



Setting recovery targets for a charismatic species in an iconic protected area complex: The case of tigers (*Panthera tigris*) in Chitwan–Parsa National Parks, Nepal

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Abstract

The Global Tiger Recovery Program has identified enhancing prey populations as a crucial component in achieving its target of doubling wild tiger (*Panthera tigris*) numbers, as prey density is a key determinant of tiger density. We estimate prey abundance and ecological carrying capacity (ECC) of tigers in the 1579 km² Chitwan–Parsa source site complex within a globally significant tiger conservation landscape in south-central Nepal. Surveying 605.1 km of line transects in the Terai plains and Chure hills of Chitwan–Parsa, we estimated an overall density of 55.43 (36.98–83.45) ungulates/km², and a biomass of 244,630 (151,520–334,270) kg/100 km² of five abundant ungulates. Chitwan supports 71.58 (49.02–104.71) and Parsa 30.91 (18.70–51.19) ungulates/km². The prey base can support 177 (119–263) adult tigers based on energetic requirement models. The tiger ECC was ~3.5× higher in Chitwan than in Parsa at a park level. Although opportunities for further recovery of tiger and prey through targeted habitat management exist, the current population of 170 tigers indicates that this population has likely reached its current ECC. We recommend that policymakers and park managers change focus from increasing tiger numbers to developing pre-emptive conflict mitigation strategies to allow the site to retain the successes it has realized.

KEYWORDS

distance sampling, ecological carrying capacity, line transects, prey density, recovery target

1 | INTRODUCTION

Ensuring the effective conservation and management of endangered species requires accurate and timely information on their populations' distribution, size, and limits.

This is particularly critical for large terrestrial carnivores that naturally occur at low densities in human-dominated environments and rely on conservation measures to secure and recover their populations (Estes et al., 2011; Ripple et al., 2014). Tigers, *Panthera tigris*,

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typify the problems faced by most large carnivores. With around 4000 wild tigers occupying a mere 6% of their historical range and 70% of the global population concentrated within ~40 “source sites,” the protection and effective management of these populations constitute the cornerstone of global tiger conservation strategies (Goodrich et al., 2022; Walston et al., 2010). Therefore, site-specific assessments of these source sites’ current and potential population sizes are necessary to guide conservation investment and actions (Harihar et al., 2018).

In 2010, the governments of tiger range countries committed to doubling wild tiger numbers across the range. Although countries such as India and Nepal have been making significant progress (DNPWC and DFSC, 2022; Jhala et al., 2020), there is an urgent need to estimate tigers’ Ecological Carrying Capacity (ECC) at sites to ensure that conservation goals are defined on site-specific ecological parameters. This need is acutely felt in Nepal, which supports 355 adult Bengal tigers (*P. t. tigris*, hereafter referred to as the tiger) and has exceeded its initial commitment to increasing its population to 250 individuals from a baseline of 121 (100–191) individuals in 2010 (DNPWC and DFSC, 2022; GTRP, 2010). In addition, management agencies are increasingly concerned about the escalating human-tiger conflict with limited habitat and prey availability (Aryal et al., 2016; Thapa et al., 2016).

The maximum number of individuals of a species (tigers, in this case) supported by the resources in a specified area refers to the site’s ECC. Among terrestrial carnivores, population density is positively correlated with prey availability (Carbone & Gittleman, 2002). In the case of tigers, populations within well-protected reserves are primarily regulated by prey availability, given that they are socially dominant obligate carnivores (Karanth et al., 2004). Wild ungulates, ranging in body size from 10 to 250 kg, compose the principal prey (Hayward et al., 2012). However, over 50% of ungulate species that tigers prey upon are threatened, and over 80% of these species have declined due to habitat loss and degradation, overhunting, and/or conflict with agriculturalists (Wolf & Ripple, 2016, 2017). Therefore, estimating prey abundance constitutes a crucial first step in evaluating a site’s potential to function as a source site, identifying recovery targets, and informing appropriate interventions.

In this study, we estimate prey densities and biomass in the Chitwan–Parsa source site complex within a globally significant tiger conservation landscape in south-central Nepal to determine the tiger ECC recognizing that prey densities themselves may possibly be below carrying capacity. Nonetheless, given the known relationship between prey abundance and tiger density, prey availability provides a strong foundation for determining a realistic goal for tiger densities (Karanth et al., 2004;

Miquelle et al., 2010). Using data from line-transect surveys we conducted in 2019, we estimate species-specific densities of five of the most abundant ungulates, which are also the primary prey of tigers within this complex. We then calculate the potential tiger population size that can be supported. As the source site complex is managed as two protected areas, we provide reserve-specific estimates of ungulate densities and tiger ECC. Finally, considering the debates on whether to manage for continued growth or enact appropriate management interventions to conserve and manage the population effectively, we assess the potential for increasing prey and/or tiger population size, and what potential conservation interventions may be needed for effective species conservation.

2 | METHODS

2.1 | Chitwan–Parsa complex

Chitwan–Parsa is comprised of two national parks (NP), together encompass 1579 km² (Chitwan 952 km² and Parsa 627 km²) embedded within the eastern section of the transboundary Terai Arc Landscape (TAL) of northern India and southern Nepal. This source site complex is critical for sustaining tiger population recovery in ~5000 km² of potential tiger habitat in the region (DNPWC & DFSC, 2018; Seidensticker et al., 2010; Wikramanayake et al., 2010).

The plains of east Rapti and Narayani rivers support alluvial grassland habitats comprising the genera *Saccharum*, *Themeda*, and *Imperata*, and riverine forests dominated by *Acacia catechu*, *Dalbergia sissoo*, *Trewia nudiflora*, and *Bombax ceiba*. The Chure (Shivalik) hills (ranging up to 900 m) comprise *Shorea robusta* and *Terminalia-Anogeissus*, with seasonal streams draining these slopes. Although the habitat types are similar across the two protected areas, Parsa is hillier (63%) with plains (37%) along the northern and southern boundaries. In contrast, Chitwan comprises 48% of Chure hills and 52% plains (PNP, 2018; Thapa & Kelly, 2017). The region experiences a subtropical climate with a monsoon period from June to September, followed by a cool, dry season from October to February and a hot, dry summer from March to May (Carter et al., 2015; Karki et al., 2015).

Chitwan–Parsa supports an ungulate assemblage of 10 species comprising red muntjac *Muntiacus muntjac*, Himalayan goral *Naemorhedus goral*, hog deer *Axis porcinus*, wild pig *Sus scrofa*, spotted deer *A. axis*, Himalayan serow *Capricornis thar*, sambar *Rusa unicolor*, nilgai *Boselaphus tragocamelus*, gaur *Bos gaurus* and the greater one-horned rhinoceros *Rhinoceros unicornis* (DNPWC & DFSC, 2018; Karki et al., 2015). However, given that the goral, serow, nilgai, gaur and rhino either occur at low

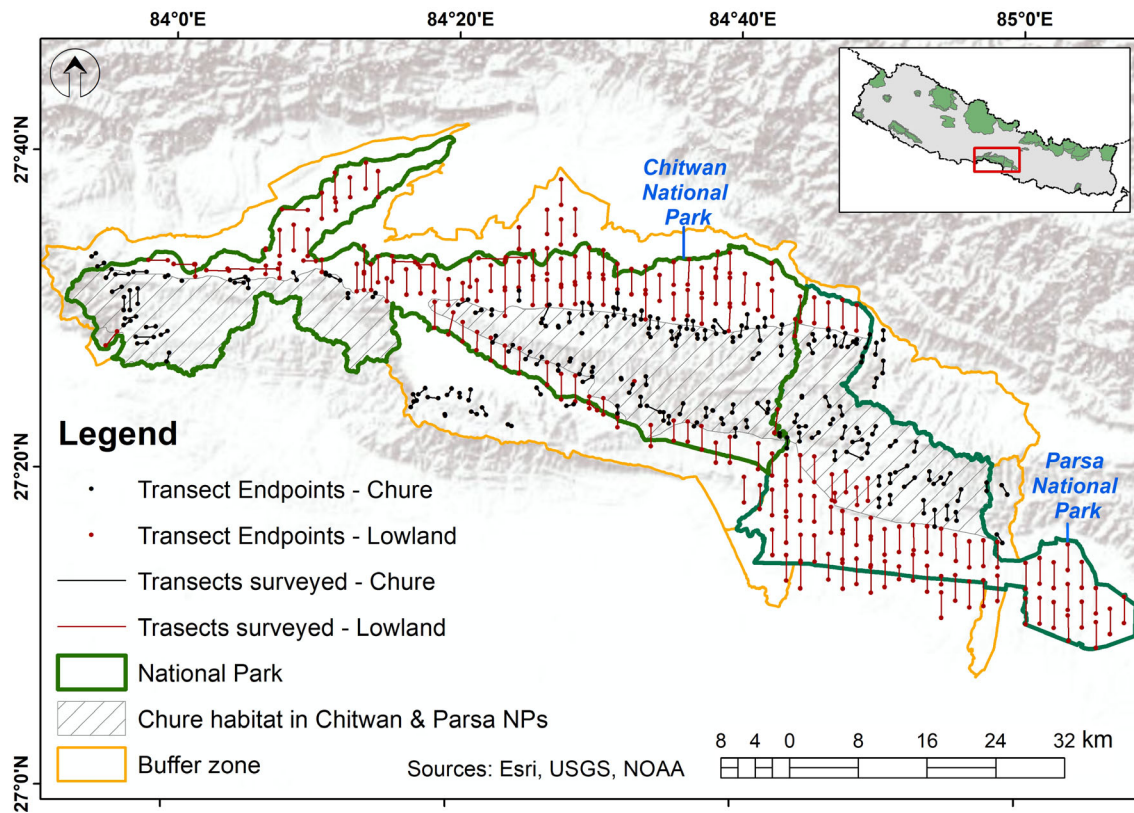


FIGURE 1 Location of Chitwan–Parsa source site in south-central Nepal, with the 302 line transects distributed across the Terai plains and Chure hills of the two protected areas.

densities and/or are not significant prey for tigers, we did not include these species in this study.

Chitwan NP, established in 1973, is Nepal's oldest NP and has been a site of significant research and conservation attention. Parsa NP was, first established as a Wildlife Reserve in 1984, then was upgraded to a NP in 2017. Since 2012, Parsa has received increased management attention leading to the relocation of villages and the subsequent recovery of tigers. In 2018 it was estimated that there were 93 (89–102) tigers in Chitwan and 18 (16–24) in Parsa (with a total of 111 adult tigers) (DNPWC & DFSC, 2018), while in the most recent survey (DNPWC and DFSC, 2022), tiger estimates are now 128 (121–40) and 41 (38–50) in Chitwan and Parsa, respectively (totaling 170 adult tigers).

2.2 | Estimating tiger prey densities and biomass

Past national tiger surveys were conducted only in the plains due to logistic constraints (Dhakal et al., 2014; Karki et al., 2009). However, Thapa and Kelly's (2017) survey of prey in the Chure hills of Chitwan suggested that the region retains prey densities capable of

supporting tiger recovery. Therefore, we carried out line-transect surveys covering the plains and hills to assess prey status and estimate the ECC for tigers across this complex. A total of 320 line transects were laid across Chitwan (106 in the Terai plains and 101 in the Chure hills) and Parsa (63 in the plains and 50 in the Chure) (Figure 1). We surveyed between April 29, 2019 and May 25, 2019, after controlled burning had removed much of the understory and increased visibility, covering a distance of 372.3 km (270.5 km in the plains and 101.8 km in the hills) in Chitwan and 232.8 km (160.9 km and 71.9 km in the plains and hills, respectively) in Parsa. The transects were laid out systematically with a random start point and north–south or east–west orientation in the plains, while in the hills, a random start point was chosen, but the direction was decided based on the terrain. Given the extreme ruggedness of the Chure hills, some areas in the central parts of the PAs were not covered. The transects in the plains were surveyed from elephant back, while the transects in the hills were surveyed on foot (Lahkar et al., 2020; Thapa & Kelly, 2017; Wegge & Storaas, 2009). The surveys were conducted in the mornings (0630–0930 h) and/or afternoons (1530–1830 h) by 10 survey teams. Each team had two observers, with one recording observations with the species name, group size,

angular distance (using a digital laser range-finder) and sighting bearing using a compass following standard protocols used in previous national assessments (Dhakal et al., 2014; DNPWC & DFSC, 2018).

We estimated the population densities of ungulates from the detection data using the program DISTANCE (Thomas et al., 2010). We expected two primary sources of heterogeneity in detection probability: one related to species and the other to the two habitat types sampled (also corresponding to the survey method). So, we conducted two sets of analyses to accommodate these variations while obtaining management-relevant estimates of ungulates in the two protected areas. Given that body size and grouping behavior influence detectability (Table S1), we first constructed species-specific detection models in the Conventional Distance Sampling (CDS) engine and derived PA-specific and habitat-specific density estimates through post-stratification. Second, a combined species dataset was analyzed for each habitat type using species as observation covariate within the multiple covariate distance sampling (MCDS) engine in the program DISTANCE. Here, we modeled species to influence the scale of the detection function but not its shape. Both global and separate species detection function estimation was also selected in the analysis, and PA-specific density estimates were derived through post-stratification. For all analyses, the smooth function of perpendicular distance from line transects was modeled using uniform, half-normal, and hazard rate key functions. Cosine, simple polynomial, and Hermite polynomial adjustment terms were included where necessary to ensure the detection function was monotonically decreasing for the CDS analyses. No adjustment terms were used in MCDS analyses. Model selection among candidate models was performed by comparing AIC (Akaike information criterion) values. Model fit was assessed using the Chi-square test statistic. Finally, the estimated prey densities were converted to biomass by multiplying estimated prey densities with $\frac{3}{4}$

of average prey body weight estimates derived from the literature (presented in Table S1) following (Hayward et al., 2007).

2.3 | Estimating tigers ecological carrying capacity

To estimate the ECC, we reviewed and used two established relationships. The first is based on prey density (Karanth et al., 2004), and the second is on prey biomass (Carbone & Gittleman, 2002). First, assuming tigers crop $\sim 10\%$ of available prey with a kill rate of ~ 1 per week, ECC was estimated from prey density (individuals/km²). Then, following the generalized scaling relationship between prey biomass and population density across the order Carnivora, which suggests that 10,000 kg of prey biomass supports 90 kg of a given carnivore species, ECC was estimated from prey biomass (kg/100 km²). In our estimates, we assumed that one adult tiger would weigh 180 kg in Nepal (Carbone & Gittleman, 2002). Therefore, 20,000 kg could support one adult tiger.

3 | RESULTS

3.1 | Ungulate prey densities and biomass

We recorded 7 ungulate species with 642 independent detections/observations across the Chitwan–Parsa source site. Spotted deer was the most sighted ungulate (34.6%; 222 independent detections), followed by Sambar (26.2%; 168), red muntjac (13.4%; 86), wild pig (12.5%; 80), and hog deer (10.9%; 70). During our surveys, Nilgai (5) and gaur (11) sightings were too few to include in further analysis (Table 1). In Chitwan, we recorded 425 independent detections of 6 ungulate species at an average

TABLE 1 The number of independent detections and individuals observed (in parentheses) of ungulate species recorded along line transects in Terai plain and Chure hills of the Chitwan–Parsa source site, 2019.

Prey size	Species	Chitwan			Parsa		
		Terai plains	Chure hills	Total	Terai plains	Chure hills	Total
Small	Barking deer	43 (55)	7 (7)	50 (62)	33 (35)	3 (3)	36 (38)
Medium	Hog deer	67 (173)	3 (4)	70 (177)	–	–	–
	Spotted deer	153 (1354)	18 (262)	171 (1616)	45 (285)	6 (27)	51 (312)
	Wild pig	20 (30)	7 (14)	27 (44)	49 (78)	4 (14)	53 (92)
Large	Nilgai	–	–	–	5 (18)	–	5 (18)
	Gaur	6 (58)	4 (25)	10 (83)	1 (1)	–	1 (1)
	Sambar	62 (108)	35 (74)	97 (182)	64 (126)	7 (11)	71 (137)

TABLE 2 Estimated individual animal density (individuals/km²) and biomass density (kg/km²) and associated 95% confidence interval for the five abundant ungulates in the Chitwan–Parsa source site in 2019.

Prey size	Species	Individual animal density			Biomass density		
		Chitwan	Parsa	Overall	Chitwan	Parsa	Overall
Small	Barking deer	3.5 (2.33–5.25)	2.69 (1.67–4.33)	3.18 (2.07–4.88)	55.12 (36.69–82.68)	42.36 (26.30–68.19)	50.05 (32.56–76.93)
Medi-um	Hog deer	5.67 (3.51–9.16)		3.42 (2.12–5.52)	182.85 (113.19–295.41)		110.24 (68.24–178.11)
	Spotted deer	51.95 (36.14–74.68)	13.96 (8.07–24.13)	36.86 (24.99–54.61)	1831.23 (1273.93–2632.47)	492.09 (284.46–850.58)	1299.47 (881.03–1924.91)
Large	Wild pig	2.81 (1.67–4.73)	9.44 (5.72–15.56)	5.44 (3.28–9.03)	67.44 (40.08–113.52)	226.56 (137.28–373.44)	130.62 (78.67–216.731)
	Sambar	7.65 (5.37–10.89)	4.82 (3.24–7.17)	6.53 (4.52–9.41)	768.82 (539.68–1094.45)	484.41 (325.62–720.58)	655.88 (454.68–945.99)
Total		71.58 (49.02–104.71)	30.91 (18.7–51.19)	55.43 (36.98–83.45)	2905.49 (2003.6–4218.5)	1245.43 (773.67–2012.8)	2246.3 (1515.2–3342.70)

Note: Refer to Table S2 for distance analysis output.

encounter rate of 1.29 detections/km, while in Parsa, we obtained 217 independent detections of 6 ungulates at an encounter rate of 0.93 detections/km. Detections were higher in the plains (85.4%) at an average encounter rate of 1.27 detections/km than in the hilly Chure habitat (14.6%, 0.54 detections/km).

From the species-specific CDS models, we estimated an overall density of 55.43 (36.98–83.45) individuals/km² for the five ungulates in the Chitwan–Parsa source site, with Chitwan supporting 71.58 (49.02–104.71) and Parsa supporting 30.91 (18.70–51.19) individuals/km² (Table 2). Spotted deer was the most abundant prey (66.5% of overall density), followed by Sambar (11.8%), wild pig (9.8%), hog deer (6.2%), and red muntjac (5.7%). The Terai plains supported around twice the density (66.19 [44.41–99.09]) compared to the Chure hills (34.8 [23.3–52.2]) (Table S2). The combined density for the five ungulates in the Chitwan–Parsa source site from the MCDS analyses was 57.19 (26.93–102.79) individuals/km², with the plains supporting higher densities than the Chure hills (Terai 66.2 [31.18–118.95]; Chure 34.81 [16.35–62.65]; Table S3). Although similar to our CDS analyses, confidence intervals from the MCDS analyses were wider.

We used prey density estimates derived from species-specific detection functions to estimate an overall prey biomass density of 224,630 (151,520–334,270) kg/100 km² in the Chitwan–Parsa source site (Table 2). Spotted deer contributed the highest proportion of biomass (53.1%), compared to Sambar (36.2%), wild pig (5.4%), hog deer (3.6%), and red muntjac (1.7%).

3.2 | Tigers' ecological carrying capacity

Based on our estimates of prey, we estimated ECCs of 177 (119–263) adult tigers based on prey biomass and 175 (117–264) adult tigers based on prey density across the source site. The tiger ECC was $\sim 3.5\times$ higher in Chitwan than in Parsa (Table 3).

4 | DISCUSSION

Our study highlights that, given prey densities estimated across the plains and hills, the Chitwan–Parsa source site in south-central Nepal can support 177 (95% CI 119–263) adult tigers, indicating that the population of 111 (105–126) estimated in 2018 was below the carrying capacity (DNPWC & DFSC, 2018). More specifically, Chitwan, with a population of 93 (89–102) in 2018, could support an additional $\sim 40\%$, while Parsa can double its tiger population from 18 (16–24) to 39 (24–64). More recently, national surveys reported that populations have recovered at these two

TABLE 3 The ecological carrying capacity of tigers ($ECC_{\text{prey biomass}}$) based on prey biomass density ($\text{kg}/100 \text{ km}^2$) and $ECC_{\text{prey density}}$ -based based on individual animal density ($\text{individuals}/\text{km}^2$), Chitwan–Parsa source site, 2019.

Site	Biomass density ($\text{kg}/100 \text{ km}^2$)	$ECC_{\text{prey biomass}}$	Individual density (ind/km^2)	$ECC_{\text{prey density}}$
Chitwan NP (952 km^2)	290,549 (200,360–421,850)	138 (95–200)	71.58 (49.02–104.71)	136 (93–199)
Parsa NP (627 km^2)	124,543 (77,367–201,280)	39 (24–63)	30.91 (18.7–51.19)	39 (23–64)
Chitwan–Parsa (1579 km^2)	244,630 (151,520–334,270)	177 (119–263)	55.43 (36.98–83.45)	175 (117–264)

sites to a total of 170 adults in the Chitwan–Parsa landscape and surrounding areas (DNPWC and DFSC, 2022), suggesting that the landscape is now likely to be close to the ECC.

The estimated prey density of 55.43 (37.05–83.58) individuals/ km^2 for Chitwan–Parsa is comparable to several source sites in the TAL, such as Bardia (65.2) and Shuklaphanta (59.98) NPs in Nepal, Rajaji (40.22), and Corbett (59.03) NPs in India, and to other alluvial grassland and moist woodland habitats, such as Kaziranga (58.1) and Manas (42.66) NPs in eastern India (Dhakal et al., 2014; Harihar et al., 2014, 2020; Karanth et al., 2004; Lahkar et al., 2020). These sites either support some of the highest recorded tiger densities globally (e.g., Corbett; $14/100 \text{ km}^2$ and Kaziranga; $13/100 \text{ km}^2$; Jhala et al., 2020) or are hosting rapid tiger population recoveries (e.g., Bardia and Rajaji; DNPWC and DFSC, 2018; Harihar et al., 2020). In our study site, Chitwan supports Nepal's largest tiger population, while Parsa has rapidly recovered in recent years (DNPWC and DFSC, 2022; Karki et al., 2015; Lamichhane et al., 2018). Together, these results highlight the critical role of sites with high prey density in supporting high-density tiger populations. Therefore, ensuring they remain secure is vital to sustaining population recovery at landscape scales. However, the source site's linear shape and the high human density surrounding the parks may limit tigers' movements and territories.

Across the source site, Chitwan's higher ungulate densities than Parsa are likely due to differences in available habitat and conservation legacy. Although forest types across the source site are similar, Chitwan comprises more extensive plains with productive grasslands and riverine forests than Parsa. In particular, 9.6% of Chitwan comprises grasslands along three major river systems and >80 permanent wetlands compared to 0.85% of Parsa comprising alluvial grasslands along the river Rapti towards the northern boundary (CNP, 2016; PNP, 2018). Given that these habitats are preferred by hog deer and spotted deer (Lamichhane et al., 2020; Odden et al., 2005; Wegge et al., 2009), these differences in the extent of the preferred habitat likely resulted in $>3.5\times$ higher densities of spotted deer in Chitwan, and hog deer not being encountered in Parsa (Table 2). Also, the Chure hills, where seasonally water is not available

and therefore supports lower prey densities (Thapa & Kelly, 2017), make up over 63% of Parsa, in contrast to 48% of Chitwan. Additionally, because Chitwan is Nepal's oldest NP and has received significant conservation attention for nearly five decades, ungulate densities are likely closer to the carrying capacity. In contrast, although established in 1984, Parsa was upgraded to a NP in 2017. Consequently, efforts to reduce anthropogenic pressures such as poaching, livestock grazing, and illegal natural resource extraction have occurred relatively recently (Lamichhane et al., 2018). Therefore, while recovering, prey densities are likely still not close to the carrying capacity (Dhakal et al., 2014; DNPWC & DFSC, 2018). Hence, we believe that the estimated potential density of tigers for Chitwan is probably close to the ECC, while the continued recovery of prey in Parsa suggests that the potential ECC for the tiger could still increase over time. Collectively these two protected areas constitute over 1500 km^2 of contiguous protected habitat, making Chitwan–Parsa a quintessential source site that can support a large tiger population with over 50 breeding females, assuming a stable demographic structure and support recoveries across the eastern TAL (Walston et al., 2010; Wikramanayake et al., 2011).

Using prey availability to estimate ECC inherently suggests that ECC for tigers will be altered with prey density/biomass changes. Given that tigers prefer prey approximately their own size (Hayward et al., 2012), it is worth considering management options that will support populations of large prey and hence more tigers. Recent studies suggest some grasslands are successional into forests, which could adversely affect ungulate densities (DNPWC, 2020). Habitat management, such as controlled burns, may effectively maintain grasslands and increase prey abundance. Targeted habitat improvement measures to increase gaur densities, which are low in this landscape, could also benefit the tiger population at the site.

An unintended negative consequence of recovering predator and prey species is increased human-wildlife conflict. Past research documents how tiger recovery in Chitwan has led to increased conflict with buffer zone communities and highlights conservation actions that have helped mitigate and reduce loss (Bhattarai et al., 2019; Gurung et al., 2008; Lamichhane et al., 2018). Given that

our analyses suggest that the ECC for tigers has essentially been reached in Chitwan (while small gains are still likely as prey populations recover [recovered both in Chitwan and Parsa based on recent survey]), policymakers and park managers need to change focus from increasing tiger numbers to developing pre-emptive conflict mitigation strategies to allow the Chitwan–Parsa source site to retain the successes it has realized.

In conclusion, estimating the carrying capacity of tigers in any given landscape provides defensible and quantifiable recovery goals. Basing estimations on prey biomass also allows considerations as to what may influence their abundance and how management actions may induce increases in prey species, thereby increasing the ECC of tigers. Managers should recognize that there is inherent fluctuation in tiger populations; however, by setting clearly defined recovery goals based on the ecological capacity of the landscape, managers can prioritize conservation investment and action towards recovery in a timely and adaptive manner.

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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