K. Ullas Karanth · James D. Nichols
Editors

Methods For Monitoring Tiger And Prey Populations

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Foreword

If wild tigers were easy to study, every aspiring field researcher would want to do so. The elegance, ecological role, and aura of this top predator exert a magnetic pull that extends far beyond biologists. Surveys undertaken by conservation groups show that among the general public, tigers consistently come out as the most popular wild species on Earth. The irony, of course, is that catching a glimpse of a tiger outside of zoos and in its natural habitats is often, at best, a once-in-a-lifetime event. It should thus come as no surprise that since George Schaller's pioneering study of wild tigers in India's Kanha National Park over 50 years ago, relatively few long-term field studies have been successfully carried out on this highly territorial, secretive large carnivore. The authors in this volume make up a large subset of those intrepid biologists who have crouched on jungle trails to set camera traps, pick up scats, and look for other signs or monitored the prey of this big cat.

Even though few biologists have had the good fortune to study tigers in the wild, everyone wants to know about their numbers, especially conservationists, for without accurate counts and projections, it's difficult or even impossible to devise adequate conservation strategies. Those who have studied tigers are repeatedly plied with the same four questions: How many tigers are left in the wild? Are their numbers increasing or decreasing? Will they go extinct? What can we do to save them? These are the questions to which government wildlife officials in the tiger range states are hounded to provide answers by concerned citizens and the popular press. Unless we have robust, repeatable methods to answer questions accurately about changes in tiger numbers and forces affecting them, officials must answer by reverting to guessing or crude surveys. The reliance on outdated and less accurate approaches does little to advance science and even less to determine the true fate of wild tigers.

Enter this volume. A gathering of scientists, under the leadership of Ullas Karanth and Jim Nichols, addresses the most important topics related to accurately assessing the status of tigers and their prey and, we can hope, monitoring their recovery. It is a critical task to share information on best ways of analyzing numbers for tiger and tiger prey researchers, for concerned others, and for those who study other species in the region. In the ongoing effort to save and recover wild Asia, the content of this book provides the monitoring bible.

In the 1970s and even today, India has been home to the majority of the world's wild tigers, and it is on that country that the authors focus much of their attention. In the late 1960s, wildlife officials became aware that poaching of tigers and prey and loss of habitat were leading to precipitous drops in the number of tigers in the wild. The prevalent technique at the time to estimate tiger numbers was the well-worn pugmark method, relying on the claim that the footprints of tigers, measured in the appropriate substrate, served as identifying "fingerprints," and adult and subadult tigers could be identified as distinct individuals from tedious field measurements. Ullas Karanth in the 1980s illustrated the inaccuracy of this approach through a clever controlled experiment: allowing a known number of zoo tigers to make tracks and inviting official "tiger pugmark identification experts" to attempt to determine how many tigers had actually been present. The results of this experiment put to rest the idea that "seasoned experts" could eyeball correctly the number of tigers in an area based on an examination of pugmarks. Tracks were useful for establishing the presence of tigers but not to determine their numbers. Karanth and coauthors followed this up with a rigorous overall critique of the pugmark census method (Karanth et al. 2003: "Science deficiency in conservation practice: the monitoring of tiger populations in India," *Animal Conservation* 6:141–146), which eventually led to the method's official demise in 2005.

From the early 1990s, Karanth and his WCS colleagues worked to replace the pugmark method with a new technology—automatically triggered camera traps—that, when used with a systematic sampling design, could begin to improve estimation techniques. Guided by statistical guru Jim Nichols from USGS, the team revolutionized how best to sample wild tigers and, by extension, how populations of many other cryptic but individually identifiable animal species that occur at low densities could be reliably, and noninvasively, estimated.

By 1995, researchers were also using new GIS mapping techniques to determine the tiger's range as a series of landscapes called tiger conservation units (TCUs), formed by the known presence of tigers or their suspected presence and by their ability to disperse. The resulting exercise identified places where tigers could be conserved. It also identified giant polygons as "survey landscapes," large blocks of presumed habitat where no information on tiger status was available. These polygons, mapped in purple, caught the attention of Karanth and his disciples and became the targets of field efforts, many of these far from the boundaries of India. Ten years later, all of the survey TCUs had been thoroughly camera-trapped or at least visited by camera-trapping teams.

These results were collated again in 2005 and published in a series of papers, one of which, "The Fate of Wild Tigers" by biologists from the World Wildlife Fund and the Wildlife Conservation Society, divided the tigers' truncated ranges into 76 tiger conservation landscapes. The critical finding of their analysis could be termed "range collapse": tigers occupied 40% less habitat in 2005 than they had a decade earlier according to a 1995 study. The structural habitat was still present to support tigers, but either the tigers, their large prey, or both had been hunted out. Even accounting for some error in the comparison, the interpretation of the

intensive camera-trapping campaign between 1995 and 2005 can be summed up in a depressing, short phrase: learning a lot more about fewer tigers.

Recognizing that a shift in strategy was needed to avoid the extirpation of tiger populations, several tiger biologists hatched the idea of a Global Tiger Initiative (GTI), which culminated in staging a Global Tiger Summit in 2010 in St. Petersburg, Russia. The attending heads of state, hosted by Vladimir Putin, and subsequently other range state leaders not in attendance agreed to the global goal of doubling the wild tiger population from about 3200 in 2010 to upward of 6500 by 2022, the date of the next Year of the Tiger. Suddenly, the work of Karanth and Nichols took on a fresh new urgency: how to provide reliable information to monitor the path to this milestone of recovery.

That work continues in earnest to this day, and the initial chapters here focus on the latest approaches to answering several basic questions: Why are you undertaking the monitoring program? What aspect of tiger or prey biology are you trying to address? How do you go about it in the most robust way? It is an ideal beginning, to state the questions clearly at the outset, to avoid wasting time and money in what could otherwise be glorified fishing expeditions.

A subsequent chapter (Chap. 5) discusses five other questions that biologists and technicians should ponder before proceeding. Another reason this book needs to be widely circulated is that we need to ensure that the estimates of tiger numbers and occupancy are accurate to make sure that the interventions on behalf of tiger conservation are actually working. The GTI helped catalyze a number of range states to allocate more funds for tiger protection. By answering the questions laid out here and adopting the best practices described in this volume, we stand the best chance of these resources being invested wisely.

A further pathbreaking finding of Karanth and his co-workers was that tiger density can be predicted by prey density (Karanth et al. 2004: "Tigers and their prey: Predicting carnivore densities from prey abundance," *Proceedings of the National Academy of Sciences*, USA 101:4854–4858). This insight builds on work of Karanth's mentor, felid biologist Mel Sunquist, who remarked at a conference in 1980 that "to be a tiger biologist, you really need to be a deer biologist." So it is welcome that this volume includes several important chapters on monitoring prey density. If being a tiger biologist means being a deer biologist, one could argue that being a deer biologist requires an understanding of plant ecology, soil science, and geology. Underpinning the correlation of tiger densities with large prey densities is another rarely discussed feature: alluvial soils produce the densest population of tigers because they support the highest concentrations of large herbivores. Soil fertility thus may be one of the ultimate drivers of tiger densities.

By incorporating techniques for monitoring tigers and their prey that can apply to many other large mammals, the authors greatly extend the reach and value of their work. A further benefit of the volume is the penultimate chapter, a treatise on connectivity, a vital aspect of conserving many large terrestrial mammal populations. If tigers are to have a future in Asia, they must be managed as metapopulations—populations linked by dispersal. The fact remains that not a

single tiger reserve among the 350 or so in the tiger's range is large enough to maintain a viable population. Establishing corridors connecting tiger conservation areas and developing a healthy matrix through which to disperse are vital.

What will tiger and prey monitoring look like 15 years hence? Advances in camera trapping, remote sensing, and GIS modeling led to a quantum leap in how we have studied tigers and tiger habitats over the past 20 years. Could the emerging technologies of computer vision, machine learning, miniaturization of electronics, smart drones, and long-range (LoRa) radio frequency communication further revolutionize how we count or detect wildlife? Sensors that use cryptic cameras equipped with computer vision algorithms to detect humans (poachers) and relay such information via GSM or LoRa networks will soon be in place in African wildlands. It is only a half-step more to insert new low-cost, computer vision chips into such cameras that can do "onboard" processing to detect tigers, sort and identify them, and transmit photos in real time to a researcher connected to the Internet. When these sensors are mass produced at "cents to the dollar" per unit, it would be only another small step to expanding camera-trapping grids to systematically cover the entire tiger landscape using linked sensors and thus obtain a total census.

These potential developments raise a final question: Will our sophisticated ability to monitor tigers and their prey then be matched by the development of the necessary political will, interest in protecting enough habitat, ability to gain the local buy-in to save tiger landscapes, and then mobilization of sufficient resources to restore thriving populations of tigers and other populations of large Asian mammals? If we only set aside large blocks of habitat and left tigers and their prey alone, there would be much less need for a book like this. But because the development of the tiger range states, among the fastest in the world, has ramped up the pressures, this volume becomes even more vital.

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Preface

The tiger is a global conservation icon. Because of its popular appeal, which has religious, cultural, aesthetic, and social roots, an impressive array of leaders in these spheres has also seriously engaged with tiger conservation over the past 50 years. A quick chronological, but nonstatistical, sample includes Indira Gandhi (post-1969), King Birendra of Nepal (1970s), Dalai Lama (1990s), and Vladimir Putin (2000s). Tiger range state officials, tiger scientists, national and international NGOs, and conservation advocates at various levels have all toiled hard to stem the tiger's slide, into what appeared to be inevitable extinction by the mid-1960s. Some of these efforts have succeeded, while many others have failed.

One of us (Karanth) got involved in tiger conservation as an amateur naturalist in the 1970s, around the same time as the other (Nichols) began his professional career as a quantitative ecologist. At that time, in spite of conservation efforts, rigorous science was excluded from the critical task of assessing how tiger populations were faring. Such assessments required a thoughtful synthesis tiger biology and quantitative ecology, relevant to specific conservation contexts. Such a methodological synthesis was simply not available.

In the late 1980s, we met for the first time, somewhat serendipitously, at the University of Florida, Gainesville. Soon after, we decided to collaborate to develop and apply rigorous and defensible methods for monitoring tigers and their principal prey species. With lots of help from various field personnel, wildlife managers, as well as other tiger biologists and quantitative ecologists, we developed a set of monitoring methods that we believed to be useful and representative of the state of the art in inference methods for animal populations.

Application of these methods in India demonstrated their feasibility and utility to the point where we believed that we should recommend them to others involved with tiger conservation monitoring. We organized an international technical workshop, sponsored by the Wildlife Conservation Society (WCS) at Nagarahole Reserve, India, in January 1999. The workshop was conducted in association with Indian government's Project Tiger and some state forestry departments and included several wildlife managers, carnivore biologists, and biostatisticians. Several population monitoring approaches were discussed in detail, with topics ranging from the collection of field data to their final statistical analysis.

As a direct result of this workshop, we produced the edited volume, *Monitoring Tigers and Their Prey: A Manual for Wildlife Researchers, Managers and Conservationists in Tropical Asia* (Karanth and Nichols 2002). The intent of this volume was to provide guidance about field monitoring and statistical methods that we believed to be superior (in the sense of yielding stronger inferences), compared to methods that had been used for decades in India and the rest of tiger range. Recognizing the natural reluctance of practitioners to discard such historical methods in favor of new approaches, we made a special effort to present the logic and rationale underlying our recommended approaches. We tried to describe field methods in sufficient detail that they could be duplicated by others and to provide simple numerical examples to aid understanding of some of the analytic approaches that we were recommending. In 2008, WCS collaborated with Trust for Environmental Education, India, to produce a 47-minute video guide that clearly depicted the various monitoring methods described in Karanth and Nichols (2002). Both PDF version of the book and the video guide were made freely available to all users by WCS on the Internet (http://wcsindia.org/home/media-library/).

As a result, the methods recommended in Karanth and Nichols (2002) have been widely used by carnivore ecologists, conservationists, and wildlife managers. Many users have adapted these methods to monitor not only tigers but also other big cats, such as jaguars, *Panthera onca*; cheetahs, *Acinonyx jubatus*; leopards, *Panthera pardus*; and snow leopards, *Panthera uncia*. We have been surprised and pleased that some of the ideas (e.g., on camera trapping, occupancy modeling of sign survey data) have been applied to conservation problems extending well beyond tigers and prey, to varied species and conservation issues across the globe.

We ended the penultimate paragraph of the preface to Karanth and Nichols (2002:xv) with the following two sentences: "However, we are well aware that, eventually, the methods that we present in this manual will be replaced by better methods generated through the very same process of scientific review that we endorse. In fact, we look forward to such improvements."

This methodological evolution has proceeded even more rapidly than we anticipated, to the point where we believed it necessary to develop this new volume to incorporate these advances. We were fortunate to have collaborated, once again, with an outstanding group of authors who have produced what we believe is an exceptional set of methodological chapters representing the current state of the art in animal monitoring in general and as applied to tigers and their prey specifically.

This new volume differs from the 2002 volume in important ways, and we believe that the relationship between the two volumes merits some discussion here. For the purpose of brevity, in this comparison, we will refer to the earlier manual as *KN (2002)* and the present volume as *KN (2017)*.

First, we note that the methods presented in *KN (2002)* are still foundational and useful. Unlike the earlier tiger census methods that they replaced, these methods have sound conceptual underpinnings and still "work." Rather than scrapping these methods, many of the chapters of *KN (2017)* extend the modeling of *KN (2002)* in exciting and novel ways that increase their value. Even the major "new" method

in *KN (2017)*, spatially explicit capture-recapture modeling, can be viewed as a marriage between two classes of methods described in *KN (2002)*, classical capture-recapture models and distance sampling.

An additional distinction between the two volumes is in simplicity of explanations. In both editions, we made special efforts to simplify explanations to the degree possible, hoping that readers can develop an understanding of how the described methods work. However, many of the extensions and new developments in *KN (2017)* were made possible by advances in computing power and associated numerical methods, which are not as amenable to simplified explanations and examples as the initial models described in *KN (2002)*. We have thus come to view the two volumes as complementary. The 2002 volume is probably a better starting place for readers who have never been exposed to these inference methods yet seek to develop an understanding of them. Explanations in the current volume have been simplified to the degree possible but will be more readily understood by those who have some prior familiarity with these general classes of methods. Therefore, we have made the *KN (2002)* volume and its associated video guide to readers of this volume available on the Internet (http://wcsindia.org/home/media-library/). The video guide and related visual material are also available at http://www.conservationindia.org/ and the publisher's online support (www.springer.com). We hope readers will find these features helpful.

An additional feature of this volume is a final chapter describing how the rigorous monitoring approaches explained and recommended here can fit into, and contribute to, adaptive natural resource management (Walters 1986, Nichols et al. 2007) and structured decision-making (Martin et al. 2009), which are being increasingly applied by conservation practitioners and wildlife managers in varied contexts globally. We urge tiger conservationists to seriously consider these suggestions in their own specific situations.

We both continue to strongly believe that the scientific process of peer review and publication in high-quality journals should guide the choice of appropriate methods for monitoring tigers and their prey. Therefore, we are somewhat dismayed that, in spite of availability of superior methods, tiger conservation practitioners are sometimes slow to adopt them or even use demonstrably flawed or obsolete methodologies. We believe this is largely because of intellectual inertia, rather than resource constraints, given the current levels of investment. Unfortunately, we can offer no methodological cure for this problem.

As is the way of all scientific progress, the animal monitoring approaches that authors in this volume recommend too will eventually be superseded by superior ones. As editors, we hope that this volume will inspire cohorts of talented carnivore biologists and quantitative ecologists who will follow, to seriously engage with the innovations necessary to rapidly render our current effort obsolete. The still precarious fate of the wild tiger populations urgently demands such a proactive engagement.

Bengaluru, India — K. Ullas Karanth
Crofton, MD, USA — James D. Nichols

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*Any use of trade, firm, or product names by the author is for descriptive purposes only and does not imply endorsement by the US Government.

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Blurbs

This book brings together the best minds and decades of experience in tiger conservation. We must continue to improve the way we monitor wildlife to measure the impact of our work. This authoritative volume will be an invaluable tool for us in this important task, for decades to come.

Cristián Samper
President and CEO of the Wildlife
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CEO, Panthera
New York

This book is well written and exciting to read. The focus on tigers allows the reader to understand the deep complexities in estimating demographic parameters in animal populations. The valuable contribution here is to showcase the relevant spatial estimation theory and methods—these new thrusts are very important and useful for tigers and for a wide variety of other animal species.

David R. Anderson
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Compendious, enlightening, and monumental with relevance far beyond tigers: if you don't know what you've got, you can't know how you are doing or how to do better, which is why counting animals and monitoring trends in their numbers are fundamental to conservation. Counting tigers is difficult, and the answers are policy dynamite, which is why the opening chapter of this benchmark book is right in asserting that its contents are critical and, while technically sophisticated, happily not daunting. In 2002, these editors compiled an earlier book in which they looked forward to their then cutting-edge ideas being superseded by others who would follow. It turns out that others didn't need to do the job; Karanth and Nichols have done it themselves!

David W. Macdonald
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I was a sponsor of the technical workshop held in January 1999, which led to the popular manual compiled by Karanth and Nichols, titled *Monitoring Tigers and their Prey*, in 2002. I am sure this new book by the same editors titled *Methods for Monitoring Tiger and Prey Populations* will prove to be as popular and useful as its predecessor.

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About the Editors

K. Ullas Karanth (b:1948) is the Director for Science, Asia with the Wildlife Conservation Society (WCS)-New York, besides being Emeritus Director at the Centre for Wildlife Studies (CWS), and WCS, India Program based at Bengaluru. Originally trained as a mechanical engineer, he subsequently obtained his graduate education in wildlife biology from the University of Florida, Gainesville, USA, and Mangalore University, India. The ecology of tigers, sympatric carnivores, and their prey species and issues of monitoring of wild animal populations have been his focal areas of research since 1986. Dr. Karanth has published over 125 scientific articles. He has authored or edited 15 technical and popular books. Over the years, Dr. Karanth has served on India's Forest Advisory Committee, the National Tiger Conservation Authority, the Governing Body of the Wildlife Institute of India, and the Indian Board for Wildlife. He is a Fellow of the Indian Academy of Sciences and has received the J. Paul Getty Award from WWF-USA for conservation leadership. Dr. Karanth has been honored with India's presidential award *Padma Shri* and *Rajya Prashasti* by Karnataka State, in recognition of his services to wildlife conservation and science.

James D. Nichols (b: 1949) is now retired after 40+ years of service as a senior scientist at the Patuxent Wildlife Research Center for the US Fish and Wildlife Service and then the US Geological Survey. He received his undergraduate degree in biology from Wake Forest University, his master's degree in wildlife management from Louisiana State University, and his doctorate in wildlife ecology from Michigan State University, in the USA. His research interests are animal population dynamics and wildlife management with a special focus on the estimation of demographic parameters. He has published over 400 scientific articles and is widely recognized for his contributions to wildlife ecology and management. Dr. Nichols is a fellow of the Ecological Society of America and the recipient of various awards including the Outstanding Publication Awards from The Wildlife Society and the American Statistical Association. He is a recipient of the Aldo Leopold Award (The Wildlife Society), Wetland Conservation Achievement Award (Ducks Unlimited), Award of Excellence (Biometrics Working Group of The Wildlife Society), US Presidential Rank Award (Meritorious Senior Professional), and Wings Across the Americas Award (US Forest Service for outstanding contributions to bird conservation).

Role of Monitoring in Global Tiger Conservation

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1.1 Introduction

This chapter sets the overall context by providing a brief overview of the historical and current status of wild tiger populations and social, cultural, and scientific perspectives on the tiger. It also covers aspects of population biology of tigers, history of conservation efforts, and the need for reliable monitoring for advancing

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tiger science as well as conservation. We also touch upon typical monitoring goals relevant to different ecological and social contexts. Our primary goal here is to convince field practitioners that approaches presented in this volume are not as daunting as they may appear at first glance: they are more sound and practical, compared to many of the methods on which large investments are currently being made.

1.1.1 Status of Wild Tigers

Tigers (*Panthera tigris*) were once widespread across Asia, with a distributional range spanning 30 present-day countries, stretching across a vast region (latitudes 53^0 52′ N to S 8^0 51′ N and longitudes 46^0 42′ E to 134^0 24′ E). After modern humans colonized Asia (∼60,000 years BP), forest clearance for shifting cultivation, followed by settled agriculture and livestock raising (∼10,000 years BP), squeezed tiger habitats. Expanding human settlement brought tigers under great pressure. In the escalating conflict with people over land and livestock, tigers were systematically hunted out. Finally, with the advent of steel traps and snares—and later firearms, explosives, and chemical poisons—hunters virtually extirpated tigers from most agricultural tracts (Karanth 2001). For example, a molecular genetic estimate (Mondol et al. 2009b), with wide variance, suggests a median estimate of 58,000 tigers for peninsular India ∼500 years ago. Just 150 years ago, the extent of tiger habitat across Asia may have exceeded 13 million km^2, an area the size of China and India combined (computation based on Walston et al. 2010, Goodrich et al. 2015).

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During the nineteenth and twentieth centuries, the following threats to tigers ratcheted up:

1. Agricultural encroachments through large- and small-scale forest conversions.
2. Major infrastructure and industrial development, such as railways, roads, mines, irrigation, and power projects.
3. Intensive industrial-scale logging by governments and companies as well as severe forest biomass exploitation by rural communities and their livestock.
4. Large-scale sport hunting by social elites and bounty hunting of tigers for conflict mitigation. Depletion of wild ungulate populations by local hunters. For example, in the British Indian Empire, in 50 years between 1875 and 1925, over 80,000 tigers were killed off by sportsmen and bounty hunters (Rangarajan 2001).
5. In the late twentieth century, increased demand for tiger body parts as medicinal curatives and decorative trophies from newly affluent consumers in China and East Asia has emerged as another major threat (Nowell and Ling 2007).

Under such intense pressures, tigers were successively extirpated: from Bali Island by the 1940s, from West Asia by the 1950s, and from Java, Korean Peninsula, Central China, Cambodia, and Vietnam by the late twentieth century (Goodrich et al. 2015). In the last 200 years, the tiger's range has shrunk by >95%, down to $\sim$ 638,000 km^2 spread across 11 countries: India, Nepal, Bangladesh, and Bhutan (all in South Asia) and Myanmar, Thailand, Malaysia, Indonesia, and Lao PDR where they may be virtually extinct (all in Southeast Asia). Tigers also survive in the Russian Far East and adjacent areas of China in Northern Asia (Goodrich et al. 2015; Fig. 1.1).

An educated guess is that ~4000–5000 wild tigers may now survive in Asia, with 75% occurring in Southern Asia, which supports only 30% of remaining habitat. Tiger populations are now secure only in a few protected areas, mostly in India. They are virtually confined to "source populations" occupying about 6% of overall habitat range wide (Walston et al. 2010, Wikramanayake et al. 2011).

1.1.2 Social and Cultural Underpinnings of Tiger Conservation

The tiger is the largest among living felid species. It is an apex predator in ecological communities as diverse as the snow-bound taiga to steaming tropical jungles. Its primary prey are large ungulates. Undoubtedly, the tiger must have made a deep impression on the first humans who colonized Asia ~60,000 years ago. Tigers preyed on human beings and were feared greatly for that reason (McDougal 1987). Both admired and feared, the tiger is deeply embedded in Asian cultures: from the early animistic ones to the Hindu, Taoist, Buddhist, Christian, and Islamic faiths that historically swept across Asia. Tiger iconography is pervasive: in caves and shrines of tribal cultures as deities or spirits and in association with various gods, saints, prophets, warriors, and kings (Boomgaard 2001, Thapar 2011). However, this human fascination has not helped the tiger much in its historical struggle for survival

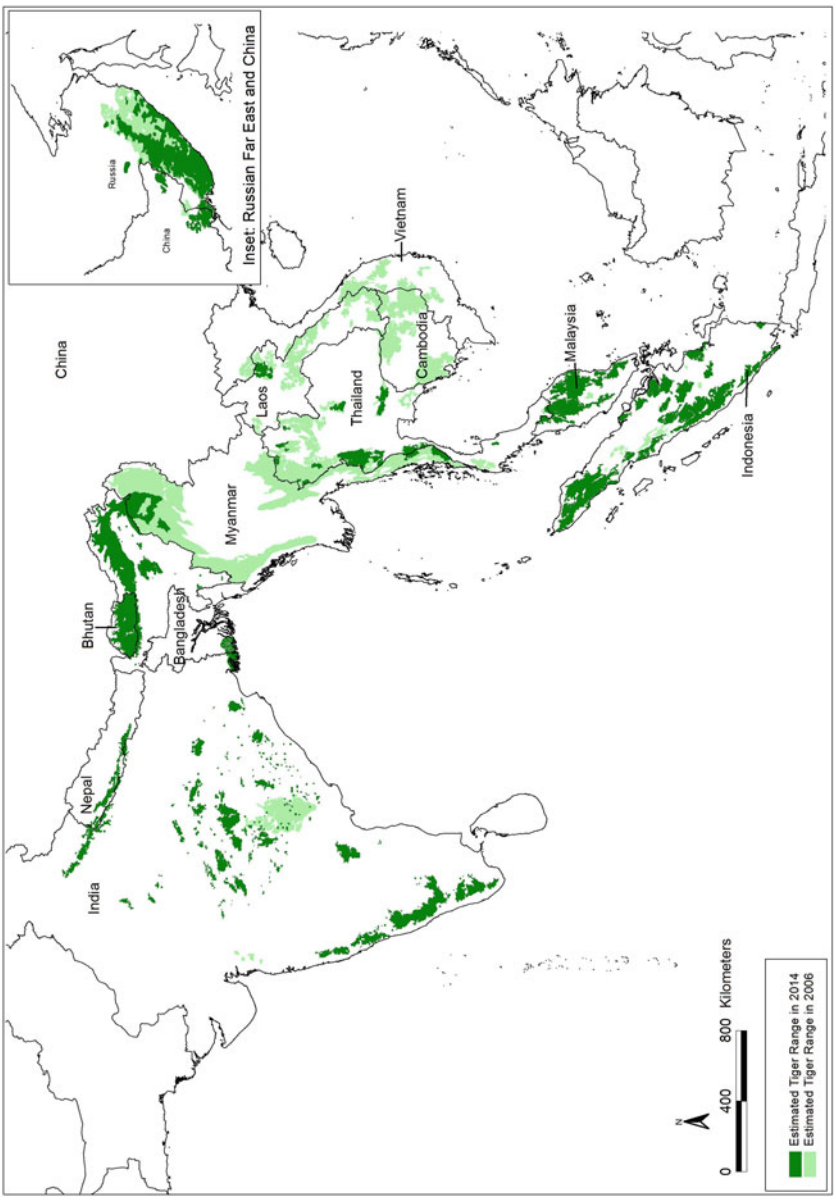

Fig. 1.1 Distribution of wild tiger populations (tiger range) 2006–2014 (Goodrich et al. 2015)

(Karanth 2001). Overhunting of tigers for sport in the past and their continued killing for human consumption are both culturally rooted.

More recently, this fascination for tigers has turned benign, with the cat serving as a mascot of commerce for diverse products such as beer, petrol, breakfast cereals, sports teams, and even hedge funds. The same fascination is now inspiring a rearguard action to save tigers. Because of its wide cultural appeal, the tiger is now a flagship of all global species conservation efforts.

1.1.3 Scientific Underpinnings of Tiger Conservation

Until the 1960s, all knowledge of tiger ecology came from accounts by hunters and amateur naturalists. The first application of methods of modern wildlife biology, such as analyses of tiger scats and kills to understand their food habits or observations at baits to study tiger behavior, was by George Schaller in Central India (Schaller 1967).

Scientific tiger studies advanced greatly with the application of the newly developed radiotelemetry techniques in the early 1970s in Nepal (Sunquist 1981, Smith 1993), in India (Karanth and Sunquist 2000) and Russia (Goodrich and Miquelle 2010) in the 1990s, and in Thailand after 2000 (Simcharoen et al. 2014). These studies have generated fine-grained data on the tiger's spatial ecology, social organization, and behavior.

Application of molecular genetic techniques to tiger DNA obtained from tissue and blood samples has opened up new paths to study tiger taxonomy and evolution (Luo et al. 2004, Mondol et al. 2009b, Wilting et al. 2015). Individual identification using fecal DNA has advanced noninvasive population studies (Mondol et al. 2009a; Chap. 11).

The critical need for practically estimating wild tiger numbers with sufficient statistical rigor was addressed only in the 1990s, with the availability of inexpensive, rugged camera traps activated by tiger movement (Karanth 1995). Such traps could obtain "samples" of tiger photos from wild populations, enabling identification of individuals from their unique stripe patterns. In combination with capture–recapture statistical models (see Chaps. 9 and 10), photographic "capture histories" of individuals were obtained. These enabled rigorous estimation of tiger numbers (Karanth and Nichols 1998).

Many photographic capture–recapture studies have been conducted across the tiger's range, for example, Karanth et al. (2004a, b) and Jhala et al. (2011, 2015) in India, Simcharoen et al. (2007) in Thailand, Rayan and Mohamad (2009) in Malaysia, Sunarto et al. (2013) in Indonesia, Thapa and Kelly (2016) in Nepal, and Xiao et al. (2016) in China. Systematic, long-term camera trap studies using "open-model" analyses in India (Karanth et al. 2006) and Thailand (Duangchantrasiri et al. 2016) have enabled even the estimation of difficult parameters such as rates of survival, recruitment, and transience, providing a comprehensive understanding