## LIVING ON THE EDGE: TIGERS AT THE NORTHERN LIMITS OF THEIR RANGE

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Most of us, when asked to conjure up an image of the tiger, imagine a magnificent predator skulking through the steamy jungles of southern Asia, more often than not somewhere on the Indian subcontinent. Despite this stereotype, the tiger is in fact at home in a great variety of environments across a surprisingly wide range of latitudes. Our studies of the tiger living on the very edge of its range in the Russian Far East have emphatically demonstrated how elastic tiger behavior is and how capable it is of adapting to environmental variation.

It is surprising how "at home" Amur tigers appear in the snowy forests of Russia. The orange background with black stripes, assumed to provide camouflage in tropical forests and grasslands, also conceals these animals in masterly fashion in oak forests (where the leaf litter is a dingy orange) and temperate forest thickets (where vertical striping can make the animal "disappear" before your very eyes). A thick winter coat, absent in animals from other populations, provides adequate protection against winter temperatures that can drop to  $-40^{\circ}$ C ( $-40^{\circ}$ F). Despite repeated claims in popular literature that members of the Amur population are the largest of all tigers, our measurements on more than fifty captured individuals suggest that their body size is similar to that of Bengal tigers.

As with all predators, the population density of Amur tigers is ultimately limited by prey availability. As elsewhere across their range, Amur tigers prey on medium-sized and large cervids (deer) and wild boar, although wild cattle, an important component of their diet in some areas, are absent in the north. Amur tigers make kills at a similar rate as in the south, despite slightly higher energy requirements associated with the cold temperatures. Rapid decay of carcasses

in the tropics prevents tigers from fully utilizing meat from large kills, whereas in the north 90 percent of meat is normally consumed. However, because plant productivity declines with latitude, ungulate carrying capacity in northern temperate forests is reduced by an order of magnitude in comparison to southern areas. Prev-biomass estimates in high-quality habitats in India range from 2,000 to nearly 7,500 kilograms per square kilometer (5 to 18.5 tons per square mile), whereas in the Russian Far East high-quality habitat can support a prey biomass of less than two hundred kilograms per kilometer (about half a ton per square mile). Amur tigers must traverse home ranges that are dramatically larger to find sufficient food: tigresses in prime habitat in India use home ranges of only twenty square kilometers (eight square miles), while tigresses in Russia maintain home ranges that on average are twenty-two times as large. As a result, tiger densities at the northern limits of their range rarely exceed one animal per hundred square kilometers, whereas some parts of India can boast of more than sixteen animals in a similar-sized area.

The conservation implications of these ecological differences are vast. While India is attempting to conserve its tigers in small, isolated islands of habitat (tiger reserves), such a tactic would be impossible in the north. The largest protected area in Russia within tiger range (Sikhote-Alin Reserve), which covers four thousand square kilometers (nearly 1,600 square miles), harbors fewer than thirty animals, at least half of which regularly use areas outside the boundaries of the reserve. Because Amur tigers require such vast home ranges, no single protected area can retain a viable population of tigers. Conservation in Russia will therefore depend upon development of a core network of protected areas interspersed with multiple-use lands that integrate tiger conservation with sustainable use of natural resources by humans.

Despite the dramatic differences in the scale at which tigers use the landscape across their ranges, their social structure is similar in India and Russia. In both areas, females generally occupy exclusive home ranges, and males attempt to secure exclusive access to females by retaining territories that overlap with those of one or more females but exclude other males. Surprisingly, despite the low densities of prey, the reproductive rate of Amur tigers appears to be similar to that of Bengal tigers. Contrary to some theories, our data suggest that tigers are not particularly resilient in the face of human poaching and that relatively low levels of human-caused mortality can result in dramatic decreases in population size.

Although India still retains the largest number of tigers in the world, its burgeoning human population has fragmented remaining tigers into small subpopulations isolated from one another. Because the remaining habitat is so productive, tigers there require only small home ranges, and reasonably large numbers of tigers can be retained in these protected areas. At least in the short term, this tactic is working to retain tigers in the Indian landscape. In contrast, although Amur tigers require vast home ranges, Russia retains the largest existent single population of tigers in the world in a single, unbroken forest tract that exceeds 180,000 square kilometers (70,000 square miles). Although future development and timber harvest are unavoidable, a decreasing human population there provides hope that this landscape may not undergo serious fragmentation in the near future. If suitable management regimes can be developed on existing forest tracts to provide minimum requirements for tigers, and if incentives can be found for local people to benefit from—or at least tolerate the presence of-tigers, the future of tigers in the Russian Far East is bright.

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