

Estimating the abundance of Nepal's largest population of tigers *Panthera tigris*

JHAMAK B. KARKI, B. PANDAV, S. R. JNAWALI, R. SHRESTHA, N. M. B. PRADHAN,
B. R. LAMICHANE, P. KHANAL, N. SUBEDI and Y. V. JHALA

Abstract Information on the abundance of tigers *Panthera tigris* is essential for effective conservation of the species. The main aim of this study was to determine the status of tigers in Chitwan National Park, Nepal, including the Churia hills, using a camera-trap based mark–recapture abundance estimate. Camera traps ($n = 310$) were placed in an area of 1,261 km² from 20 January to 22 March 2010. The study area was divided into three blocks and each block was trapped for 19–21 days, with a total effort of 3,582 man-days, 170 elephant-days and 4,793 camera-trap nights. The effectively camera-trapped area was 2,596 km². Camera stations were located 1.5–2 km apart. Sixty-two tigers (age ≥ 1.5 years), comprising 15 males, 41 females and six of unidentified sex, were identified from 344 photographs. The heterogeneity model Mh (jackknife) was the best fit for the capture history data. A capture probability (\hat{p}) of 0.05 was obtained, generating a population estimate (\hat{N}) of $125 \pm \text{SE } 21.8$ tigers. The density of tigers in the area, including Churia and Barandabhar (buffer zone forest linked with mid hill forest), was estimated to be $4.5 \pm \text{SE } 0.35$ tigers per 100 km², using a Bayesian spatially explicit capture–recapture model in *SPACECAP*. Our study showed the use of Churia by tigers and we therefore conclude that the Chitwan tiger population serves as a source to maintain tiger occupancy of the larger landscape that comprises Chitwan National Park, Parsa Wildlife Reserve, Barandabhar buffer zone, Someswor forest in Nepal and Valmiki Tiger Reserve in India.

Keywords Camera trap, capture–recapture, Churia, Nepal, *Panthera tigris*, tiger

Introduction

The tiger *Panthera tigris* is an umbrella species for the protection of biodiversity in forested ecosystems in Asia (Dinerstein et al., 2007). Despite various efforts to protect tigers by range states and global conservation partners, their numbers declined by >96% during 2000–2010 (GTRP, 2010). The decline has been caused by illegal trading of tiger parts, habitat loss, loss of prey species, and conflict with humans over livestock. During 1996–2006 the species' range was reduced by 41% (Dinerstein et al., 2007), and a scenario projecting habitat loss in Tiger Conservation Landscapes suggests a possible further reduction of 43% during the coming decade (Wikramanayake et al., 2010).

Tigers are charismatic animals and are the focus of human attention for many reasons. They compete and conflict with humans for food and space and have done so across both evolutionary and historical time scales (Inskip & Zimmermann, 2008). Cultural perceptions of tigers are shaped by factors as diverse as fear, admiration and superstition, and by the utilitarian values of meat, pelts and tourism potential. Thus, because of the tiger's cultural and utilitarian value, the public predominantly has a positive attitude towards tiger conservation despite the occurrence of conflict where people reside close to tiger habitat (Karanth & Chellam, 2009).

Across tiger range states there remain 43 source sites, which have the potential to maintain > 25 breeding females. These source sites are embedded in larger landscapes with the potential to maintain > 50 breeding females. Together, these sources hold 70% of the current tiger population in a mere 6% of the recent range (Walston et al., 2010). If connectivity between adjacent tiger conservation landscapes could be created and conserved the habitat range could increase to 10% of its historical extent, from 7% in 2006 (Wikramanayake et al., 2010).

The forests of lowland Nepal and northern India were once continuous along the base of the Himalayas and supported dense populations of tigers and their prey (Seidensticker, 2010). In this area Chitwan National Park is home to one of three isolated tiger populations in Nepal (Smith et al., 1998), which has c. 3,000 km² of tiger habitat (including Parsa Wildlife Reserve, Barandabhar buffer zone forest, Someswor forest in Nepal and Valmiki Tiger Reserve in India) and is an important source population within the Terai Arc Landscape (Walston et al., 2010).

JHAMAK B. KARKI (Corresponding author) Department of National Parks and Wildlife Conservation, P.O. Box 860, Babarmahal, Kathmandu, Nepal. E-mail jbkarki@gmail.com

B. PANDAV and Y. V. JHALA Wildlife Institute of India, Dehradun, Uttarakhand, India

S. R. JNAWALI, B. R. LAMICHANE and N. SUBEDI National Trust for Nature Conservation, Lalitpur, Nepal

R. SHRESTHA, N. M. B. PRADHAN and P. KHANAL WWF Nepal Programme, Kathmandu, Nepal

Received 8 August 2012. Revision requested 18 October 2012.

Accepted 4 March 2013. First published online 30 October 2013.

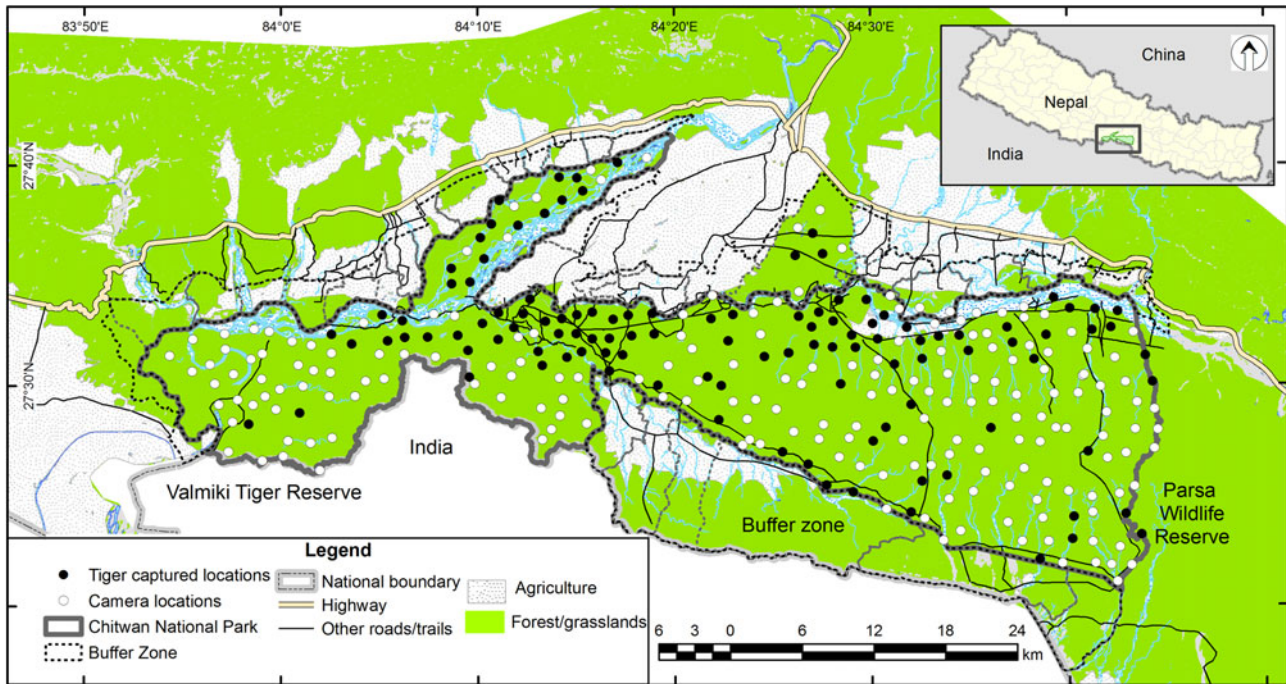


Fig. 1 Camera-trap stations in Churia hills and flood-plain habitat of Chitwan National Park. The rectangle on the inset indicates the location of the main map in Nepal.

Previous investigations of tiger status in Nepal were primarily based on radio-telemetry (Sunquist, 1981; Smith, 1993; Smith et al., 1999), pugmark surveys (McDougal, 1999) and limited camera-trap surveys (Barlow et al., 2009). Although these methods can provide estimates of population size they do not deal explicitly with the two key issues of animal population estimation: incomplete spatial sampling of the area of interest and incomplete detection of animals, even within the area that is sampled. It is now recognized that population sampling approaches that deal explicitly with these problems by employing appropriate statistical models are essential for robust estimation of animal abundance (Seber, 1982; Williams et al., 2002; Thompson, 2004). A capture–recapture framework based on a spatially explicit approach overcomes these issues (Efford, 2009; Royle et al., 2009; Singh et al., 2010). In this study we used camera-trap-based mark–recapture in a closed-population framework to assess the tiger population in Chitwan National Park.

Study area

Chitwan National Park (Fig. 1) was the first national park established in Nepal, in 1973. It is a world heritage site and an important tiger conservation landscape (Dinerstein et al., 2007), situated in the south central lowlands in the Inner Terai. The Park lies between the Siwalik (Churia) Outer Range and the Mahabharat Range. It is covered by forest (80%), grassland (12%), exposed surfaces (5%) and water bodies (3%; Thapa, 2011). The Narayani River marks the

western boundary of the Park, Rapti River marks the northern boundary, Harda River and forest of the Parsa Wildlife Reserve mark the eastern boundary, and Reu River and the border with India along the Valmiki Tiger Reserve mark the southern boundary. The mean monthly maximum and minimum temperatures are 24–38 °C and 11–26 °C, respectively. For 2004–2007 the mean annual rainfall was 2,437 mm per year. More than 50 mammal species, > 526 bird species, 49 reptile and amphibian species, 156 butterfly species, and 120 fish species have been reported in the Park (Gurung, 1983; Edds, 1986; BPP, 1995; Shah & Tiwari, 2004; Baral & Upadhyay, 2006; Bhujju et al., 2007). The major carnivore species present include tiger, leopard *Panthera pardus*, wild dog *Cuon alpinus*, jungle cat *Felis chaus*, fishing cat *Prionailurus viverrinus*, toddy cat *Paradoxurus hermaphroditus*, and jackal *Canis aureus*. Prey species include chital *Axis axis*, sambar *Rusa unicolor*, wild pig *Sus scrofa*, hog deer *Heylaphus porcinus*, barking deer *Muntiacus muntjak*, gaur *Bos gaurus*, nilgai *Boselaphus tragocamelus*, rhesus macaque *Macaca mulatta*, common langur *Semnopithecus entellus*, black-naped hare *Lepus nigricollis*, porcupine *Hystrix indica*, four-horned antelope *Tetracerus quadricornis*, one-horned rhinoceros *Rhinoceros unicornis*, and Asian elephant *Elephas maximus*.

Methods

The camera-trap survey was conducted in three blocks of 414–433 km², covering a total area of 1,278 km². Each block was camera-trapped for 19–21 days between 20 January and

22 March 2010. Camera-trapping was employed (Karanth, 1995; Karanth & Nichols, 1998; Karanth et al., 2001; O'Brien et al., 2003; Kawanishi & Sunquist, 2004; Wegge et al., 2009) to estimate the tiger population in a closed-population framework (Otis et al., 1978; White et al., 1982). Between 7 December 2009 and 6 January 2010 we conducted a preliminary sign survey in the Churia region by walking most of the available trails, ridges and river beds. We selected potential sites for cameras along sections of the trail or river bed with tiger signs (pug marks, scats, scrapes, claw marks), in passages between hills, and on narrow trails leading to ridge lines from river beds or valleys. We plotted these sites and similar sites identified in previous camera-trapping surveys in the flood plain (Karki et al., 2009), along with altitude, aspect and substrate, in a geographical information system. The final selection of camera locations was based on adequate trap spacing, ease of access, availability of camping sites and a sampling effort that covered all areas where tigers were likely to occur (Karanth & Nichols, 2002).

We identified 310 camera-trap locations, with a spacing of 1.5–2 km (Wegge et al., 2004), following guidelines for survey design (Karanth & Nichols, 1998, 2002; Karanth et al., 2001) and considering the results of our sign survey. The Park and Barandabhar buffer zone forest were divided into three blocks to cover the 310 sites, with 107 pairs of camera traps. Camera traps were deployed for a total of 62 days, with 21 days and 98 traps in block I, 19 days and 107 traps in block II and 22 days and 105 traps in block III. Each sampling event (Otis et al., 1978) was for a duration of 24 hours, except at nine sites in block III, where sampling was for 16 hours (16.00–08.00). Moultrie (Moultrie Feeders, Alabaster, USA) and Stealth Cam (Stealth Cam, Bedford, USA) camera traps were checked once every 2–3 days and Trail Master TM1550 cameras (Goodson Associates Inc. Kansas, USA) were checked every day. Memory cards were viewed at the site during every visit and were replaced if a tiger was recorded, to minimize the loss from damage by wild elephants or theft by poachers. Photographic films were sent for processing and scanning and a digital ID was prepared for all digital photographs.

Ninety-seven photographs of both sides of an animal and 76 left-flank photographs were used to identify individual tigers from their unique stripe patterns (Karanth & Nichols, 1998). Identification was carried out individually by three trained personnel, who then reached a consensus on the identity of each tiger.

We developed capture histories (Otis et al., 1978; Nichols, 1992) on the basis of the stripe patterns (Schaller, 1967; McDougal, 1977; Karanth, 1995). The tiger population was estimated in a closed-population mark–recapture framework in *CAPTURE* (Rexstad & Burnham, 1991). *CAPTURE* uses a series of discriminant function tests to compare the null (M_0), time effects (M_t), behaviour effects (M_b) and

TABLE 1 Parameters for our survey of the tiger *Panthera tigris* population in Chitwan National Park, Nepal (Fig. 1), with minimum convex polygon, number of tigers estimated by a capture–mark–recapture model with time variation, trap effort, effective trapping area based on half the mean maximum distance moved, density estimates from various models, Park area, and estimated total population.

Parameter	Value
Minimum convex polygon (km ²)	2,086
Estimated number of tigers	125 ± SE 21.8
Trap effort (days)	3,920
Effective trapping area (km ²)	2,596
Density, based on ½MMDM (per 100 km ²)	4.6 ± SE 0.8
Density, based on maximum likelihood spatially explicit capture–recapture (per 100 km ²)	2.7 ± SE 0.4
Density, based on Bayesian spatially explicit capture–recapture model (per 100 km ²)	4.5 ± SE 0.4
Park area (km ²)	932
Estimated total population	41.9

individual heterogeneity (M_h) models, and combinations of these, and rate them on a relative scale of 0 to 1.

We used two approaches to estimate tiger density: (1) the traditional approach of adding a buffer width of half the mean maximum distance moved (1/2 MMDM) by recaptured tigers to the camera-trap polygon to estimate the effectively sampled area (Karanth & Nichols, 1998), and (2) a spatially explicit approach developed by Efford (2009) and Royle et al. (2009) that estimates density directly from spatial capture histories of individual animals without the need for an ad hoc method of determining the effectively sampled area. These spatially explicit analyses were carried out using *DENSITY* (Efford, 2009) and *SPACECAP* (Singh et al., 2010). A habitat mask that removed non-tiger habitat from the sampled area was applied to both approaches for estimating tiger density.

Results

We identified 62 tigers (15 male, 41 female and six whose sex could not be determined) from 314 exposures, with a trapping effort of 3,920 trap days. New individuals continued to be photographed until the 21st day after camera installation. Tigers were photographed at 106 sites, including 23 locations in the Churia hills (Fig. 1).

CAPTURE selected the jackknife model (M_h) as the best fit. There was heterogeneity in trapping probabilities (M_0 vs M_h ; $\chi^2 = 51.655$, $df = 3$, $P < 0.001$). As our sampling duration was short (62 days) in comparison to the lifespan of tigers, we could therefore assume demographic closure. We could also reasonably assume geographical closure over this short sampling duration as we camera-trapped the entire habitat occupied by tigers in this landscape.

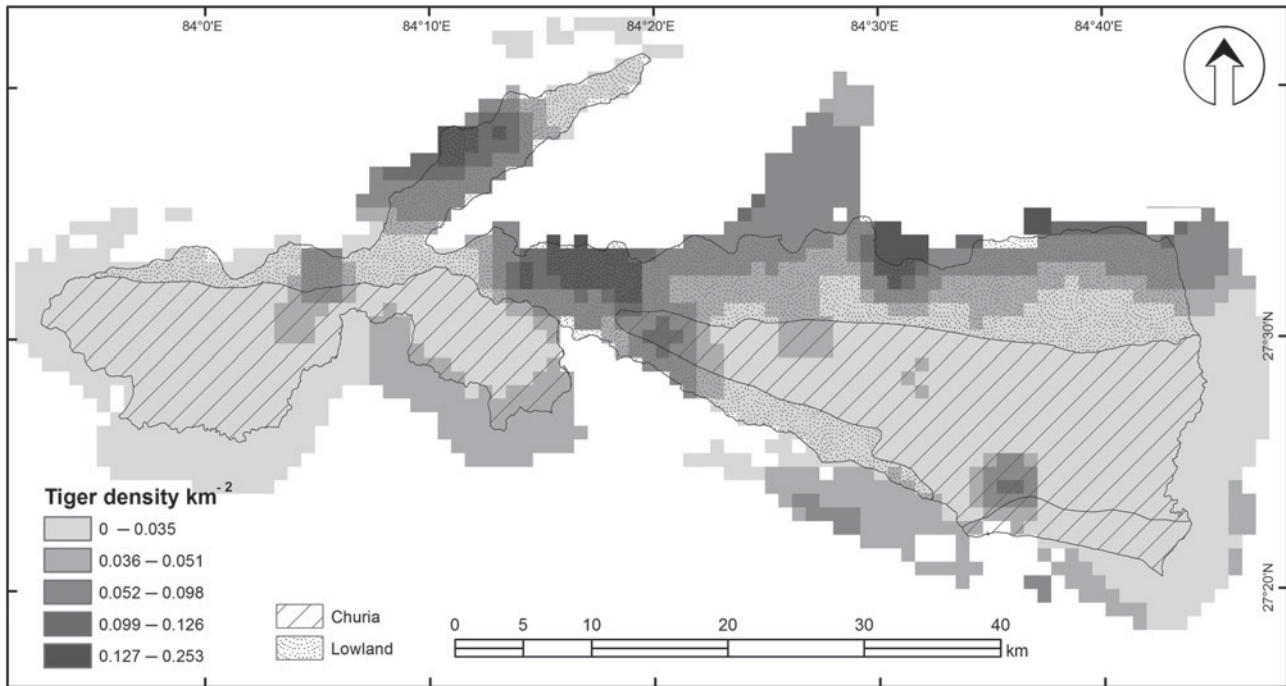


FIG. 2 Tiger density in the Churia hills and lowland habitat in Chitwan National Park.

The model M_h estimated a mean capture probability of 0.057 and the population size (\hat{N}) was estimated to be $125 \pm \text{SE } 21.8$ tigers (95% CI 95–183). The effectively sampled area with habitat mask was estimated to be $2,596 \text{ km}^2$ by the $1/2$ MMDM method and the tiger density was estimated to be $4.6 \pm \text{SE } 0.84$ tigers per 100 km^2 , whereas *SPACECAP* estimated the tiger density to be $4.5 \pm \text{SE } 0.4$ tigers per 100 km^2 and *DENSITY* estimated $2.3 \pm \text{SE } 0.32$ tigers per 100 km^2 (Table 1). There was a clear gradient in tiger density, with a higher density in the flood plain habitat compared to the Churia hills (Fig. 2).

Discussion

Capture–recapture analysis using camera-trap photographs has been used in other studies to estimate tiger density in India (Jhala et al., 2011a,b; Karanth, 1995; Karanth & Nichols, 1998, 2000, 2002; Karanth et al., 2004a,b), Nepal (Wegge et al., 2004, 2009; Barlow et al., 2009), Indonesia (O'Brien et al., 2003), and Bhutan (Wang & McDonald, 2009). However, this study has invested one of the largest sampling efforts, involving 4,793 camera-trap nights and covering an entire tiger-occupied landscape in Nepal. This high sampling effort has yielded reasonable capture rates, given the medium density of tigers.

There has been a general tendency to use 10–15-day trapping sessions in camera-trap surveys of tigers in India (Chauhan et al., 2005; Harihar et al., 2006) and Nepal (Mishra et al., 2008; Karki et al., 2009; Wegge et al., 2009). We used trapping sessions of 19–21 days in three blocks.

Three, four, one, two and one new tigers were photographed on the 17th, 18th, 19th, 20th and 21st days of a session, respectively, which suggests that longer sessions may be needed to obtain sufficient recaptures for precise results, particularly in mixed terrain such as that of Chitwan, with undulating hills and tall grassland flood plains. Longer sessions were not possible in our study because of the limited number of cameras (107 pairs) and the size of the landscape being sampled. We circumvented this limitation by sampling smaller blocks of habitat for shorter duration, to ensure population closure. Ideally the entire landscape would be camera-trapped simultaneously, with more cameras and sessions.

We estimated a population of 125 tigers, with a density of 4.5 per 100 km^2 , in Chitwan. This is the highest estimate of tigers so far in the Park and compares to estimates of 26–36 in 1978 (Tamang, 1982), 65 in 1987 (Smith et al., 1987), 50 in 1998 (Smith et al., 1998), 38 in 2000 (KMTNC/NCRTC, 2001), and 91 in 2009 (Karki et al., 2009). All of these earlier studies estimated tiger numbers and densities in small areas of the Park and are therefore only partly comparable to our study, which covered the entire Park. Tiger densities reported for Chitwan have been lower than those reported for similar habitats in India. Corbett and Kaziranga Tiger Reserves in India are comparable tiger habitats to Chitwan in terms of habitat, prey availability and topography but the tiger densities reported for both these reserves are 3–5 times higher than that observed in Chitwan (Jhala et al., 2011a,b). The lower density of tigers in Chitwan is probably a result of prey depletion by subsistence and illegal poaching of tigers during the political insurgency of

1996–2006. There has been a reduction in wildlife crime since the end of this period of political unrest, as a result of improved cooperation between police, the Forest Department, national and international NGOs, local communities and district administration. Improved law enforcement and enhancement of prey species (perhaps with the re-introduction of locally extinct species such as water buffalo *Bubalis bubalis arnee* and swamp deer *Cervus duvauceli duvauceli*) could potentially result in recovery of the tiger population to match densities observed in comparable habitats in India.

A study conducted on the periphery of Chitwan National Park suggests that tigers can coexist with humans at fine spatial scales (Carter et al., 2012). Our data, which cover the entire Park, including the study site of Carter et al. (2012), suggest that tigers and humans often co-occur on the periphery of large tiger-occupied areas, the cores of which are devoid of human settlements. This is the basic concept of zonation and management of protected areas for tigers: core areas are maintained free of human settlements to foster high tiger densities and in buffer zones spill-over tigers coexist with humans (Fig. 2). Buffer zones are managed to minimize land uses that are not compatible with the conservation objective of the protected area. However, it seems unlikely that areas of tiger–human coexistence would arise independently, without a human-settlement-free core zone that harbours a large source population of tigers (Gopal et al., 2007).

Twelve tigers (five female, three male and four whose sex could not be determined) were photographed exclusively in the Churia hills, indicating that this area, although it has a lower tiger density than the floodplain habitat (Fig. 2), is an important tiger habitat. Churia experiences low disturbance by humans and is therefore a comparatively less disturbed habitat for wild prey species such as sambar, wild pig, chital, barking deer, serow *Capricornis thar*, goral *Naemorhedus goral*, and gaur. It has a cooler microenvironment during the summer, and water is available from perennial rivers, making the habitat suitable for tigers and their prey. Chitwan National Park is an important source of tigers in the Eastern Terai Arc complex, from where tigers disperse south to Valmiki Tiger Reserve in India (Jhala et al., 2008, 2011b; Sharma et al., 2011), east to Parsa Wildlife Reserve, and west to the Dumkibash forest of Nepal. The Churia hills are the conduit for these dispersing tigers, providing rugged vegetated terrain, with prey and water, that forms ideal corridor habitats. The Churia hills also provide space for the expanding tiger population of Chitwan National Park. A landscape that provides a large area for tigers is important for its long-term persistence (Walston et al., 2010; Wikramanayake et al., 2011). The existing continuous tiger habitat, encompassing Chitwan, Parsa, Barandabhar, Someswor and Valmiki (Fig. 1), covers an area of c. 3,000 km². This population, if managed through transboundary

initiatives with India, could ensure long-term persistence of tigers for the entire landscape and assist in the goal of doubling tiger numbers globally by 2020 (GTRP, 2010).

The information generated from this survey will serve as a basis for future population monitoring and management planning and will facilitate objective assessment of the effectiveness of conservation interventions. A press release issued by the Department of National Parks and Wildlife Conservation on 29 July 2013 reported 120 individual tigers (95% CI 98–123), with a density of 3.84 tigers per 100 km², which is close to our findings in 2009.

Acknowledgements

Funding for this study was provided by the Save the Tiger Fund, the US Fish and Wildlife Service, WWF–US, WWF–UK and WWF–International. The field work was jointly undertaken by the Department of National Parks and Wildlife Conservation, the National Trust for Nature Conservation and WWF–Nepal. We acknowledge personnel from Chitwan National Park and the Nepalese Army, nature guides, university and local volunteers, Terai Arc Landscape, National Trust for Nature Conservation–Biodiversity Conservation Centre and domestic elephant staff engaged in the survey, concessionaire hotels in the Park, and local people for their assistance with this project.

References

- BARAL, H.S. & UPADHYAY, G.P. (2006) *Birds of Chitwan*, 4th edition. GoN Department of National Parks and Wildlife Conservation, Participatory Conservation Programme II and Bird Conservation Nepal, Kathmandu, Nepal.
- BARLOW, A.C.D., MCDUGAL, C., SMITH, J.L.D., GURUNG, B., BHATTA, S.R., KUMAL, S. et al. (2009) Temporal variation in tiger (*Panthera tigris*) populations and its implications for monitoring. *Journal of Mammalogy*, 90, 472–478.
- BHUJU, U.R., SHAKYA, P.R., BASNET, T.B. & SHRESTHA, S. (2007) *Nepal Biodiversity Resource Book: Protected Areas, Ramsar Sites, and World Heritage Sites*. ICIMOD, MoEST, Kathmandu, Nepal.
- BPP (BIODIVERSITY PROFILE PROJECT) (1995) *Biodiversity profile of the Terai/Siwalik physiographic zones*. Publication No. 12. Department of National Parks and Wildlife Conservation, Kathmandu, Nepal.
- CARTER, N.H., SHRESTHA, B.K., KARKI, J.B., PRADHAN, N.M.B. & LIU, J. (2012) Coexistence between wildlife and humans at fine spatial scales. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 15360–15365. <http://www.pnas.org/cgi/doi/10.1073/pnas.1210490109> [accessed on 13 October 2012].
- CHAUHAN, D.S., HARIHAR, A., GOYAL, S.P., QURESHI, Q., LAL, P. & MATHUR, V.B. (2005) *Estimating Tiger Population using Camera Traps in Ranthambore National Park*. Wildlife Institute of India, Dehradun, India.
- DINERSTEIN, E., LOUCKS, C., WIKRAMANAYAKE, E., GINSBERG, J., SANDERSON, E., SEIDENSTICKER, J. et al. (2007) The fate of wild tigers. *Biosciences*, 57, 508–514.
- EDDS, D. (1986) *The Fishes of Royal Chitwan National Park*. Department of Zoology, Oklahoma State University, Stillwater, USA.

- EFFORD, M. (2009) *DENSITY 4.4.1.2 Spatially Explicit Capture-recapture*. University of Otago, Dunedin, New Zealand.
- GOPAL, R., SINHA, P.R., MATHUR, V.B., JHALA, Y.V. & QURESHI, Q. (2007) *Guidelines for preparation of Tiger Conservation Plan*. A technical document of the National Tiger Conservation Authority. Ministry of Environment & Forests, Government of India, New Delhi, India.
- GTRP (GLOBAL TIGER RECOVERY PROGRAM) (2010) *Global Tiger Recovery Program 2010–2022*. http://www.globaltigerinitiative.org/download/St_Petersburg/GTRP_Nov11_Final_Version_Eng.pdf [accessed October 2012].
- GURUNG, K.K. (1983) *Heart of the Jungle: the Wildlife of Chitwan, Nepal*. Andre Deutsch, London. pp. 197.
- HARIHAR, A., PANDAV, B. & GOYAL, S. P. (2006) *Monitoring tiger and its prey in Chilla Range, Rajaji National Park, Uttaranchal, India*. Research Report No. 06/001. Wildlife Institute of India, Dehradun, India.
- INSKIP, C. & ZIMMERMANN, A. (2008) Human-felid conflict: a review of patterns and priorities worldwide. *Oryx*, 43, 18–34.
- JHALA, Y.V., GOPAL, R., & QURESHI, Q. (eds) (2008) *Status of Tigers, Co-predators and Prey in India*. National Tiger Conservation Authority, New Delhi, India and Wildlife Institute of India, Dehradun, India.
- JHALA, Y.V., QURESHI, Q. & GOPAL, R. (2011a). Can the abundance of tigers be assessed from their signs? *Journal of Applied Ecology*, 48, 14–24.
- JHALA, Y.V., QURESHI, Q., GOPAL, R. & SINHA, P.R. (eds) (2011b) *Status of the Tigers, Co-predators, and Prey in India, 2010*. National Tiger Conservation Authority, New Delhi, India and Wildlife Institute of India, Dehradun, India.
- KARANTH, K.U. (1995) Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological Conservation*, 71, 333–338.
- KARANTH, K.U. & CHELLAM, R. (2009) Carnivore conservation at the crossroads. *Oryx*, 43, 1–2.
- KARANTH, K.U. & NICHOLS, J.D. (1998) Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, 79, 2852–2862.
- KARANTH, K.U. & NICHOLS, J.D. (2000) *Ecological status and conservation of tigers in India*. Final technical report to the Division of International Conservation, US Fish and Wildlife Service, Washington, DC and Wildlife Conservation Society, New York, USA. Centre for Wildlife Studies, Bangalore, India.
- KARANTH, K.U. & NICHOLS, J.D. (eds) (2002) *Monitoring Tigers and their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia*. Centre for Wildlife Studies, Bangalore, India.
- KARANTH, K.U., BHARGAV, P. & KUMAR, S. (2001) *Karnataka Tiger Conservation Project*. Wildlife Conservation Society, New York, USA.
- KARANTH, K.U., NICHOLS, J.D., KUMAR, N.S., LINK, W. & HINES, J. (2004a). Tigers and their prey: Predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 4854–4858.
- KARANTH, K.U., CHUNDAWAT, R.S., NICHOLS, J.D. & KUMAR, N.S. (2004b). Estimation of tiger densities in the tropical dry forest of Panna, Central India, using photographic capture-recapture sampling. *Animal Conservation*, 7, 285–290.
- KARKI, J.B., JNAWALI, S.R., SHRESTHA, R., PANDEY, M.B., GURUNG, G. & THAPA (KARKI), M. (2009) *Tigers and their Prey Base Abundance in the Terai Arc Landscape, Nepal*. Department of National Parks and Wildlife Conservation and Department of Forests, Kathmandu, Nepal.
- KAWANISHI, K. & SUNQUIST, M.E. (2004) Conservation status of tigers in a primary rainforest of Peninsular Malaysia. *Biological Conservation*, 120, 329–344.
- KMTNC/NCRTC (KING MAHENDRA TRUST FOR NATURE CONSERVATION/NEPAL CONSERVATION AND RESEARCH TRAINING CENTRE) (2001) *Tiger monitoring in and around RCNP*. Final report submitted to WWF–Nepal, Kathmandu, Nepal.
- MCDUGAL, C. (1977) *The Face of the Tiger*. Rivington Books, London, UK.
- MCDUGAL, C. (1999) You can tell some tigers by their tracks with confidence. In *Riding the Tiger: Tiger Conservation in Human-dominated Landscapes* (eds J. Seidensticker, S. Christie & P. Jackson), p. 190. Cambridge University Press, Cambridge, UK.
- MISHRA, N., KARKI, J.B., POKHAREL, C. & THAPA, K. (2008) *Tiger monitoring in Suklaphanta Wildlife Reserve*. Unpublished report for Suklaphanta Wildlife Reserve, Kanchanpur, Nepal.
- NICHOLS, J.D. (1992) Capture-recapture models: using marked animals to study population dynamics. *Bioscience*, 42, 94–102.
- O'BRIEN, T.G., KINNAIRD, M. & WIBISONO, H.T. (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, 6, 131–139.
- OTIS, D.L., BURNHAM, K.P., WHITE, G.C. & ANDERSON, D.R. (1978) Statistical inference from capture data on closed animal populations. *Wildlife Monograph*, 62, 1–135.
- REXSTAD, E. & BURNHAM, K.P. (1991) *Users Guide for Interactive Program CAPTURE*. Colorado State University, Fort Collins, USA.
- ROYLE, J.A., NICHOLS, J.D., KARANTH, K.U. & GOPALASWAMY, A.M. (2009) A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology*, 46, 118–127.
- SCHALLER, G. (1967) *The Deer and the Tiger*. University of Chicago Press, Chicago, USA.
- SEBER, G.A.F. (1982) *The Estimation of Animal Abundance and Related Parameters*. Macmillan, New York, USA.
- SEIDENSTICKER, J. (2010) Saving wild tigers: a case study in biodiversity loss and challenges to be met for recovery beyond 2010. *Integrative Zoology*, 5, 283–299.
- SHAH, K.B. & TIWARI, S. (2004) *Herpetofauna of Nepal: A Conservation Companion*. IUCN, Kathmandu, Nepal.
- SHARMA, R., STUCKAS, H., BHASKAR, R., KHAN, I., GOYAL, S.P. & TIEDEMANN, R. (2011) Genetically distinct population of Bengal tiger (*Panthera tigris tigris*) in Terai Arc Landscape (TAL) of India. *Mammalian Biology*, 76, 484–490.
- SINGH, P., GOPALASWAMY, A.M., ROYLE, A.J., KUMAR, N.S. & KARANTH, K.U., MUKHERJEE, S., et al. (2010) SPACECAP—A Program to Estimate Animal Abundance and Density using Spatially Explicit Capture-Recapture.
- SMITH, J.L.D. (1993) The role of dispersal in structuring the Chitwan tiger population. *Behavior*, 124, 165–195.
- SMITH, J.L.D., WEMMER, C. & MISHRA, H.R. (1987) A tiger geographic information system: the first step in global conservation strategy. In *Tiger of the World: the Biology, Biopolitics, Management and Conservation of an Endangered Species* (eds R.L. Tilson & U.S. Seal). Noyes Publications, Park Ridge, USA.
- SMITH, J.L.D., AHEARN, S.C. & MCDUGAL, C. (1998) Landscape analysis of tiger distribution and habitat quality in Nepal. *Conservation Biology*, 12, 1338–1346.
- SMITH, J.L.D., MCDUGAL, C., AHEARN, S.C., JOSHI, A. & CONFORTI, K. (1999) Metapopulation structure of tigers in Nepal. In *Riding the Tiger: Tiger Conservation in Human-dominated Landscapes* (eds J. Seidensticker, S. Christie & P. Jackson). Cambridge University Press, Cambridge, UK.

- SUNQUIST, M.E. (1981) The social organization of tigers (*Panthera tigris*) in Royal Chitwan National Park, Nepal. *Smithsonian Contribution to Zoology*, 336, 1–98.
- TAMANG, K.M. (1982) *The status of the tiger (Panthera tigris) and its impact on principal prey populations in Royal Chitwan National Park, Nepal*. PhD thesis. Michigan State University, East Lansing, USA.
- THAPA, T. (2011) *Habitat suitability evaluation for leopard (Panthera pardus) using remote sensing and GIS in and round Chitwan National Park, Nepal*. PhD thesis. Saurashtra University, Rajkot, India.
- THOMPSON, W.L. (2004) *Sampling Rare or Elusive Species: Concepts and Techniques for Estimating Population Parameters*. Island Press, Washington, DC, USA.
- WALSTON, J., ROBINSON, J.G., BENNETT, E. L., BREITENMOSE, U., DA FONSECA, G.A.B., GOODRICH, J. et al. (2010) Bringing the tiger back from the brink—the six percent solution. *PLoS Biology*, 8, e1000485. doi:10.1371/journal.pbio.1000485.
- WANG, S.W. & MACDONALD, D.W. (2009) The use of camera traps for estimating tiger and leopard populations in the high-altitude mountains of Bhutan. *Biological Conservation*, 142, 606–613.
- WEGGE, P., POKHAREL, C. & JNAWALI, S.R. (2004) Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. *Animal Conservation*, 7, 251–256.
- WEGGE, P., ODDEN, M., POKHREL, C.P. & STORAAS, T. (2009) Predator–prey relationships and responses of ungulates and their predators to the establishments of Protected Areas: a case study of tigers, leopards and their prey in Bardia National Park, Nepal. *Biological Conservation*, 142, 189–202.
- WHITE, G.C., ANDERSON, D.R., BURNHAM, K.P. & OTIS, D.L. (1982) *Capture–recapture and Removal Methods for Sampling Closed Populations*. Los Alamos National Laboratory, New Mexico, USA.
- WIKRAMANAYAKE, E., DINERSTEIN, E., FORREST, J., LOUCKS, C., SEIDENSTICKER, J., KLENZENDORF, S. et al. (2010) Roads to recovery or catastrophic loss: How will the next decade end for wild tigers? In *Tigers of the World: the Science, Politics, and Conservation of Panthera Tigris*, 2nd edition (eds R. Tilson & P. Nyhus). Elsevier/Academic Press, Oxford, UK.
- WIKRAMANAYAKE, E., DINERSTEIN, E., SEIDENSTICKER, J., LUMPKIN, S., PANDAV, B., SHRESTHA, M. et al. (2011) A landscape-based conservation strategy to double the wild tiger population. *Conservation Letters*, 4, 219–227.
- WILLIAMS, B.K., NICHOLS, J.D. & CONROY, M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, San Diego, USA.

Biographical sketches

JHAMAK B. KARKI has served 23 years in protected-area conservation and management within the Department of National Parks and Wildlife Conservation in Nepal. B. PANDAV is a tiger expert, with research interests in tiger, prey and landscape management. S. R. JNAWALI managed field programmes for Nepal's National Trust for Nature Conservation for over 2 decades. R. SHRESTHA was a conservation biologist and worked in Nepal and the Eastern Himalayas. N. M. B. PRADHAN is a conservation biologist and has served more than 2 decades in the Department of National Parks and Wildlife Conservation, managing protected areas. B. R. LAMICHANE has been actively engaged in research implementation activities for Chitwan National Park. P. KHANAL works on biodiversity conservation and livelihood improvement programmes in Nepal. N. SUBEDI runs biodiversity research and monitoring programmes in Nepal's Terai region. Y. V. JHALA coordinates the implementation of tiger monitoring studies for the Government of India.