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TIGER ECOLOGY AND CONSERVATION IN THE INDIAN SUBCONTINENT

(*With one text-figure and one plate*)

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The tiger has served as an effective umbrella species in conserving many forms of biodiversity in the Indian subcontinent. During the last three decades, scientific research employing modern methods has generated reliable information on tiger ecology in a range of habitats in the Indian subcontinent. These studies show that tigers evolved as solitary predators of large ungulates, and their social organisation pivots around breeding females that try to maintain and defend home ranges. Across the Subcontinent, tiger population densities vary from a low of <1 tiger/100 sq. km to a high of 20 tigers/100 sq. km, depending primarily on densities of ungulate prey. Although over 300,000 sq. km of potential tiger habitat still exists in southern Asia, breeding 'source' populations for wild tigers are primarily confined to effectively protected reserves that occupy less than 2% of the overall landscape, the rest of which acts as a population 'sink'. Tiger demography is characterised by both high productivity and mortality. Consequently, the depletion of their prey base due to human over-hunting appears to be a major threat to tigers, besides habitat loss and poaching. After being persecuted for centuries and pushed to the verge of extirpation, tigers received official protection over the last thirty years. However, their future is still not secure because of newly emergent misplaced priorities in conservation policies. Protecting viable tiger populations in reserves and buffering them against incompatible human uses of their habitats must continue to be at the core of the conservation strategy if tigers are to survive this century and beyond.

INTRODUCTION

Saving tigers: a landscape species approach to biodiversity conservation

Through centuries, the tiger *Panthera tigris* has been a predominant cultural icon in the Indian subcontinent (Jackson 1990, Karanth 2001). At the same time, however, commoners, kings and colonial adventurers have ruthlessly persecuted tigers. Thereafter, since the early 1970s, several South Asian countries have tried to use the tiger as an umbrella species for wildlife conservation through species recovery plans like India's ambitious 'Project Tiger' (Karanth 2001). As a result, in the Indian subcontinent, about 13,181 sq. km temperate forest, 9,043 sq. km wet evergreen forest, 13,736 sq. km moist deciduous forest, 19,360 sq. km dry deciduous forest, 6,927 sq. km alluvial grassland and 873 sq. km mangrove forest have been proclaimed as protected nature reserves

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(Dinerstein *et al.* 1997), thereby benefiting a whole range of other species and the overall biodiversity in general. Thus, in the Indian subcontinent, survival prospects for biodiversity in its myriad forms are inextricably linked to effective conservation of tiger habitats. The anxiety that the focus on tigers is some form of benign neglect of other species is thus clearly not justified.

Beginning with Jim Corbett, conservationists have repeatedly predicted the imminent extinction of tigers in the Indian subcontinent for the last 70 years (Karanth 2001). However, these predictions have failed to materialise because of the ecological resilience of the tiger (Sunquist *et al.* 1999) and due to timely conservation interventions (Karanth 2001). On the other hand, governments have also exaggerated their conservation successes (Panwar 1987) based on "tiger numbers" they generated using demonstrably failure-prone techniques (Karanth 1987, 1999; Karanth *et al.* 2003). Such widely divergent perceptions about the fate of the tiger arise from inadequate scientific understanding of tiger ecology and conservation issues. The purpose of this paper is to briefly review tiger ecology in the Indian subcontinent based on recent and ongoing scientific studies and to explore future directions for tiger conservation.

Generating a knowledge base for tiger conservation

Many hunters and naturalists have produced anecdotal accounts of tiger biology during the past two centuries (see Thapar 2001 for some examples): accounts by Brander (1923), Champion (1929), Corbett (1944), Singh (1984) and Thapar (1989) can be cited as good examples from India. Although qualitative in nature, they provided useful insights into tiger biology.

Despite the widespread interest in tigers among hunters of the past, and more recently among conservationists, and despite the massive efforts and investments made to recover tiger populations, knowledge about the species remains scanty, even within the conservation community. Most popular literature published even today repeats the same old flawed clichés: that there are five 'subspecies' of surviving tigers; that the largest wild tiger population in the world exists in Sundarbans; that white tigers have conservation value; that there is a need for releasing captive-bred tigers into the wild to save the species; that we reliably know the tiger numbers in specific reserves, regions or even over the entire country; and above all, that human beings and tigers had lived in harmony during some past golden age, and therefore, special reserves that try to curtail incompatible human uses of tiger habitats are unnecessary now.

Although ecological studies of tigers within a modern scientific framework began forty years ago with George Schaller's pioneering work in Kanha (Schaller 1967) and have advanced tremendously thereafter as a result of research by other scientists, much of this new knowledge appears to have escaped the notice of wildlife managers and conservationists in the Indian subcontinent. Therefore, there is an urgent need to summarise this knowledge that can provide a foundation for effective action to save tigers.

Major scientific advances in understanding tiger ecology were made in the 1973-1985 period through radio telemetry studies in Chitwan, Nepal, under the Smithsonian Tiger Ecology Project (Seidensticker 1976, Sunquist 1981, Smith *et al.* 1987, Sunquist and Sunquist 1988, Smith 1993, Seidensticker and McDougal 1993). During the1990s, long-term ecological studies in Nagarahole (Karanth and Sunquist 1992, 1995, 2000, Karanth *et al.* 1999), Panna (Chundawat *et al.* 1999) and other areas of India (Karanth and Nichols 1998, 2000) that employed modern techniques such as radiotelemetry, camera trapping, dietary analyses and prey density estimation, generated substantial new knowledge about wild tigers. At the same time, new studies by taxonomists, geneticists, evolutionary biologists and biogeographers (Wentzel *et al.*

1999, Kitchener 1999, Kitchener and Dugmore 2000) generated fresh insights into issues of evolutionary origin, radiation, and classification of tigers. In the following section, I will try to provide a brief overview of this new knowledge about tiger biology in the Indian subcontinent.

BIOLOGY OF THE TIGER

Morphology

The tiger is the largest of all living wild cats. Its body is adapted for stalking and ambushing ungulate prey up to five times its own size. Its strong but light skeletal structure and powerful muscles permit speedy short rushes, leaps and grappling. The jaw muscles and long canines enable a strong bite necessary to quickly kill struggling prey. Although quite spectacular, the tiger's coloration and stripes camouflage it well in the forest brush (Karanth 2001).

The standard body measurements (Riney 1982) and weights of tigers in South Asia (Pocock 1929; Sunquist 1981; Karanth, unpubl. data) are as follows: body mass of 175-260 kg for males and 100-160 kg for females; total length of 270-310 cm for males and 240-265 cm for females inclusive of an 85-110 cm long tail. The height at the shoulder is 90-110 cm. Contrary to earlier perceptions, measurements obtained from tigers captured for radiotelemetry studies in the Indian subcontinent (Sunquist 1981; Karanth, unpubl. data) show that they are not smaller than tigers captured in the Russian Far East (Dale Miquelle and John Goodrich, unpubl. data).

Tigers possess 30 teeth, with 6 upper and 6 lower incisors, 2 upper and 2 lower canines, 6 upper and 4 lower premolars and 2 upper and 2 lower molars. The upper canines are 50-60 mm long, and the lower ones 40-50 mm. Like other cats, tigers have five front toes (only four leave prints) and four hind toes. The toes have sheathed claws that can be extended for grasping. Their large, round eyes possess excellent night vision and ability to detect movement, but appear to have poor colour discrimination capability. Their hearing is acute and is used to locate prey, but the sense of smell is used primarily for detecting scent from the ground or vegetation. The cat's sense of "touch", with its padded feet as well as long vibrissae, is critical for silent movement through dense cover. Tigers possess several scent glands around their cheeks, toes, tail and the anal region, like other cats do (Ewer 1985).

Evolution, radiation and taxonomy of tigers

Tiger evolution has been studied using fossil evidence and molecular genetic techniques (Hemmer 1987, Herrington 1987, Kitchener 1999, Kitchener and Dugmore 2000). Tigers belong to the family Felidae and the genus *Panthera*, within which they branched off as a distinct species even before lions (*Panthera leo*), leopards (*Panthera pardus*) and jaguars (*Panthera onca*) and were widely distributed over China and Southeast Asia even about 2 million years ago. Tigers had managed to expand their range northwards into Russia, Japan, the Bering land-bridge, and south and westwards into the Indian subcontinent and the Caspian regions by about a million years ago. By the beginning of the Holocene (about10, 000 years ago), tigers were found on the islands of Java and Bali, but not in Sri Lanka (Kitchener and Dugmore 2000).

The climatic changes that shaped the expansion of tiger range across Asia during the Pleistocene and Holocene primarily operated through changes in connectivity of land-bridges and landscapes, which in turn was driven by changes in sea level and vegetation patterns. These environmental factors led to the evolution and radiation of large ungulates, particularly several species of deer (Cervidae) and wild cattle (Bovinii), opening up an ecological niche for a large, solitary, forest predator (Sunquist *et al.* 1999).

Although tigers tolerate high ambient temperatures up to 48 °C in northern India, they are not adapted to the arid, water-scarce environments in which lions and leopards still survive. However, tigers can tolerate severe cold climate (-35 °C) in the Russian Far East. They live at altitudes ranging from sea level to 3,000 m sometimes crossing Himalayan passes at 4,700 m. Tigers occur in the cold Temperate Zone forests of northeastern Asia as well as in the hot, humid, wet or dry forests further south. In the Indian subcontinent, they are found in Tropical Dry and Moist Deciduous Forests, Evergreen and Mangrove Forests, Riparian Grassland-forests of the *terai* and in mixed subtropical forests of Himalayan foothills. Their distribution seems to be determined primarily by availability of large ungulate prey rather than by vegetation types (Sunquist *et al.* 1999, Karanth 2001).

The tigers that successfully evolved and adapted to these varied environments and prey types, now 'look' somewhat different in different parts of their range. Based on such perceived morphological differences, taxonomists had classified tigers into four subspecies (*tigris* in South Asia, *virgata* in the Caspian region, *altaica* in Russia, *sondaica* in Java) by the19th century. Four more tiger subspecies were described in the 20th century: (*amoyensis* in southern China, *balica* in Bali, *sumatrae* in Sumatra and *corbetti* in mainland Southeast Asia). These traditional "eight tiger subspecies" were segregated based on body measurements and pelage details (Hemmer 1987, Herrington 1987) obtained from very few museum specimens (Kitchener 1999).

However, more recent syntheses (Wentzel *et al.* 1999, Kitchener 1999, Kitchener and Dugmore 2000) of the genetic, morphological and biogeographic evidence suggest that this traditional classification of "eight subspecies" of tigers is not reliable. New data suggest that morphological variation in tigers occurs along a gradient, rather than at the level of discrete subspecies. Therefore, the more plausible current models of tiger evolution lump all mainland Asian tigers into one or two subspecies that are distinct only from the other subspecies from the Sundaic Islands. Tigers now surviving in Russia, China, Indo-China and southern Asia, all appear to belong to one subspecies that is distinct only from the island subspecies surviving in Sumatra. Such studies also highlight the critical importance of representatively conserving the much wider range of ecological and behavioural variations in wild tigers as adaptations to their specific habitats, rather than merely trying to save traditional "subspecies" (Wikramanayake *et al.* 1998, Karanth 2001) that have little basis in reality.

Communication and social behaviour

Communication and sociality:

Because tigers are solitary animals that live at very low densities (Sunquist 1981, Sunquist *et al.* 1999), communication between individuals, either to seek out or to avoid one another, is crucial for maintaining their social organisation. The tigers' communication system involves an elaborate repertoire of chemical, visual and vocal signals. Common chemical and visual signals include exuding scent mixed with urine and scats, leaving visual marks by scraping or rolling on the ground and clawing trees (Smith *et al.* 1989, Smith 1993). A variety of long and short-range vocal signals, including roars, grunts, growls and purrs are also used. Among all these modes of communication, spraying scent mixed with urine is perhaps the most effective one overall (Sunquist 1981, Smith *et al.* 1989).

Using a combination of such signals, tigers communicate information on their individual identity, time of passage, social status, sexual receptivity and range-ownership to other tigers, thus enabling contact or avoidance, depending on the social context. With such a communication system, tigers maintain their social organisation with relatively few aggressive encounters that can have fatal consequences for the animals involved.

Sexual behaviour:

Tigers appear to mate throughout the year in the Indian subcontinent (Sunquist 1981; Smith 1993; Karanth, unpubl. data). Tigresses advertise their oestrous status through increased bouts of roaring and scent marking that help male tigers find them. The mating session lasts from 2-7 days and involves dozens of copulations of about 15 seconds duration every day. Mating tigers indulge in a lot of aggressive play. The tip of the male's penis has backward pointing 'spines', which may provide stimulation to induce ovulation in the female (Ewer 1985). Once the mating period is over, the two animals go their own separate ways.

Relationship between mother and cubs:

Following a gestation of 102-108 days, litters of 2-5 (usually 3) cubs are dropped in a secluded hideout. The cubs are born blind and helpless, and, are aggressively protected by the tigress. However, rarely, through a temporary hormonal imbalance, a tigress may kill or even eat her newborn cubs. The cubs are nursed on milk for the first two months and effectively hidden from other predators and even other tigers. Because the tigress must nurse and guard her cubs closely, her home range shrinks to a fraction of its usual size (Sunquist 1981, Smith 1993). When the cubs are 2-3 months old, the tigress starts to take them to her kills. At about 12 months old, they accompany the mother over her entire home range (Schaller 1967, Sunquist 1981, Smith 1993). Cubs learn to hunt by watching their mother. Sometimes, several prey animals may be killed within a few hours, when the tigress teaches her cubs to kill effectively.

Sometimes, the adult male that sired the cubs may temporarily associate with the tigress to share a kill or even play with the cubs (Schaller 1967, Thapar 1989). A tigress with cubs may sometimes share kills with her older daughter, who may have her own litters, leading to temporary associations of 7-8 related tigers. On the other hand, the tigress zealously guards her cubs from strange males, which often exhibit the infanticide behaviour common to many mammalian species (Smith 1993; Karanth, unpubl. data).

Between 12-18 months age, tiger cubs acquire their permanent teeth and become proficient killers. They learn to search, stalk, capture and kill potentially dangerous prey. By the age of 18 months, juvenile males make forays away from their mother's range to begin a transient life. Juvenile females stay close to their mother, but eventually disperse by 20-28 months, as their mother becomes increasingly aggressive towards them (Smith 1993). By then, the tigress would have come into oestrus again and mated.

Population structure and social organisation:

The structure of the typical tiger population can be described in terms of the sex and age categories of its members. Tigers of both sexes can be categorised into demographic stages (Karanth and Stith 1999) such as cubs (less than 1 year old), juveniles (1-2 years old), post-dispersal floaters or transients (over 2 years old) and breeding adults (3-12 years old). A few of the transients may also be old or incapacitated breeders evicted from their ranges by more vigorous successors.

Tiger social organisation pivots around breeding females that maintain fixed home ranges within which they try to raise cubs. These tigresses acquire ranges by evicting previous residents, or by 'inheriting' a part of their mother's range (Smith *et al.* 1987, Smith 1993). Normally, in a good habitat stocked with enough prey, a tigress starts to breed at 3-4 years. Her normal residential tenure is of 5-7 years, after which she loses her range to a competitor. The degree of spatial overlap (or lack of it) between neighbouring female ranges varies, depending on prey density and other ecological factors (Sunquist 1981, Smith *et al.* 1987, Miquelle *et al.* 1999, Karanth and Sunquist 2000). Adult males have larger ranges that overlap ranges of several breeding females, the average being about three. The degree of exclusiveness of male ranges is variable, depending on factors that are as yet unclear. The land tenures of breeding males are shorter (2-4 years) than those of females (Sunquist 1981, Smith 1993).

Although the ranges of neighbouring female tigers were exclusive in Chitwan (Sunquist 1981, Smith *et al.* 1987, Smith 1993), there appears to be some overlap in Nagarahole (Karanth, unpubl. data). In Chitwan, male ranges were mutually exclusive, but this was not clear in Nagarahole. In Chitwan and Nagarahole, the size of breeding female ranges varied from 13-30 sq. km and that of males from 40-100 sq. km (Sunquist 1981, Smith 1993, Karanth and Sunquist 2000). In Panna Reserve in central India, where tiger habitats are just beginning to be restored through protection, the range sizes were 243 sq. km for a male and 27 sq. km for a female, respectively (Chundawat *et al.* 1999). While female range size seems to be determined primarily by prey abundance, the size of a male's range appears to be a function of the number of female ranges that he manages to cover.

At about 18-28 months age, juveniles either leave their natal ranges or are evicted by their mother to become transients. Such floaters, particularly males, criss-cross several breeder ranges and even disperse away into new areas. These transient tigers have large ranges, which may cover an entire ecological unit. During a six-month period, two transient males had ranges of 99 and 77 sq. km in Nagarhole and the latter's range shrank to 44 sq. km when he acquired a breeding range (Karanth and Sunquist 2000). Radiotelemetry studies in Chitwan (Smith 1993) showed 10 dispersing males travelled an average distance of 33 km, and four females a distance of 10 km, before establishing their own ranges. However, occasionally such dispersers travel great distances of 100 km or more (Smith 1993).

In productive tiger populations, there is intense competition for breeding ranges. However, breeders of both sexes tolerate the passage of their transient offspring within their ranges and transient siblings seem to tolerate each other. However, when a breeder male is replaced, the new male systematically kills cubs of resident tigresses within his range. Through such infanticide, the tigresses are induced to come into oestrus again and mate, thus conferring an evolutionary advantage to the male through propagation of his genes (Smith 1993).

Predatory behaviour and ecology

Prey types and prey selection:

The need to hunt alone and kill large ungulate prey has been the driving force behind evolution of tigers (Seidensticker and McDougal 1993, Sunquist *et al.* 1999). Although tigers kill prey ranging in size from frogs to adult gaur (*Bos gaurus*) — the bulk of their requirement must come from deer, pigs, and wild or domestic cattle, that weigh between 20-1,000 kg (Sunquist *et al.* 1999, Karanth 2001). Apart from livestock, the principal wild prey of tigers in the Indian subcontinent include: wild pig *Sus scrofa*, sambar *Cervus unicolor*, barasingha *Cervus duvaucelii*, red deer *Cervus elaphus*, chital *Axis axis*, hog deer *Axis porcinus*, muntjac *Muntiacus muntjak*, nilgai *Boselaphus tragocamelus*, chousingha *Tetracerus quadricornis*, chinkara *Gazella bennettii*, blackbuck *Antilope cervicapra*, gaur, wild buffalo *Bubalus bubalis*, takin *Budorcas taxicolor*, goral *Naemorhedus goral*, serow *Naemorhedus sumatraensis*, and, occasionally, elephant *Elephas maximus* and rhino *Rhinoceros unicornis* calves. Tigers also opportunistically kill and eat other carnivore species such as sloth bears *Melursus ursinus*, leopards and dholes *Cuon alpinus*.

Activity and hunting behaviour:

Tigers hunt primarily after dark, when their superior vision confers an advantage (Sunquist 1981, Karanth and Sunquist 2000). Tigers tend to be active at the same times of the day when their prey are also active because they can more easily detect and home in on the latter. Consequently, human activities such as forest product collection and hunting that compel prey species to become nocturnal, also compel tigers to do the same.

Usually tigers become active at dusk, and remain so through the night until dawn. During hot parts of the day, they rest under shade, often lying up in water (Schaller 1967, Thapar 1989). Radiotelemetry locations in Chitwan and Nagarahole (Sunquist 1981, Karanth and Sunquist 2000) showed that tigers moved around a lot more at night (80% of locations) compared to midday (10% of locations). They typically remain active for about 6-8 hours in a day. The linear distances between radio-locations on successive days were 1-8 km (Sunquist 1981, Karanth, unpubl. data) although the actual distance walked overnight was more (5-25 km).

Tigers pad along forest trails and locate prey through hearing (in dense cover) or visually. Occasionally, they lie in ambush at localities favoured by prey, like water holes, clearings or salt licks (Karanth and Sunquist 2000). Some observers (Schaller 1967, Thapar 1989) guess that tigers have a 5-10% success rate while hunting. Because of difficulties in observing an unbiased sample of hunts, it is difficult to validate such estimates. However, success rates are likely to strongly depend on probabilities of encountering prey, and, therefore, on prey densities in an area (Karanth and Sunquist 1995).

After locating the prey, the tiger stalks it silently to get within range for a final rush of 15-30 m (Seidensticker and McDougal 1993, Karanth and Sunquist 2000), or longer across open clearings or waterbodies (Thapar 1989). The tiger usually attacks the prey from the flanks or rear, and knocks it down by the impact of its momentum and by grappling with its forelimbs. Simultaneously, it tries to bite the prey animal's throat or nape to immobilise it (Seidensticker and McDougal 1993). The tiger tries to keep away from the flailing hooves and horns of large ungulate prey. With dangerous prey such as adult gaur or buffalo, if the initial attempt to knock down and immobilise does not succeed, tigers may even give up the attempt. Sometimes, tigers get injured or killed by such quarry. After the prey animal is brought down, it is killed by strangulation or by rupturing of the cervical vertebrae, spinal chord, brain case or major blood vessels. Tigers deliver the lethal bite to the throat of larger prey animals, whereas smaller prey, such as pigs or chital may also be killed with a nape bite.

Feeding ecology:

Tigers in Nagarahole dragged their kills over distances ranging from 0-350 m (with an average of 51 m, for a sample of 133 kills), hiding the carcasses in dense cover unless the prey was too heavy (Karanth and Sunquist 2000). Tigers consume 20-35 kg of meat in their first meal, and unless disturbed, stay close by to guard their kills from other tigers and scavengers. Depending on the kill size and the number of tigers feeding, they stay with the kill for 1-7 days, eating two thirds of the kill including some fairly putrid meat. The remaining one third, comprising of larger bones, rumen contents and intestines is normally discarded (Karanth and Sunquist 2000). When hungry, tigers scavenge kills made by other tigers or by other predator species.

Killing and cropping rates:

Tigers are provisioned 1,825-2,190 kg meat/year in captivity (Sunquist 1981). A female tiger kills about 40-45 ungulate prey/year, consuming about 2,000 kg of meat (or about 3,000 kg of live prey), just for maintenance. The quantity of live prey consumed by adult males is higher (4,000 kg/year) and by juveniles and cubs is less. A tigress raising three cubs has to kill 60-75 ungulate prey/year (Schaller 1967, Sunquist 1981, Sunquist *et al.* 1999). Thus an 'average' tiger can be estimated to take about 50 prey animals or 3,000 kg of live prey annually (Schaller 1967, Sunquist *et al.* 1999).

Tigers may crop roughly 10-15% of available prey in an area annually, depending on how much prey is additionally killed by other predators such as leopards, dholes and human hunters. Considering the natural reproductive rates of ungulate prey, a 10% cropping rate translates into the requirement of a standing prey base of about 400-500 ungulates to support a single tiger through one year. Therefore, sizes of tiger home ranges depend on prey densities. Ranges of breeding female tigers vary from a low of 10-20 sq. km in prey-rich habitats to 200-300 sq. km or more in poor quality habitats (Sunquist *et al.* 1999, Miquelle *et al.* 1999). Therefore, more tigers can 'pack' into an area at higher prey densities, although social spacing behaviours may set an upper limit on tiger numbers. In the semi-arid area of Panna, availability of water and prey distribution (rather than prey abundance alone) influences tiger home range sizes (Chundawat *et al.* 1999, R.S. Chundawat, unpubl data).

Population ecology

Population densities:

Over most of their range, tigers coexist with other predatory carnivores such as leopards and dholes. The relative densities of each predator species in such guilds appear to be determined by the relative abundance of different size classes of prey in the assemblage (Karanth and Sunquist 1995, Karanth and Nichols 1998). Furthermore, as noted earlier, densities of tigers appear to be primarily a function of prey densities (Schaller 1967, Sunquist 1981, Seidensticker and McDougal 1993, Karanth and Sunquist 1995, Karanth and Nichols 1998, Sunquist *et al.* 1999, Chundawat *et al.* 1999).

As primary predators of large ungulates, tigers cannot sustain themselves or reproduce in the absence of such prey in sufficient numbers, even if smaller prey are quite abundant (Schaller 1967, Sunquist 1981, Karanth and Sunquist 1995, Sunquist *et al.* 1999). Recent studies that estimated tiger and prey abundance using rigorous methods (Karanth and Nichols 1998, 2000, Sunquist *et al.* 1999) clearly show a strong positive relationship between abundance of large ungulates and tiger densities.

As prey densities get lower, female ranges become larger, reducing the number of such breeders the area can support. Lower prey densities also appear to result in lower densities of transient tigers (Karanth and Nichols 1998, 2000). Because survival rates of cubs and juveniles are also likely to be lower at lower prey densities (Karanth and Stith 1999), the numbers of tigers in these two demographic stages will also be lower. Therefore, while other habitat-related or managerial factors may influence tiger density at a given site, prey abundance appears to be the most critical determinant.

However, accurately estimating tiger densities is difficult (Karanth and Chundawat 2002). The Indian Government's official pugmark censuses have often yielded unreliable results (Karanth 1987, 1988, 1999, Karanth *et al.* 2003). Camera trap sample surveys within a formal Capture-Recapture modelling framework has proved to be a good method for obtaining reliable tiger density estimates in well-protected study areas, particularly at higher tiger densities (Karanth and Nichols 1998; Plate 1, Figs 1, 2). Mean densities of tigers (excluding cubs <1 year) derived using the photographic Capture-Recapture approach in some typical tiger habitats in India were: Pench (Madhya Pradesh) 4.9 tigers/100 sq. km, Kanha 11.7 tigers/100 sq. km, Nagarahole 11.9 tigers/100 sq. km, Kaziranga 16.8 tigers/100 sq. km (Karanth and Nichols 1998).

The above cited density estimates show that alluvial grassland-forest mosaics of the Himalayan foothills and moist-deciduous forests of peninsular India potentially support the highest densities of tigers anywhere in the world (15-22 tigers/100 sq. km, including cubs). At the other end of the ecological scale, in the Russian Far East, tiger densities are as low as 0.5-1.5 tigers/100 sq. km (Miquelle *et al.* 1999).

Karanth, K.U.: Camera trapping of *Panthera tigris* PLATE 1

Fig. 1: Camera trap being set up for studying tiger density in Nagarahole National Park

Fig. 2: A tiger 'photo-captured' by the camera trap

Fecundity and mortality rates:

In good habitats, tigresses appear to have an oestrous cycle of 20-30 days, beginning at around 2 years of age or earlier, but they conceive and produce cubs only at 3-4 years of age after acquiring permanent home ranges. The sex ratio is equal at birth. If cubs survive to dispersal age, usually the tigress will produce the next litter after 2-2.5 years. If the cubs die in the interim, the tigress comes into oestrus almost immediately. In prey-rich habitats, the average cub production can be estimated at roughly 1 cub/breeding female/ year (Karanth and Stith 1999). In such a productive population of 20 breeding females, roughly a third breed every year, adding about 20 new tigers to the population.

However, this high productivity of tigers is balanced by naturally high mortality rates. Tigers in all demographic stages die from a variety of causes. Male tigers that acquire new ranges try to kill the cubs of the former resident breeder. Other factors that cause mortalities among cubs include: starvation, floods, forest fires, other predators and human persecution. Hunting of tigresses also leads to indirect mortalities of dependent cubs (Sunquist 1981, Smith 1993, Karanth 2001). Juvenile tigers (1-2 years) die from starvation, hunting-related injuries and intra-specific aggression.

During dispersal phase, transient tigers move back and forth through larger ecological units, criss-crossing boundaries of breeder territories, nature reserves and even states or countries (Smith 1993). Such transient tigers suffer heavy attrition through starvation, intra-specific aggression and human persecution.

Based on data from Chitwan and Nagarahole, demographic models of tiger populations built by Kenny *et al.* (1995) and Karanth and Stith (1999) assumed the following approximate annual mortality rates in healthy tiger populations: cubs of both sexes 40%, juveniles of both sexes 10 %, transient males 35%, transient females 30%, breeder males 20% and breeder females 10%.

Factors that influence tiger population dynamics:

Karanth and Stith (1999) recently built a stochastic population model for tiger populations under different ecological scenarios. Their model of a productive (but insular) wild tiger population with a 'carrying capacity' of 24 breeding females, generated the following typical age-sex structure: 8 breeding males, 28 transients, 14 juveniles and 24 cubs. This population produces 24 cubs/year on an average, and, would be balanced by annual mortalities of the same magnitude. This model suggests that even relatively small wild tiger populations with only 12 breeding tigresses may be demographically viable. The model explains well how tiger populations could have survived the heavy pressure inflicted by hunters and poachers in the past. For example, between 1860-1960, approximately 93,000 tigers were legally killed for sport or bounties in parts of British India and some princely states (Rangarajan 1999).

The demographic model of Karanth and Stith (1999) indicates that rebounding tiger populations will quickly reach saturation densities, and remain relatively stable thereafter, because any further increase in reproduction rates is balanced by increase in mortality rates or dispersal. Therefore, in most productive tiger populations, there is potentially a 'doomed surplus', that perishes annually, without lowering the tiger population density (Karanth 2001).

The Karanth and Stith (1999) simulations also suggest that prey depletion (caused by human hunters or competition with livestock) reduces the numbers of breeding females and transients, as well as depresses cub survival rates. On the other hand, moderate levels of tiger poaching may simply remove a part of an existing annual surplus. In prey-rich habitats, a tigress may produce 3-4 litters or about 9-16 cubs during her reproductive tenure (Sunquist 1981, Karanth and Stith 1999), thereby producing a substantial 'surplus' of tigers. Consequently, human-induced prey depletion may be a far more serious threat to the viability of tiger populations than moderate levels of tiger poaching (Karanth and Stith 1999, Karanth 2001).

TIGER CONSERVATION IN THE INDIAN SUBCONTINENT

Conservation status of wild tiger populations

In historic times, tigers were found all the way from the Temperate Zone forests of the Russian Far East to the tropical forests of southwestern India. They ranged from Azerbaijan and Iraq on the West all way through the Indian subcontinent to parts of southern China, eastern Russia and Southeast Asia. Their range covered 30 present day countries, stretching over 70 degrees of latitude and 100 degrees of longitude on the earth's surface (Seidensticker *et al.* 1999, Karanth 2001).

Within the Indian subcontinent, tigers were present in a diverse array of habitats: Tropical Dry and Moist Deciduous Forests, Evergreen and Mangrove Forests, *terai* grasslands and Mixed Conifer-broadleaf Forests in the Himalayan foothills. Availability of ungulate prey, water and shade seem to determine their distribution (Sunquist *et al.* 1999, Chundawat *et al.* 1999, Karanth 2001). Tigers once overlapped with lions in a wide region stretching across northwestern India. Early human modifications of landscapes such as development of water resources, and extirpation of the more-easily hunted lions by human societies might have benefited tigers, allowing them to expand their range in drier regions of northwestern India by moving into newly-opened ecological niches (Karanth 2001).

Recent assessments (Wikramanayake *et al.* 1999) show that the current distributional range of tigers in the Indian subcontinent is around 350,000-400,000 sq. km (Fig. 1). Even within this reduced range, reproducing tiger populations are now restricted to a few better-protected reserves that may cover about 40,000 sq. km, or less than one percent of the tigers' historical range (Karanth 2001). The mountainous regions of the Himalaya, the dense evergreen forests of northeastern India as well as mangrove forests of India and Bangladesh, are inherently poor quality habitats for tigers. Lowland areas of Nepal and several Indian states have high quality habitat patches within the 50 or so protected areas that sporadically occur in a matrix of human-dominated landscapes.

Perhaps over 90% of their range, local tiger populations cannot be sustained without periodic immigration from breeding populations in protected areas. In the overall landscape, such protected areas might be the only 'sources' from which tigers disperse and perish in the surrounding 'sinks' (Karanth 2001, Karanth and Chundawat 2002).

Furthermore, many of these 'source' tiger populations are under threat from prey depletion, tiger poaching, and, habitat degradation and fragmentation. These threats arise from a variety of factors linked to local rural uses as well as economic development projects (Karanth 2001). The potential erosion of genetic variability in wild tiger populations as a result of habitat fragmentation is considered to be a major threat by some workers (Tilson and Christie 1999). However, Caughley (1994) averred that the smallness of animal populations should be viewed as a consequence rather than a cause of animal extinctions.

All the above threats to tigers are generally recognised in scientific and popular literature (Seidensticker *et al.* 1999). Therefore, the essential challenge now lies in setting appropriate priorities in responding to these threats. Such priority setting must necessarily be based on an objective evaluation of past successes and failures in tiger conservation.

A brief history of tiger conservation

It is necessary to have a brief overview of the social context and history of tiger conservation in the Indian subcontinent before exploring current conservation issues. This outline is necessarily brief, and has to be read in the context

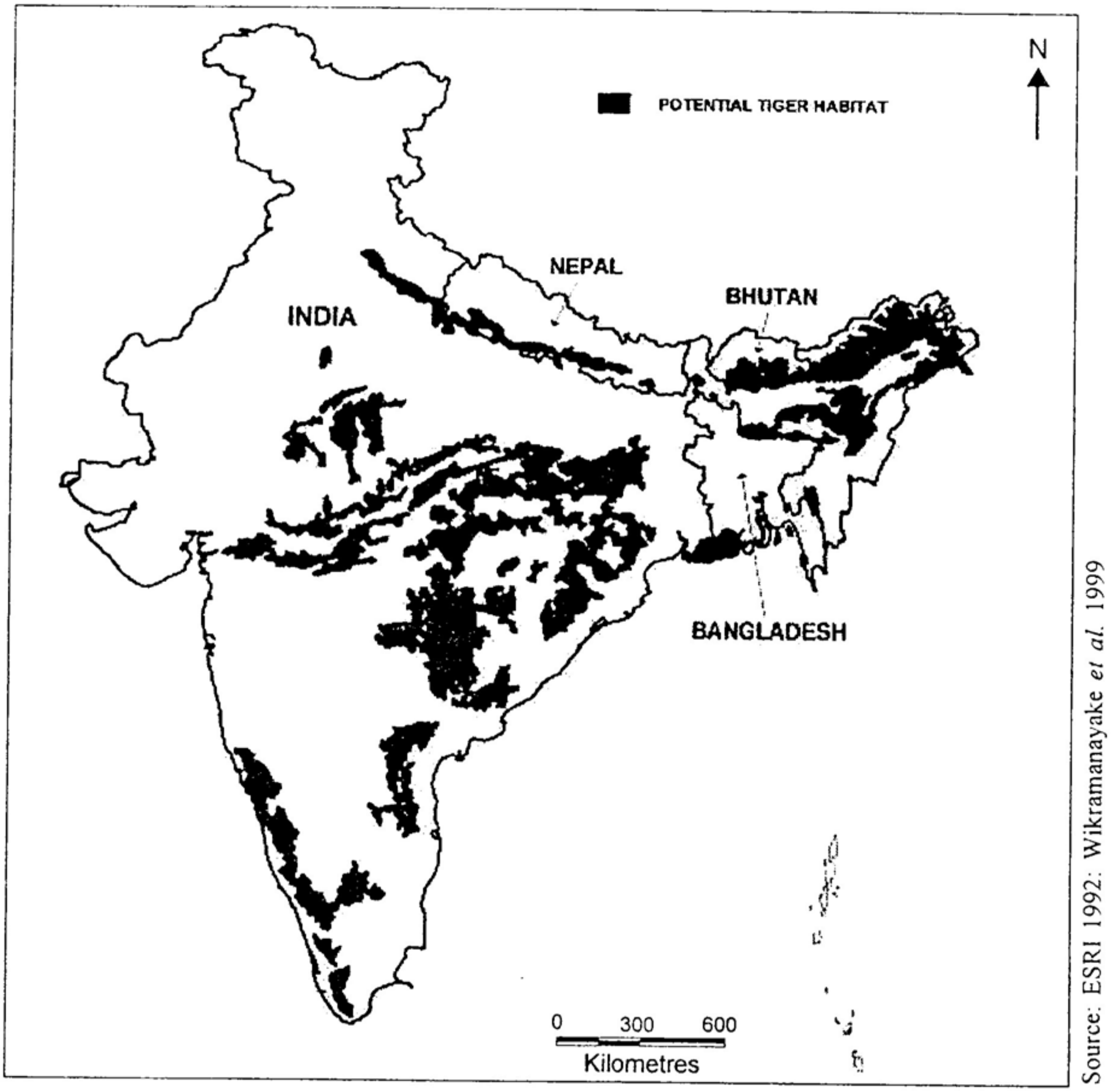

Fig. 1: Potential tiger habitat in the Indian subcontinent

of more detailed historical analyses (Rangarajan 1999, 2001).

Throughout the 19th century and during the first half of the 20th, tigers were viewed as vermin to be eradicated by giving bounties to local hunters or as glamorous game animals to be exclusively hunted by elite 'sportsmen'. Both colonial rulers and native chieftains adhered to this view. Although some local cultures have traditionally revered tigers as deities (Jackson 1990, Karanth 2001), in practice such reverence made no difference to tigers as people persistently hunted tigers and their prey, and encroached on tiger habitat to convert it to farmland. However, in a few "game reserves" established for the sportsmen of the ruling classes who wielded substantial social power, "native poachers" were kept out. Consequently, tiger populations survived despite heavy pressure from elite hunters.

In the post-colonial period (after the 1950s) the first systematic attempts at tiger conservation were made under pressure from hunter-naturalists (Rangarajan 2001). These included the introduction of the first wildlife protection laws and establishment of "game reserves" all over India. However, due to the weakness of these efforts, tigers continued to be under pressure and were in decline into the 1960s. Only a few naturalists (Gee 1964, Daniel 1970) pleaded the case for more effective laws and protected areas for tigers. Around the same time, Schaller (1967) published the first scientific study of tigers, forcefully publicising their grim conservation status in the Indian subcontinent. Despite these early warnings, commercial tiger hunting by foreign tourists as well as "sport hunting" by the local elite prevailed, particularly in the forests of Central India (Sankhala 1978). During the late 1960s assessments by Sankhala (1978) and a questionnaire survey by Daniel (1970), both re-confirmed the tiger's precarious status in India, suggesting (without much evidence) that tiger numbers in India could be lower than 2000 animals. Such concerns led to effective lobbying and support from international conservation agencies (mainly IUCN and the World Wildlife Fund) that resulted in the Governments of India and Nepal initiating stronger tiger conservation measures (Jackson 1990).

At the core of these fresh conservation initiatives were the greatly strengthened wildlife protection laws, special protected reserves for tigers and increased funding for protective infrastructures (Panwar 1987, Karanth 2001). The criticisms that such tiger recovery measures were based on a top-down perception of conservation and did not sufficiently empower or involve local people in tiger conservation (Saberwal 1997, Rangarajan 2001) are valid. However, it is equally true that in most protected areas where these "top-down" conservation measures were implemented, significant recovery of tiger populations, prey base and habitats was observed (Karanth *et al.* 1999, Karanth 2001). These recoveries resulted from measures that met the ecological needs of tigers by reducing pressures of incompatible uses of tiger habitats by local people as well as by forestry departments. Had these unpopular protective measures not been put in place, it is very likely that tigers would have been extirpated from even these protected areas, as indeed they were from forests outside them.

Shifting conservation paradigms

Unfortunately, the tiger population recoveries in the 1970s and '80s in the Indian subcontinent were not documented using rigorous science (Karanth *et al.* 2003). As a result, the conservation community at large did not draw correct inferences from these large-scale conservation "experiments". Consequently, the proposed alternative of a more "bottom-up" conservation policy (Kothari *et al.* 1995) downplays the importance of preservationist measures. Instead it emphasises "sustainable use". This alternative conservation paradigm appears to advocate "human-tiger coexistence" and multiple use of even designated priority tiger conservation areas (Kothari *et al.* 1995, Saberwal 1997). Although tigers did "coexist" with subsistence-level human use of their habitats in the past, they lost ground steadily as a result of the ensuing conflict. The tiger's distributional range shrank by more than 95 percent in the process, within a few centuries. How such coexistence can now become beneficial to tigers again remains undemonstrated.

Tigers are landscape animals that typically live at low densities. The area needed to support a wild tiger population with 25 breeding females may range from 500 to 5,000 sq. km, depending on prey density and other habitat parameters. Being large-bodied carnivores, tigers readily kill livestock and occasionally, humans. When tigers lose their natural fear of humans, they can become persistent man-eaters (McDougal 1987, Karanth 2001). Usually, increased human use of tiger habitat depresses densities of principal ungulate prey (Karanth *et al.* 1999) through hunting, competition with livestock, and over-harvest of vegetation. Consequently, productive tiger populations cannot "coexist" with activities such as agriculture, livestock grazing, minor forest product collection and intensive logging, without serious human - tiger conflict. In the long run, such conflicts inevitably lead to the extirpation of tigers from areas of intensive human use.

Therefore, the assertion that local involvement in resource extraction from tiger habitats, together with the political empowerment of 'local people' are sufficient conditions to recover tiger populations, rests on no solid evidence either in ecological theory or in conservation experience. While there could be arguments over 'who' should manage tiger reserves, there is no doubt that such special reserves are needed, and, 'someone' has to enforce the preservationist measures necessary to maintain and perpetuate them.

Currently, as a result of increasing human and livestock densities, higher rates of forest-product harvests and hunting (all linked to growing commercial markets), wild tiger populations are declining. Intensification of human use of tiger habitats, and economic development projects, both now present major threats to their ultimate survival (Karanth 2001).

Scientific knowledge of tiger biology as well as our empirical knowledge of past conservation practices (what works and what does not) reviewed above, clearly show that reducing human pressures on tiger reserves and buffering them against incompatible land use practices outside, and extending and increasing connectivity among these reserves, are the best ways to recover and sustain wild tiger populations.

A renewed commitment to such effective protected tiger reserves, under a new conservation paradigm of maintaining 'sustainable landscapes' overall, rather than implementing 'sustainable use' practices everywhere, seems to be the most fundamental paradigm change necessary to save tigers in this century and beyond. However, conservationists appear to be often distracted from this central task by a variety of 'surrogate tiger conservation activities'.

Surrogate tiger conservation activities

Because the practical measures necessary to recover wild tiger populations are socially and politically complex and difficult to implement in almost any specific local context, conservationists often escape from them by taking up 'surrogate tiger conservation activities'. As a result, currently, a substantial amount of goodwill, concern, effort and financial resources meant to support tiger conservation are being misdirected at implementing such surrogate solutions. While some of these activities simply divert scarce resources and energy away from more immediate needs, others adversely affect tiger conservation in a more direct manner.

One example of surrogate tiger conservation is the disproportionate attention paid to initiatives that involve captive breeding, assisted reproduction and reintroduction of tigers, ostensibly for augmenting wild populations or maintaining genetic viability or for promoting animal welfare. However, this approach is fundamentally flawed for reasons explained in the following paragraphs.

Wild tiger populations have been extirpated through demographic causes (increased mortality, decreased reproduction) that are driven by over-hunting, prey depletion and habitat loss. Reintroductions serve no purpose in replenishing wild populations because the introduced tigers will also be eliminated by the same causes. As to the issue of genetic viability, leading conservation geneticists and population ecologists (Lande 1988, Caughley 1994) have argued that smallness of wild populations is most likely an effect of demographic factors and not their cause. Even if infusion of new genes into an isolated tiger population is scientifically demonstrated as a real need, it is more efficient and practical to capture and translocate dispersal-age individuals between wild tiger populations, rather than reintroduce captive animals that have to be reared and trained at great cost.

Given what we know about the social organisation of tigers, even in the unlikely event that an introduced animal establishes a range and breeds, such an introduction will inevitably involve the killing or eviction of an existing resident breeder. It will also have the same disruptive influence that the natural turnover of resident breeders in a population involves. Because the number and sizes of tigers an area can support is limited by prey density, there will be no net population gain even after a successful introduction. Even in a rare (and expensive) case of successful reintroduction, the new animal simply replaces some other less fortunate individual in the population. Therefore, tiger reintroduction can neither be logically justified as a population augmentation tool, nor even be defended as an animal welfare measure.

On the other hand, if the reintroduced tiger fails to establish a home range, as is more likely, there are high probabilities of the cat turning into a 'problem animal' that kills livestock or even humans. Such an event will further aggravate the antipathy local people already feel towards tigers and exclusive reserves that protect them, thus making the job of genuine tiger conservationists even more difficult than it already is.

Another example of surrogate conservation involves diversion of tiger conservation monies to other worthy social objectives like providing schools, hospitals and other services to people living around tiger habitats. Such activities indeed should be funded, but out of the much larger pool of money earmarked for developmental and social causes. Given that resources earmarked for tiger conservation are meagre, and the demonstrated immediate needs are for improved protection, habitat consolidation, conservation monitoring and conservation education — all currently under-funded activities — diversion of conservation funds to meet social objectives that have no immediate impact on wild tigers is also a form of surrogate tiger conservation.

An extreme example of the above approach are the current "eco-development projects" of various kinds being implemented with the assistance of the World Bank-GEF combine and other multilateral aid agencies, and with enthusiastic support from a large number of Indian officials and conservationists. These projects have diverted huge amounts of money, energy and attention away from the core issue of tiger protection towards largely wasteful "developmental" activities leading to further deterioration of tiger protection (Karanth 2002).

Another oft-promoted surrogate activity is 'eco-tourism', a term often misapplied to the expensive corporate sponsored form of wildlife tourism practised in India. It is true that well-managed tourism involving charismatic animals like tigers can generate substantial revenues for the reserves and help protect tigers directly. Such schemes can also potentially generate incomes and revenues for the local people around the tiger reserves, thus engendering additional public support for tigers. Rarely, such projects can also lead to land use changes outside the reserve that are favourable to tigers (Dinerstein *et al.* 1999). However, unfortunately, the high-revenue tiger tourism practised in India is singularly devoid of any of these positive features. It simply constitutes a large net drain on the park budgets and engenders mostly apathy or even hostility among local residents whose access to and use of tiger habitats has been curtailed to meet tiger conservation needs. Therefore, in the Indian subcontinent, despite its vast potential, eco-tourism has been turned into another surrogate tiger conservation activity that confers little benefit to the target species.

Beyond the pugmark census: ecological monitoring of tigers

We need to monitor tiger populations for three fundamental reasons. Firstly, to objectively evaluate the success or failure of past conservation interventions, so as to react adaptively to solve problems. A second major goal is to establish benchmark data that can serve as a basis for future management. A third overarching goal of tiger monitoring is to improve our basic understanding of tiger ecology and behavior to develop a body of empirical and theoretical knowledge that can potentially improve our predictive capacity to deal with new situations (Karanth *et al.* 2002).

At this point, given the critical status of tigers and the substantial investments made in their conservation, wildlife managers and conservation agencies need clear and reliable answers to some basic questions given below (Karanth *et al.* 2002, Karanth and Chundawat 2002), without which they cannot even begin to evaluate the success or failure of tiger conservation:

1. What is the extent and range occupied by different individual tiger populations?

2. Where are individual tiger populations increasing their range, and, where are these ranges fragmenting or shrinking?

3. Within the distributional range of tigers, what is the proportion of the area occupied by productive, breeding populations?

4. In important individual tiger reserves, what are the tiger population trends? Are tiger populations in such reserves holding steady, declining or increasing?

The traditional approach to answering such questions has been based on attempts to obtain total counts of wild tigers all over the country through 'pugmark censuses' (Choudhury 1970, 1972). Such 'census-based' approaches have major biological and statistical weaknesses (Karanth 1987, 1999, Karanth and Chundawat 2002, Karanth *et al.* 2003). Therefore, the need to employ more reliable 'population sampling-based' methods tailored to suit a variety of practical contexts is being increasingly realised (Anon. 1997, Karanth *et al.* 2002)

During the past 35 years, our knowledge of tiger ecology has advanced significantly as a result of several scientific studies. During the same period, methodologies for assessing wildlife population parameters have also developed substantially. In particular, two conceptual approaches to population sampling, Distance Sampling and Capture-Recapture Sampling, have advanced particularly rapidly (Thompson *et al.* 1998, Williams *et al.* 2002). Such methods now offer powerful tools for ecological monitoring of tigers and other wildlife in India. The type of monitoring feasible in each specific context can be determined by considering the potential methods in relation to available resources and local conditions.

The following guidelines from Karanth *et al.* (2002) may be useful in choosing a monitoring method appropriate to any specific local context:

1. It is almost impossible to estimate absolute or even relative densities of tigers or prey if trained manpower, equipment and other resources are extremely limited, and, large regions, states or countries have to be covered. Since most of the distributional range of tigers in the Indian subcontinent typifies such conditions, one can only attempt sample surveys of presence of tigers and prey species to estimate and map their distribution at this large landscape scale.

2. Where adequately trained personnel are available, measuring the relative density of tigers from sample surveys of encounter rates with tiger tracks or scats or the relative densities of prey species from pellet or dung counts are options (Karanth and Kumar 2002). It is likely that such index-based surveys are feasible only in some individual reserves.

3. If special equipment, trained personnel and other resources are available, absolute densities of prey species can be estimated from line transects using distance sampling methods (Buckland *et al.* 1993, 2001). Even absolute densities of tigers can be estimated using photographic capture-recapture sampling from camera trap surveys (Karanth and Nichols 1998, 2002a). Such advanced methods are likely to be practical only in a few priority tiger reserves or study sites.

If there is a mismatch between available resources and the goals that tiger managers hope to achieve, failure of monitoring is almost certain. The goal (1) of monitoring tiger or prey spatial distribution is a critically important first step in implementing any landscape level conservation programmes. Gradually, over the years, one can build up the capacity and resources to try to meet objectives (2) and (3) in priority conservation areas.

I emphasise that if the goal is to *reliably* estimate parameters such as tiger densities, survival and recruitment rates, there is no escape from implementing advanced population estimation methods. However, these methods can be employed only where necessary skills and resources are available. They cannot be applied for routine population surveys over large regions. However, the two most critical needs of tiger monitoring in the Indian subcontinent, mapping spatial distributions over large regions and determining population trends in specific reserves through indices, are widely attainable goals using relatively simple methods (Karanth and Nichols 2002b).

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