pulling backward with throat bite. In a variation on the above, the tiger seizes the prey's throat in its jaws and brings it down with a backward pull.

Seizing throat with forepaw assist. In a further variation on the first, the tiger simultaneously grasps the prey by the throat and uses a forepaw to assist in bringing down the prey. The initial hold with the jaws is maintained as the killing bite.

Upon back. If the prey is moving away or the attack is from the rear, the tiger uses its forepaws before its jaws. From behind, the tiger pulls its prey's hindquarters down or collapses them with its own weight before seizing the prey with the teeth. As the prey is going down, the tiger reaches over, bites

Behavioural profile	Adults	Subadult male	Facing	Face turn	Angling away
Seizing throat Attack ➡ Bite throat	--	1	1	--	--
Pulling back with throat bite Attack ➡ Bite throat ➡ Pull back ⬇ Bring down	--	1	1	--	--
Seizing throat with forepaw assist Attack ➡ Bite throat ⬇ ⬇ Grasp ➡ Bring down	1	--	1	--	--
Upon back I Attack ↖ Bite throat ↗ ⬇ Grasp ➡ Bring down	1	3	--	2	2
Upon back-II Attack ↖ Bite ↗ ⬇⬆ Grasp ➡ Bring down	--	2	1	1	--
Upon back-III Attack ➡ Bite ↖ ⬇⬆ Grasp ➡ Bring down	--	2	--	2	--
Pulling back Attack ➡ Bite ➡ Pull back ⬆⬇ ↗ Bring down	1	6	2	3	2
Seizing with forepaw(s), bite nape Attack Nape bite ↖ ↗ ⬇ Grasp Bring down	2	--	1	1	--
Forepaw blow Attack ↖ Blow ➡ Down ➡ Bite (nape or throat)	2	--	1	1	--
Seizing nape Attack ➡ Nape bite ➡ Pin down ⬆ Forepaw assist	3	--	3	--	--

Fig. 1. Different sequences of movements used by tigers to seize and kill domestic water buffalo. The number of sequences observed for adults and a subadult tiger and the relative position of the prey during the tiger's approach are indicated. These behavioural sequences were derived from photographs and written protocols made during each event. In total 26 kill sequences were observed. One kill sequence is not included here because the tiger failed to bring the prey down in its initial attempt and used a second mode to make the kill.

its throat, and, retaining the throat hold, slides off to one side, thus pulling the prey over. When the prey is down, the tiger may adjust its throat bite one or more times. We saw only the initial bite directed toward the neck. Schaller (1967) saw initial bites directed toward the front quarters and the dorsal ridge and nape, depending on the size and position of the prey animal. Whether the tiger uses its forepaws depends upon the prey's position. The extreme case is the tiger trying to pull the prey animal down by grasping a hind leg.

Pulling back. Here the tiger initially uses teeth and jaws in concert with the forepaws to seize and bring the prey down. The killing bite is delivered later. In a variation, the tiger approaches the prey at a rapid pace from the front, side or rear, first biting it in the neck region and in some instances seizing it with the forepaws and then, using its own body weight, pulls the prey down toward itself with the prey's ventral side and hooves facing away. As the prey is falling, the tiger releases its grip, reaches over the fallen animal's neck, and seizes it by the throat and pulls back and up. This twists the neck so that the prey cannot rise.

Seizing with forepaw and biting nape. Adult tigers will kill with a nape bite after seizing with the forepaw.

Blow from forepaw. The tiger knocks the prey down with a blow from the forepaw and then seizes the nape or the throat.

Seizing nape. The tiger seizes the prey by the nape and uses its body weight to force the prey to the ground.

We saw a sequence of movements that we term 'counter rolling' used on 10 of the 26 buffalo. After the buffalo was thrown off its feet, the tiger gripped it by its throat using either the original hold or a new one and dragged it back in the opposite direction from that in which it had fallen, rolling the buffalo's body over onto the opposite side. In some cases the counter-rolling movement started before the buffalo left its feet and became part of the movement sequence to bring the buffalo down. With the tiger at one end and the weight of the buffalo at the other, this counter-rolling movement effected considerable pressure on the prey animal's neck.

Killing bite

According to Leyhausen (1979: 33), a cat's canine teeth strike the cervical vertebrae and '. . . the tooth then inserts itself between the vertebrae like a wedge, forces them apart, and thus severs the spinal cord partially or completely. . . This hypothesis alone seems to me to explain why one rarely finds any damage to the vertebrae themselves. The canine teeth are exceptionally well suited to forcing things apart, but certainly not to biting firmly with their tip on something very hard.' However, our observations on buffalo and cervids killed by tigers noted considerable damage to the vertebrae in some cases.

Damage to cervical vertebrae

Thirty-six dissections were performed on young domestic buffalo (45–90 kg) killed by tigers; these are roughly the same size as *Cervus axis*, numerically the most important prey species of the tiger in Chitwan. The killing bites were delivered to the buffalo's nape, side and throat. In 33 kills, the cervical vertebrae immediately behind the skull had been crushed by the tiger's canines. Dissection revealed angular chunks of bone and bone splinters; in some cases the vertebral column itself was severed. A 90-kg buffalo was killed by a male tiger (> 250 kg) when a canine punctured its skull just behind the foramen magnum; vertebrae were also crushed. Nineteen of the killing bites were directed to the throat or to the side of the neck with the following results: the cervical vertebrae were crushed with major contusion to the trachea ($n = 16$); the cause of death was strangulation with no damage to the cervical vertebrae ($n = 2$); the vertebrae were chipped and not crushed, with the trachea badly bruised ($n = 1$).

Killing by strangulation

Buffalo killed by strangulation showed major contusion of the trachea just behind the larynx, with frothy blood inside the trachea and pinhead haemorrhages or small blisters on the surface of the lungs. The trachea or jugular was rarely punctured. The size of the neck in very large prey animals precludes the tiger's canine teeth striking the cervical vertebrae and the only way the kill can occur is by strangulation. Dissections were performed on two large sambar (*Cervus unicolor*) males (> 270 kg) with swollen necks and heavy manes of hair. The sambar had been killed by two different adult female tigers (150 kg). There was no damage to cervical vertebrae, but there was contusion to the trachea. A large buffalo (500 kg) was also killed by one of these tigers. The buffalo was hamstrung when the tiger bit and severed the tendon and fractured the joint of the left hock. Dissection revealed major contusion to the trachea and haemorrhage on the lungs, but no damage to cervical vertebrae.

In all cases in which tigers were observed killing with a throat-oriented bite—even in cases in which the vertebrae were later found to have been fractured by the canines—the hold was maintained for several minutes. Adults retained the grip for 3–6 min and subadults for longer, but some experienced adults released their hold less than a minute after killing with a nape bite ($n = 3$).

Development of the killing bite

Differences in the method of killing between adult and subadult (< 3 years old) tigers were observed. Subadults more often killed with a throat than with a nape bite (17 vs. 2), while the opposite was true for adults (2 vs. 15). Kills by subadults accounted for all of the cases ($n = 3$) in which death was

caused by strangulation without crushing of the cervical vertebrae. Except in these three instances, the functional result of the predominantly throat-oriented bites used by subadults was the same as that of the nape bite used by adults: crushing of the cervical vertebrae.

The difference in the orientation of the bite is not simply a function of the generally smaller size of subadults because, with one exception, a young male made these kills when he was about the same size as an adult female. The young male usually used throat-oriented bites while adult females used nape bites for the same prey type. Sunquist (1981) examined 26 tiger kills to determine the factors leading to nape- or throat-oriented bites and concluded that when the weight of the prey is more than half that of the tiger it uses a throat bite to kill. This agrees fairly well with our sample if subadult tigers are not considered.

Several kills made by a male tiger cub about nine months of age with only deciduous canines were carefully examined but not dissected. One 20-kg buffalo seized by the throat had a broken neck, but only one canine had penetrated. The largest buffalo the cub managed to kill weighed 35 kg. A throat bite was used but the canines did not penetrate deeply and there was no evidence that the neck was broken. The cub failed to kill a 51-kg buffalo it attacked.

Stereotypy or plasticity in capturing prey

In this key component of predatory behaviour, tigers are plastic rather than stereotypic in their behavior. Morse (1980) defines stereotypy in resource acquisition as the tendency to exploit different (or identical) resources in the same way regardless of conditions and experience, and plasticity as the tendency to exploit different (or identical) resources in different ways under changing conditions. The variation in response by individual tigers to similar-sized prey placed in similar environmental situations displayed the range of movement options open to the tiger to counter various escape manoeuvres by the prey. These observations indicate an advantage to the tiger in not committing itself to a particular motion sequence until after the prey animal is in motion. We observed tigers fail in their first attempt to bring the prey down in five instances, and three of those involved the use of the forepaw with a bite directed toward the neck. The use of the forepaw in the initial contact appears to commit the tigers' attack along a particular motion vector from which recovery is difficult.

Eisenberg & Leyhausen (1972) concluded that, in the phylogenetic sense, prey capture with the mouth is primitive, and grasping with the mouth preceded the evolution of grasping with the forepaws. The precisely aimed killing bite was an even more recent advance. In killing large mammals, tigers showed a range of behaviours that varied with the particular tiger's experience and size. Precisely executed killing bites without the use of the

forepaws were behaviours used by adults in conservative situations. The forepaws were used when the motion vector of the prey away from the tiger was established. Rather than a fixed, stereotypic killing bite, tigers used different killing bites in concert with the movements used to bring prey down. Conservative nape- and throat-directed bites result in crushed cervical vertebrae. The strangling throat bite used to kill the largest prey is a variant. The nape of many of the animals that tigers kill is protected by horns or antlers that point upward and backward. A throat-oriented bite makes it easier for a tiger to twist a large prey's neck and anchor it to the ground, keeping the sharp horns or antlers, as well as hooves, pointed away. This allows the tiger to kill prey too large for the canine teeth to penetrate to the vertebrae. The throat bite is also the important mode for young cats learning to kill.

Dayan *et al.* (1990) suggested that canine tooth size is more likely than skull morphology to reflect resource partitioning, and they tentatively concluded that the differences in size, specifically in the diameter, of canine teeth in guilds of small felids minimize competition for prey and have been selected for this purpose. Small felids, which capture prey considerably smaller than themselves, kill by biting into the nape of the animal's neck. Leyhausen's (1979) hypothesis regarding the insertion of the felid canine between a prey's cervical vertebrae, serving as a kind of key in the lock, may be correct for smaller felids killing some prey species.

Tigers have the largest canines and jaw lengths of any felids in the assemblages of which they are a part (Kiltie 1988), and kill the largest prey. In a broad comparative analysis relating canine tooth strength to the killing behaviour of extant large carnivores, Van Valkenburgh & Ruff (1987) found that felid canines are rounder and longer than canid or hyaenid canines, and, in strength, canines scale with body weight. What is interesting here is that the set of behaviours (strangulation vs. a nape bite) that subadult tigers use while they are learning to kill prey are the same behaviours that they will use as adults to kill very large prey. The behaviours that tigers use to seize and take down prey essentially release the tiger from the constraints of a close matching of the canine diameter to the size of the cervical vertebrae of any particular size or type of prey. While tigers are the largest predator and kill some of the largest prey available, they are not restricted to taking just the largest or any specific size or type of prey. The plasticity in their prey capture and killing behaviour facilitates the exploitation of a wide range of prey types and sizes.

Searching for and approaching prey

From his studies of the predatory behaviour of cats, Leyhausen (1979) concluded that there is no single predatory mechanism and that different

behavioural elements in the predatory sequence are independent with respect to propensities and sequential order. Ruiter (1967) emphasized that the stimuli guiding and shaping appetitive behaviours into functional sequences in predatory behaviour are: (1) *search*—absence of stimuli to inform the predator of the exact location of prey; (2) *approach*—location of prey known but not within grasping range; (3) *capture*—prey within grasping range; (4) *killing*; and (5) *ingestion* (including preparation for ingestion)—contact stimulation from prey. The readiness to hunt must be high enough to permit a large predator a high proportion of failures (Curio 1976). The motivation and guiding stimuli for tigers searching for and approaching free-ranging prey are not readily amenable to observation. We approached the problem by watching how tigers responded to a standardized food source created where domestic buffalo were put out to facilitate tourist viewing of tigers. We also compared their diet of wild prey with prey availability.

Behaviour during the final approach

During the final approach, the tiger maintained visual orientation and concentrated on the prey. Tigers never vocalized. The head was held low, mouth closed or partially so, and ears were raised. The tiger appeared to spend much time assessing the overall situation, halting in cover for several minutes before committing itself to a final approach. A tiger never walked up to a buffalo casually without regard to cover or to the buffalo's position.

In 22 of 28 observed kills, the buffalo seemed aware of the tiger's presence before the tiger made its final approach. Our observations were made in daylight, suggesting that diurnal hunting is inefficient for tigers. When the buffalo did not seem aware of the tiger's presence ($n = 6$), the tiger made the approach at a rush or moved quickly from a slow pace to a rush before contact. When a buffalo seemed aware of the tiger's presence, it orientated toward the tiger, usually facing head-on, and sometimes continued a head-on stance until the tiger made contact (Fig. 1). If the buffalo turned to flee, the tiger approached in a rush, or started slowly but quickly shifted to a rush. When the buffalo continued to face the tiger, the tiger pulled up momentarily before seizing it.

The success of lions in capturing large prey is determined by the failure of the prey to see the approaching lion until the lion is within a distance at which the lion's sprinting ability exceeds that of the prey; success in subduing prey is largely dependent on prey size relative to the lion (Elliott, Cowan & Holling 1977). The key variables in determining the direction and the rate and mode of the final approach we observed in tigers were the availability of vegetation to provide concealment during the final approach and the attitude and movement of the prey. The tiger appeared to focus attention on both and adjusted its approach accordingly (Fig. 1).

Response to a standardized food source

Between November 1973 and August 1974, at least five different tigers killed 143 water buffalo that were put out for them as bait to facilitate tourist viewing at Mohan Kohla, located near the Tiger Tops tourist lodge in western Chitwan (McDougal 1980). Tigers responded to shifts in wild prey distribution which changed as a result of fires, monsoon rains and flooding-induced changes in vegetation through the year, regardless of the availability of prey at a site known to them. This was reflected in the different rates at which different individuals visited the site through the year (Fig. 2).

Individual tigers frequently killed at different times and shifted the killing times during the year (Table 1). In March, for example, an adult male killed late at night while a subadult male tended to kill before dark, as did an adult male outside his territory. Adult females tended to kill most frequently near dusk. A subadult male used this constant food source more frequently than his female sibs. When a new tigress came into the area, she made more use of the site at first than she did later, and more than did an established adult
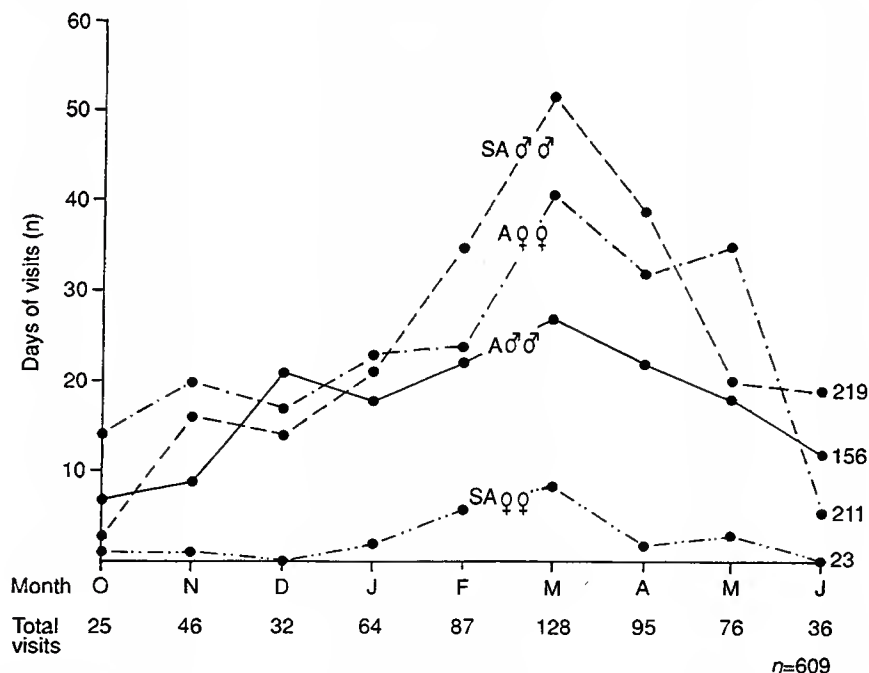

Fig. 2. The number of days different tigers were observed visiting a habitat patch where domestic water buffalo were continuously available, Mohan Kohla, Chitwan National Park, Nepal (November 1973 to August 1974). A, adult; SA, subadult.

Table 1. Times when tigers killed domestic water buffalo at Mohan Kolha, Chitwan National Park, Nepal (November 1973–August 1974)

Nepal standard time	Tiger designation					Tiger not identified
	M1	M2	MM	F1	F2	
<1600	—	—	2	—	—	1
16–1700	—	—	9	—	—	1
17–1800	—	1	21	3	—	1
18–1900	1	—	17	12	—	13
19–2000	1	—	1	4	1	21
>2000	20	—	3	1	2	7
Total	22	1	53	20	3	44

tigress. (For a description of tiger social organization see McDougal 1977 and Sunquist 1981.) Natural prey species did not markedly shift their use of habitat clumps as a result of tiger activity, and tigers occasionally encountered and killed wild prey when approaching the site.

In summary, use of the food-rich habitat patch created at Mohan Kohla was influenced by the relationships among individual tigers, their experience in searching for and finding prey, and by time spent in other activities, such as maintaining territories (Sunquist 1981). Again we were impressed with the flexibility in this component of tiger predatory behavior.

Selectiveness of tiger predation

We examined the diet of tigers in Chitwan and found that they killed prey of a wide range of sizes (Table 2). The tiger's primary prey were deer and swine, and deer and swine comprise about 75% of the wild ungulate crude biomass in Chitwan (Seidensticker 1976a). The proportion, expressed as a percentage, of the crude ungulate biomass that each available species represents is a good predictor of its frequency in the diet of tigers as revealed by scat analysis (except in the case of the rhinoceros, which is discussed below). This indicates that tigers are searchers, taking prey in proportion to its availability in terms of biomass.

However, tigers were not taking ungulates in proportion to their numerical abundance in the environment (Table 2). Larger prey, *Cervus unicolor* and *Sus scrofa*, were taken more frequently relative to their numerical abundance than the smaller cervids, such as *C. axis*.

Several large ungulates are missing from the Chitwan assemblage that were present historically (Seidensticker 1976a), including swamp deer (*Cervus duvauceli*) and perhaps wild water buffalo. While gaur (*Bos frontalis*) did occur in very low numbers in the Chitwan hills, they did not occur in the lowland and tall grass areas when and where we made our

Table 2. Crude density and biomass of ungulate prey in Chitwan National Park, Nepal (1974), compared to relative numbers of those species in the tiger diet as determined from 160 scats

Prey species	No./km²	Percentage of crude biomass weight (%)	Percentage of diet items in scats (%)	Diet/ abundance index[a]
Ungulate prey				
Rhinoceros unicornis	0.3	26	0	0
Cervus unicolor	2.5	25	32	2.9
Sus scrofa	1.1	4	9	1.8
Cervus axis	10.1	32	36	0.8
Cervus porcinus	5.5	10	16	0.7
Muntiacus muntjak	3.3	3	5	0.4
Other prey				
Presbytis entellus			1	
Lepus nigricollis			1	
Hystrix indica			1	

Crude biomass and density estimates from Eisenberg & Seidensticker (1976).
[a] Index = percent diet in scats/percent crude density

observation. (With protection, gaur have since expanded in both number and distribution.) Wild elephants (*Elephas maximus*) were once present, but now occur only as trained animals. *Rhinoceros unicornus* is the dominant megaherbivore in this forest-grassland system, forming about 25% of the crude ungulate biomass.

Tigers occasionally take rhinoceros calves (Seidensticker 1976b) and elephant calves (Johnsingh 1983), but adult rhinoceroses and elephants are too big for adult tigers to kill. These megaherbivores can form an enormous proportion of the mammalian herbivore biomass in south and south-east Asian habitats (Table 3). Tigers do take the largest suids, bovids and cervids. In Kanha National Park in central India, Schaller (1967) found that tigers killed gaur and swamp deer when they were part of the ungulate assemblages. Karanth (1988) reported heavy predation on solitary adult gaur in Nagarahole National Park in southern India. Tigers obviously kill prey as encountered, including prey in the smaller size classes (Table 2), but they seek and kill large ungulate prey, thereby gaining access to a considerable portion of the mammalian biomass that is maintained by relatively few individuals.

Flexibility in prey-catching behaviour should be reflected in success-of-capture curves relative to the frequency distribution of available prey sizes and types (Wilson 1975). Differences in body size, or canine tooth size, may facilitate specialization and increase efficiency in killing prey of a certain size (MacArthur 1972). Tigers perform a wide range of behaviours to kill prey and their prey search-and-capture behaviour is shown here to be quite flexible. We would expect this to be expressed in a success-of-capture curve

Table 3. Structure of wild ungulate assemblages expressed as percent crude biomass in selected south and south-east Asian national parks

Ungulate species	National parks				
	Chitwan	Kaziranga	Kanha	Nagarahole	Ujung Kulon
Elephas	E	50	E	47	NP
Rhinoceros	26	32	NP	NP	20
Bos	<1	NP	52	30	43
Bubalus	E	10	NP	NP	NP
Cervus unicolor	25	1	18	5	NP
C. duvauceli	E	3	5	NP	NP
C. timorensis	NP	NP	NP	NP	22
Sus	4	<1	1	<1	15
C. axis	32	NP	19	16	NP
C. porcinus	10	4	NP	NP	NP
Muntiacus	3	<1	<1	<1	1
Others	NP	NP	<3	<1	NP
Total crude biomass (kg)	1790	2942	738	14508	584

E = Extirpated; NP = Not present
Biomass estimates from summaries presented by Eisenberg & Seidensticker (1976) and Karanth (1988) for Nagarahole. Habitat types: Chitwan National Park (Nepal): moist semi-deciduous forest/gallery forest and alluvial plain; Kaziranga National Park (Assam, India): gallery forest and alluvial plain; Kanha National Park (India): moist, semi-deciduous forest with meadow; Nagarahole National Park (India): moist, tropical dry deciduous forest, moist deciduous forest, and teak plantation with meadow; Ujung Kulon National Park (Java, Indonesia): tropical lowland evergreen forest with meadow.

that has a broad plateau, perhaps tapering off rather sharply with adult elephants and rhinoceroses that are physically impossible for tigers to kill and with smaller prey that produce a poor return energetically, rather than a curve with a sharp peak of efficiency for a particular prey size or type. In Chitwan, Seidensticker (1976b) found that the tiger took a wider range of prey sizes than the leopard (*Panthera pardus*), and the tiger's average prey size was larger than that of the leopard, 97 kg vs. 28 kg. The tiger killed large prey that was unavailable to the smaller leopard, but the leopard is very efficient in switching prey type and killing smaller prey (Seidensticker 1983; Seidensticker, Sunquist & McDougal 1990). If the full assemblage of large ungulate prey were present in Chitwan, we would expect the tiger to efficiently exploit those large bovids and cervids, and thus gain access to substantial additional prey biomass (Table 3).

Predatory behaviour, ecology and conservation

A look at the plasticity and constraints in resource acquisition by tigers is a step toward understanding their basic ecological needs. By identifying basic

ecological needs, it becomes possible to recommend corrective actions and control mechanisms for ecologically disturbing activities and environmental changes.

Phenotypic adaptation to habitat and prey type

Are all tigers across their vast geographical range interchangeable? Would a tiger from the temperate forests of the Amur Valley survive in Sumatran rainforests and vice versa? We think this is unlikely because of the major differences in those environments and the difference in the size of tigers that live in those contrasting habitats.

Adult male tigers are larger than females by a factor of 1.3 to 1.6. Size also varies within populations and between different subspecies (Table 4). The difference between the smallest extant tiger from Sumatra (*P. t. sumatrae*) and the largest from Siberia (*P. t. altaica*) or India (*P. t. tigris*) is truly remarkable when you see them side by side. The former can be half or less than half the size of the latter (Table 4). The island male tigers are the size of the largest jaguars (*P. onca*); a female Sumatran tiger is the size of a northern male puma (*Felis concolor*).

Is body size in tigers determined mainly by the frequency distribution of the size of prey available and the presence of species that use the same food resources? This idea has a long history in ecology (Pimm & Gittleman 1990). However, when you consider that the smallest tigers, such as those once found on Java, killed banteng (*Bos javanicus*) males that weighed 825 kg (Hoogerwerf 1970), and the largest prey that tigers ever kill is about 900 kg, a simple predator-size to prey-size comparison becomes very murky. In Table 4, we contrast the adult weights of the ungulates in the assemblages that occur with two tropical tigers, a large form (Indian/Nepal monsoon forest) and small form (island rainforest), and the large temperate-zone tiger.

While the tiger is a very versatile predator, we would not predict the smaller tiger morph to be as efficient a predator with some large prey types or the larger tiger as efficient with smaller prey types. This prediction is confirmed in part in a recent study of tiger and leopard densities and food habits in Thailand.

The Huai Kha Khaeng Wildlife Sanctuary is the largest remaining uninhabited natural area in Thailand (Seidensticker & McNeely 1975). In those monsoon forests, Rabinowitz (1989) found that *Bos javanicus*, *Bos frontalis* and *Cervus unicolor* were greatly reduced in number, *Muntiacus feai* was very rare or extinct and *Cervus eldi* was extinct. Leopards occurred in reasonable numbers; tigers were far less abundant than expected and had very large home ranges. *Muntiacus muntjak* was the major food item of both leopards and tigers (Rabinowitz 1989). Leopards seemed to be

Table 4. Mass of adult tigers and adults in the ungulate assemblages in selected Asian tropical rainforest, monsoon forest and temperate forest

	Females (kg)	Males (kg)
Tropical rainforest		
Java, Indonesia		
Panthera tigris sondaica now extinct	75–115	100–141
Rhinoceros sondaicus	—	2280
Bos javanicus	600	825
Cervus timorensis	—	160
Sus verrucosus	44	107
Sus scrofa	59	73
Muntiacus muntjak	30	35
Tragulus javanicus	1	2
Monsoon forests		
Nepal & northern India terai		
Panthera tigris tigris	100–160	180–258
Elephas maximus	3200	5900
Rhinoceros unicornis	2000	2300
Bubalus bubalis	800	1200
Bos frontalis	650	900
Cervus unicolor	193	320
Cervus duvauceli	140	250
Sus scrofa	90	230
Cervus axis	61	91
Cervus porcinus	36	68
Muntiacus muntjak	20	25
Temperate forest		
Soviet Far East		
Panthera tigris altaica	100–167	180–306
Alces alces	350	400
Cervus elaphus	250	300
Sus scrofa	100	270
Cervus nippon	83	130
Capreolus capreolus	59	52
Nemorhaedus goral	34	35
Moschus moschiferus	16	16

Ungulate weight data from Hoogerwerf (1970) for Java; Sunquist (1981) and Schaller (1967) for Nepal and India; and Heptner, Nasimovich & Bannikov (1988) for Soviet Far East; tiger weights from Mazak (1981).

successful on a mixture of small ungulates, rodents and other small mammals; tigers obviously were not doing well.

It remains to be determined whether the tiger inhabiting tropical rainforest in mainland south-east Asia is significantly different from the extant rainforest island form on Sumatra. The former may kill larger prey, if it takes gaur. We also note that adult wild swine in mainland forests can be much larger than those found on the island of Java (Table 4).

The island tiger morph is much smaller than mainland monsoon-forest

and temperate-forest tigers and there is good reason for keeping them separate in captive breeding programmes and considering them as different in possible translocation and reintroduction programmes. At this time we do not know if there is a good ecological reason based on the size of prey to consider the mainland monsoon-forest (e.g., Bengal tiger) and temperate-forest tigers (Amur tiger) as different ecotypes.

These considerations become important to advance ideas (legal and philosophical) about tiger conservation beyond the problems of subspecies designations and towards the management of tigers, both captive and wild, as a metapopulation or as metapopulations. And recent advances in assisted reproduction technology (Wildt *et al.* 1992), when applied to tiger conservation, are making such determinations important.

Tigers as a keystone species

Do tigers act as 'keystone' species, and, if so, what are some of the likely consequences of their removal from assemblages? We know of no area where tigers live today that has not been changed in some significant way by man. We are without baselines in assessing the role that tigers play in structuring the communities where they occur. Eisenberg (1989) predicts that the likely consequences of the removal of a top carnivore from an ecosystem are a change in the relative abundance of herbivore species within a guild and an increase in the number of smaller predators. Expected results of these changes are a direct alteration of the herbaceous vegetation fed on by the herbivore assemblage and a change (decrease) in the density of prey taken by the smaller predators.

Terborgh (1990) reviewed some well-known large mammal predator–prey systems and concluded that the ability to kill prey in the prime of life and the ability to congregate in proportion to the size of herds of prey are key factors in determining the role large predators have in structuring communities. In Terborgh's view, because of the non-selective feeding habits of big cats, in neotropical forests at least, particular prey populations may be reduced to low density, so big cats may have some of the attributes of 'keystone' predators, but not to the outstanding degree found in some marine intertidal communities.

In tropical and monsoon forests in Asia, the adults of *Rhinoceros*, *Elephas* and probably *Tapirus* escape predation by tigers. In monsoon forests, both *Rhinoceros* and *Elephas* can constitute the majority of herbivore biomass (Table 3) and have significant roles in structuring habitat (Mueller-Dombois 1972; Dinerstein & Wemmer 1988). Tigers, or tigers and leopards together, can be expected to take adults of all the other ungulates, with the potential for reducing the reproductive potential of prey, and thereby exerting some effect in structuring the community. Following the control of human hunting of tigers in the early 1970s in Asia, tiger

numbers in protected areas increased. In Chitwan, for example, adult tiger numbers approximately doubled in 15 years. We have yet to have a study situation in which we can observe the full potential impact of a tiger population on an assemblage of ungulate prey.

In temperate forests (Table 4) it appears that tigers, especially where they occur with wolves (*Canis lupus*) and leopards, can take adults of all ungulate prey and would be expected to exert considerable influence on prey populations. Until recently there have been no areas in these northern habitats where the numbers of tigers have not been suppressed by man-induced mortality. A potentially important factor is that, in cool climates, big prey last far longer and provide food for more days than in hot, humid climates, where the flesh of a big prey animal literally turns to soup in two days. This may slow the rate of predation in northern habitats and result in an increase in the rate in hot, humid areas.

An important difference between temperate and monsoon forests and the neotropical forest described by Terborgh (1990) is that neotropical forest prey of large felids mostly eat fruit. The cervids and bovids in the monsoon systems browse and graze and have a great potential to modify vegetation structure. We would expect fruit to be an important food of tiger prey in some Asian rainforests, and tigers, if they are not depressed in numbers through man-induced mortality, may strongly depress prey numbers, as large cats do in neotropical forests. In Java and in mainland Asian rainforests, various species of *Bos* occur in the assemblage of tiger prey. In Java's rainforest jewel, Ujung Kulon, where the tiger is now extinct, tigers regularly killed adult banteng when Hoogerwerf (1970) studied them in the 1930s. With the tiger gone, leopards have increased in numbers from Hoogerwerf's day (Seidensticker 1986). Apparently so have banteng, to the point where their browsing has had a noticeable effect on the vegetation (R. Tilson pers. comm.). Leopards do not usually kill banteng adults. In the absence of abundant cervid prey, leopards shift their diet to smaller mammals including primates (Seidensticker 1983). In Ujung Kulon, tigers apparently did have a strong structuring effect on the community, both in killing adult banteng and thus depressing numbers and in limiting the presence of leopards. Tigers are socially dominant to leopards. Tigers kill leopards when they can catch them, and even eliminate them from some habitats (Seidensticker 1976b, 1986), including rainforests.

Killing of humans

Hand in hand with the success in tiger conservation in some parts of Asia in the last two decades has been an increase in the number of people killed by tigers (McDougal 1987). One of the puzzling aspects of tiger predatory behaviour is why tigers do not kill far more people than they do.

Our observations of tiger predatory behaviour suggested that the key

variables in determining direction, rate and mode of the final approach were the availability of adequate cover and the attitude and movements of the prey. Walking in a normal upright posture, a person does not represent the 'right' form for a prey animal. A standing person's head and neck are in the wrong place and most adult human beings are taller than many large prey species. (In a defensive mode, the sloth bear (*Melursus ursinus*) and brown bear (*Ursus arctos*), the other big carnivores in the tiger's mainland range, also stand up.) A person standing up presents a very different image to a tiger than a person sitting or squatting down or bending over, and it seems that tigers often kill people in the latter positions. Tigers kill rubber tappers who go out in the early morning dark and bend down to make their cuts, and grass cutters who are bending over, and people who go out at night to relieve themselves. Each year in the Sundarbans mangrove swamps at the mouths of the Ganges, tigers kill many people who are in the area to extract resources such as palm fronds, fish and honey. Honey collectors, for example, frequently travel alone or at least well apart from other collectors, and bend down to get under the branches of the mangroves. We have described how the tiger closes from behind as prey are moving away. Indian wildlife authorities are providing workers with face masks to wear on the back of their head (Sanyal 1987), and apparently tiger attacks are reduced by this method.

Where people are regularly using and travelling through tiger habitat, tigers can become habituated to their presence, as they are in the Sundarbans. We found that the use of the food-rich habitat patch we created in Chitwan was influenced by the relationships among individual tigers and their experience in searching for and finding prey. As densities of tigers in protected areas have increased, socially subordinate and subadult tigers can be expected to occur more frequently at the edges and be more active in daylight, thereby increasing the frequency of encounters with people engaged in various activities there. This sets the stage for an attack.

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