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VIEWPOINT

Defensible Inference: Questioning Global Trends in Tiger Populations

Abishek Harihar^{1,2}, Pranav Chanchani^{3,4}, Milind Pariwakam⁵, Barry R. Noon^{3,4}, & John Goodrich¹

¹ Panthera, 8 West 40th Street, 18th Floor, NY, 10018, USA

² Nature Conservation Foundation, 3076/5, IV Cross, Gokulam Park, Mysore, 570002, Karnataka, India

³ Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO, 80523, USA

⁴ Colorado State University, Fort Collins, CO, 80523, USA

⁵ Wildlife Conservation Trust, 11th floor, Mafatlal Center, Nariman point, Mumbai, 400021, Maharashtra, India

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Correspondence

Abishek Harihar, Panthera, 8 West 40th Street, 18th Floor, NY 10018, USA. Tel: +1(646) 786 0400 E-mail: harihar.abishek@gmail.com

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Reports claim a dramatic 22% increase in wild-tiger Panthera tigris abundance within 5 years (3,200-3,890 individuals; Associated Press 2016). Such significant population increases could potentially change the status of tigers from endangered to vulnerable on the IUCN Red List, and substantially contribute to the global target of doubling wild-tiger numbers by 2022 (GTRP 2010). While this purported increase has been attributed to improved conservation practices in India, Nepal, Bhutan, and Russia, the claimed increase is questionable given unreported methodology (Russia), lack of comparable baselines (Bhutan and Russia), and failure to adjust population estimates to account for expanded survey effort and methodological changes (Nepal and India). The latter source of bias requires explanation as it accounts for a large portion of the assumed population increase.

Photographic capture–recapture sampling of tigers from 2013 to 2015 yielded the most comprehensive country-wide estimates of tiger abundance to date for Bhutan, Nepal, and India (Dhakal *et al.* 2014; DoFPS 2015; Jhala *et al.* 2015). These estimates suggest 63% and 30% increases in Nepal and India's tiger populations since 2009 and 2010, respectively. However, there have concurrently been significant changes in the sampling frame (area sampled and thus target populations) and inconsistent modeling procedures, making temporal comparisons invalid for both countries. To assess the validity of purported increases in Nepal and India, we compared survey effort (number of trap-locations and trap-nights), minimum population sizes (number of unique photo-captured individuals), sampling duration, and density estimates from camera-trapping sites (Tables S1 and S2; Karki *et al.* 2009; Jhala *et al.* 2011b, 2015; Dhakal *et al.* 2014).

Apparent increases in population size correspond with 47% (+316) and 538% (+7,642) increases in traplocations and 44% (+4,485) and 301% (+240,691) increases in trap-nights resulting in 65% and 144% more tigers photo-captured between consecutive surveys in Nepal and India, respectively. Both countries added new

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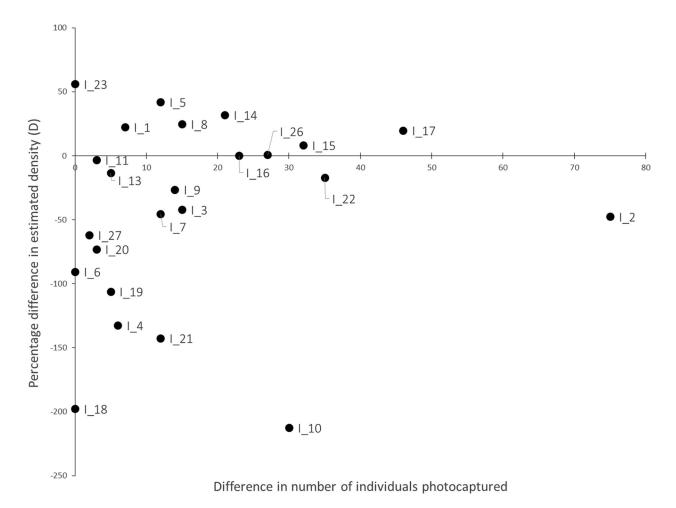


Figure 1 The difference in the number of individual tigers photo-captured (x-axis) versus percent difference in estimated density (y-axis) using a maximum likelihood spatially explicit capture–recapture formulation (MLSECR), between 2014 and 2010 at sites in India. Note that three sites, Kanha (I_12), Pakke (I_24), and Nameri (I_25) Tiger Reserves, could not be directly compared as sampling frame in 2010 differed significantly at these sites. For site identification numbers, refer Table S2.

sites (1 in Nepal; 32 in India) and expanded survey effort in previously sampled sites, each of which could result in increased abundance estimates regardless of population trend. Increases in the area sampled with cameras over time violate the critical requirement that the sample frame remains constant over time (Reynolds 2012). While spatial capture-recapture models are relatively robust to variations in area sampled, to infer trend, it is critical that the state space (the region over which individual animals exposed to detectors) remains similar (Royle et al. 2014). Importantly, neither the India nor Nepal surveys defined the target population(s) or indicated how they may have changed over time. The effects of increased survey effort resulted in lower estimates of tiger density in 15 of 24 Indian sites sampled in both years even though the number of individuals photo-captured was higher in most sites (Figure 1). Such changes often occur when the initial study areas are centered on areas of known tiger occurrence and subsequently expanded to include areas of lower density. Additionally, population estimates may be positively biased as sampling durations at 29 of 59 sites (with known sampling dates) exceeded the recommended 45–60 days (Tables S1–S3), violating the assumption of temporal closure (Kendall 1999; Karanth & Nichols 2002).

Finally, comparisons between abundance and density estimates across years are complicated by changes in analytical methods. In Nepal, 2009-estimates were based on nonspatial capture–recapture models, while, in 2013, spatial capture–recapture models were used (Karki *et al.* 2009; Dhakal *et al.* 2014). Methodology for developing country-wide estimates was not described, but appears to have been derived as a sum of all site-based estimates (Table S1). Methodological concerns also dominate estimates of tiger abundance in India. For example, claims of a 16% increase in tiger numbers between 2006 and 2010 by the Indian government were criticized owing to lack of methodological details (Karanth et al. 2011). In 2010, India used a double-sampling method to calibrate an index of tiger abundance (tiger sign) with a smallscale, rigorous estimate of abundance (Jhala et al. 2011a, 2011b). The method has been criticized because it yields poor inferences unless the survey design ensures that all sampling process parameters lie within a limited range (Gopalaswamy et al. 2015). In contrast, 2014-estimates were derived from models that predicted the locations of tiger activity range centers based on capture-recapture data and environmental covariates (Jhala et al. 2015). Without across-model calibration, it is impossible to disentangle true changes in abundance from those that are an artifact of changes in methods. The application of more recent methods to extrapolate tiger density using occupancy data needs to be explored (Dey et al. 2017).

Based on the aforementioned issues, we conclude that it is impossible to infer country-wide and global increase in tiger abundance. We believe the way forward is to shift the emphasis of monitoring from 4-year national estimates to annual or biennial, intensive site-level estimates based on consistent survey and analytical methods, and periodic meta-analysis of these data at relevant spatial scales. This shift will facilitate understanding of complex population dynamics that may underlie stable population sizes (Karanth et al. 2006; Sharma et al. 2014). A good example of a protocol for the implementation, meta-analysis, and reporting on the status and trend of multiple populations of an imperiled species has been developed and applied to the conservation of the Northern Spotted Owl (Strix occidentalis occidentalis) (e.g., Forsman et al. 2011). At the core of the spotted owl protocol is an objective assessment of data quality and subsequent statistical analysis of the data by independent analysts.

Estimates of population trend are essential to assessing the success or failure of ongoing conservation efforts for example, assessments of conservation performance according to international criteria. However, reliable estimates of trend require close attention to elements of sample design, changes in study area boundaries, and statistical methods of abundance estimation. We applaud increased efforts to assess the status of tigers, but caution that the focus on counting "all tigers" to develop countryand range-wide population estimates has distracted from reliably measuring trends in tiger numbers, which is more informative and relevant to conservation planning.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. Comparison of effort (in terms of camera points and trap-nights), number of individuals photocaptured, sampling start and end dates, and sampling duration, estimated tiger density (per 100 km) and population size (\hat{N}) between those reported by Dhakal *et al.* (2014) for 2013 and Karki *et al.* (2009) for 2009

Table S2. Comparison of effort (in terms of camera points and trap-nights), number of individuals photocaptured, index of sampling area (minimum bounding polygon in km², 2014, and estimated sampling area in km², 2010), sampling start and end dates, and sampling duration and estimated tiger density (per 100 km) between those reported by Jhala *et al.* (2015) for 2014 and Jhala *et al.* (2011b) for 2010

Table S3. Summary of information on sampling dates and durations at camera trapping sites that are adjacent to one another reported by Dhakal *et al.* (2014) and Jhala *et al.* (2015)

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