Agricultural lands offer seasonal habitats to tigers in a human-dominated and fragmented landscape in India

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Abstract. Conserving wide-ranging large carnivores in human-dominated landscapes is contingent on acknowledging the conservation value of human-modified lands. This is particularly true for tigers (Panthera tigris), now largely dependent on small and fragmented habitats, embedded within densely populated agroecosystems in India. Devising a comprehensive conservation strategy for the species requires an understanding of the temporal patterns of space use by tiger within these human-modified areas. These areas are often characterized by altered prey communities, novel risks resulting from high human densities and seasonally dynamic vegetative cover. Understanding space use within these areas is vital to devising human-tiger conflict prevention measures and for conserving landscape elements critical to maintain functional connectivity between populations. We documented seasonal space-use patterns of tigers in agricultural lands surrounding protected areas in the Central Terai Landscape (CTL) in northern India. We estimated the probability of space use and its drivers by applying dynamic occupancy models that correct for false-positive and false-negative errors to tiger detection/non-detection data within agricultural areas. These data were generated by conducting local interviews, sign surveys, and camera trapping within 94 randomly selected 2.5-km² grid cells. We found that agricultural areas were used with high probability in the winter (0.64; standard error [SE] 0.08), a period of high vegetative cover availability. The use of agricultural lands was lower in the summer (0.56; SE 0.09) and was lowest in the monsoon season (0.21; SE 0.07), tracking a decline in vegetative cover and available habitat across the landscape. Availability of vegetative cover and drainage features positively influenced space use, whereas use declined with increasing distance to protected areas and the extent of human settlements. These findings highlight the role of agricultural areas in providing seasonal habitats for tigers and offer a basis for understanding where tigers and humans co-occur in these landscapes. These findings help expand our current understanding of what constitutes large carnivore habitats to include human-dominated agricultural areas. They underscore the need for greater integration of land-sharing and land-sparing initiatives to conserve large carnivores within human-dominated agroecosystems.

Key words: false-positive detection error; habitat use; India; interview surveys; land-use planning; large carnivores; occupancy models.

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INTRODUCTION

Terrestrial, large-bodied carnivores have experienced dramatic range contractions and are among the world’s most threatened species (Wolf and Ripple 2017). Population extirpations of these species have largely occurred in areas with high human and livestock densities, and with extensive conversion of natural habitats to agriculture. Most of the biosphere is impacted by human modification (Kennedy et al. 2019), and collectively humans and livestock constitute about 96% of the global mammalian biomass (Bar-On et al. 2018). Unsurprisingly, extant ranges of many large carnivore species such as tigers (Wikramanayake et al. 2011), lions (Panthera leo; Stephens 2015), jaguars (Panthera onca; Boron et al. 2018), and wolves (Canis lupus; Chapron et al. 2014) increasingly occur within human-dominated and human-modified landscapes. Protected areas (PAs) within these landscapes remain vital to protecting breeding populations of these species and their prey from illegal harvest—a leading driver of large carnivore population declines (Ripple et al. 2014). These species are, however, not restricted to PAs and are characterized by their extensive presence within multiple-use forests (Chanchani et al. 2016), agricultural lands (Athreya et al. 2013), and peri-urban areas (Chapron et al. 2014). While biodiversity declines have prompted calls for the expansion of the global PA network (Dinerstein et al. 2017), it is also increasingly acknowledged that the persistence of large carnivores into the future, particularly in nations with dense human populations, requires greater emphasis on the conservation value of human-dominated lands (Stephens 2015).

About 40% of global human modification of terrestrial areas has resulted from the conversion of forests and grasslands to agriculture (Foley et al. 2005, Kennedy et al. 2019). Agriculture is predicted to increase in extent and intensity globally, alongside an increase in global human populations (Zabel et al. 2019), sparking debates on how best to reconcile biodiversity conservation efforts with agriculture. An important debate focuses on whether conservation efforts should be extended to sustainably managed small-scale farms (land sharing), or if agricultural areas should be intensively cultivated, while sparing large tracts of land exclusively for conservation (land sparing; Phalan et al. 2011). While land sharing is increasingly being recognized as vital to carnivore persistence within human-modified landscapes (Chapron et al. 2014, Stephens 2015), operationalizing this concept has been complicated by a limited understanding of carnivore ecology within agroecosystems. While many studies on large carnivore use of human-modified areas exist (Woodroffe 2011, Boron et al. 2018, Majgaonkar et al. 2019), there remain critical gaps in our understanding of carnivore ecology within agricultural areas. In a review of carnivore use of agroecosystems, Ferreira et al. (2018) found that the extent to which agricultural areas offer foraging habitats, dispersal routes, or cover for large carnivores remains unclear. They also found that the literature is dominated by studies conducted in tree plantations, whereas the use of annual croplands by large carnivores has not been adequately explored. Moreover, human-modified areas, and agroecosystems in particular, may show high seasonal variation in the availability of resources such as cover and prey (Karanth 2016). Since most studies are conducted over a single season, it is also unclear how this seasonal variation in resource availability impacts the use of these areas by large carnivores.

Reconciling agricultural production and conservation efforts is especially vital to the conservation of tigers. Nearly 70% of the global tiger population occurs within India (Jhala et al. 2015), the second most populous nation in the world, with a large proportion of its population dependent on subsistence agriculture (Ahmad et al. 2011). While PAs remain central to India’s tiger conservation efforts, the existing network of PAs encompasses only a fraction of the landscape necessary to sustain viable tiger populations. PAs cover only about 5% of India’s land area, and a third of India’s tigers are currently estimated to occur outside PAs, within multiple-use forests (Jhala et al. 2015). Moreover, the average size of a tiger reserve in India is 300 km² (Karanth and Nepal 2012), whereas the median home range of a single adult male tiger is 160 km² (Chundawat et al. 2016). In addition, many of these PAs and multiple-use forests are fragmented and embedded within a matrix comprising of agriculture and dense human populations.
Despite the structural discontinuity among habitats supporting tiger populations, these populations remain functionally connected via the movement of tigers through a matrix of unprotected agricultural, and community-owned lands (Thatte et al. 2018). In many instances, the presence of tigers within the agricultural matrix is also promoted by the availability of dense vegetative cover and wild prey and facilitated by high human tolerance for wildlife (Athreya et al. 2014, Karanth 2016).

The conservation benefits to tigers offered by a permeable and resource-rich agricultural matrix are undermined by two factors. First, matrix areas surrounding protected parks worldwide, and particularly in India, are experiencing accelerated human population growth rates and land-use conversion (DeFries et al. 2007, Wittemyer et al. 2008). India is projected to experience both an intensification of agriculture (Zabel et al. 2019) and an increase in urbanization as its population grows (Sanderson et al. 2019). Conversion of matrix habitats to land-use types more resistant to tiger use and movement reduces matrix permeability and results in a net loss of functional connectivity between fragmented populations (Crooks et al. 2011, Joshi et al. 2013). Second, the presence of tigers amidst dense human populations increases the probability of adverse human-tiger interactions, leading to livestock, human, and tiger casualties (Goodrich 2010). Designing a conservation strategy that addresses these challenges requires an understanding of the spatial ecology of tigers within the agricultural matrix, information that is currently lacking (Ghosal et al. 2013). This information is vital to informing measures aimed at sustaining functional connectivity between populations. In addition, understanding the factors that drive spatial overlap between tigers and humans can help clarify the circumstances under which humans and tigers co-occur with and without conflict—information that is critical to determining long-term conflict prevention measures. The extent to which tigers use agricultural areas surrounding PAs can also help inform land conservation measures such as the delineation of eco-sensitive zones (ESZ) around PAs. In India, ESZs are mandatory buffer zones, extending up to 10 km around PAs as per the directive issued by the Ministry of Environment and Forests (Banerjee et al. 2010). Land-use alterations and development activities are regulated within ESZs with the explicit intention of reducing adverse human impacts on native wildlife. While it regulates land conversion, the ESZ notification also includes provisions to promote sustainable agricultural practices within its boundaries.

We conducted a study to examine the use of agricultural areas by tigers to address some of these knowledge gaps. We documented space-use probabilities of tigers in the agricultural corridor between two protected areas in the Central Terai Landscape (CTL) in northern India. Our objective was to determine the temporal patterns of variation in space use by tigers and the underlying environmental drivers of use. Estimating space-use probabilities requires detecting tigers when they use agricultural areas. Conventional and noninvasive species detection methods such as camera trapping and sign-encounter surveys are characterized by low detection probabilities for tigers because of the species’ cryptic behaviors and low densities. We therefore used a novel sampling strategy to generate detection/non-detection data for tigers that combined camera trapping and sign surveys with interview surveys of farmers resident within the matrix (Zeller et al. 2011). While interview surveys are cost-effective and associated with higher detection probabilities for elusive species, they are prone to false-positive detection errors (Petracca et al. 2018). A false-positive detection results when an interviewed person reports a species as present at a site where it is truly absent. This error may arise if the interviewee misidentifies the species or more insidiously from assigning a detection to an incorrect spatial or temporal domain. These errors can bias inferences about habitat use and its drivers (Pillay et al. 2014). To address these biases, we applied a dynamic occupancy model that corrected for false-positive detection errors (Miller et al. 2013) to our data. We discuss the implications of our results for tiger conservation in the CTL and in broadening our understanding of the role that human-dominated, agricultural areas may play in supporting populations of large carnivores.
**Materials and Methods**

**Study area**

Our study was conducted within the Central Terai Landscape (CTL) in the state of Uttar Pradesh in northern India. The study area was a 1550-km² agricultural region lying between two tiger reserves—Dudhwa Tiger Reserve (Dudhwa National Park and Kishanpur Wildlife Sanctuary) and Pilibhit Tiger Reserve (PTR) and bounded on the north by the India–Nepal international border (Fig. 1). The area is composed of extensive sugarcane agriculture, dense human settlements, and remnant patches of riparian habitats associated with the Sharada River. These riparian habitats lie within the jurisdiction of the North and South Kheri Forest Division and are designated as multiple-use forests allowing harvest of forest resources. The remaining land within the study area is composed of privately owned agricultural land, village clusters, and small towns; the average human population density is 500/km² (Chandramouli 2011). The area is subject to humid subtropical climatic conditions with four dominant seasons: summer (April–June), monsoon (July–September), post-monsoon (October–November), and winter (December–March). During the monsoon season, substantial portions of the area experience flooding (Midha and Mathur 2014). Besides tigers, the CTL supports multiple species of threatened fauna including the greater one-horned rhinoceros (*Rhinoceros unicornis*), swamp deer (*Cervus duvaucelli duvaucelli*), hog deer (*Axis porcinus*), and Asian elephants (*Elephas maximus*).

**Study design and field methods**

We estimated the space-use patterns of tigers and other large mammals within the study area using a spatially balanced sample of 94 randomly selected 1.6 × 1.6 km cells (Fig. 1), chosen using Generalized Random Tessellation Stratified sampling (Stevens and Olsen 2004). We were interested in how tigers use non-PA lands and multiple-use areas, so we excluded cells that overlapped PA from our sampling frame. To determine how tiger space use changed with available vegetative cover, we conducted repeated surveys over three survey seasons defined according to the growth and harvest cycle of sugarcane, the dominant cover crop in the matrix. Other sources of vegetative cover include native riparian grasslands and forested areas, occurring primarily along the Sharada River. Seasons were defined as follows: winter/high cover, summer/low cover, and monsoon/moderate cover. These survey seasons coincided with the prevailing climatological seasons, characterized by marked differences in vegetation growth and cover, temperature, and precipitation (Table 1).

In each season, we employed three different survey methods: farmer surveys (FS), animal sign surveys (SS), and camera surveys (CS; Table 1). Farmer surveys involved independent interviews of 1–12 farmers opportunistically encountered while walking a random path within each cell. Each farmer was shown images and given verbal descriptions of mammalian species that occur in the landscape along with a description of their signs (e.g., tracks and scat) and asked if they observed these species on their lands within the past month. Farmer surveys yielded uncertain species detections, allowing for the potential of false positives. Farmers could incorrectly report the presence of a species due to species misidentification, memory lapses, etc.

Sign surveys (SS) were conducted in a random subset (69 cells) of surveyed cells. Within each of these cells, SS were conducted over 1–6 temporal occasions per season. On each survey occasion, two independent observers walked a random path (>500 m) searching for sign (spoor, scat, direct sightings) of wild mammals within the cell. We treated all detections of a given species along the length of these transects as a single detection. We assumed sign identification represented certain detections for tigers (i.e., no false positives); however, sign identification was less reliable for species such as hog deer and wild boar (*Sus scrofa*) and was deemed uncertain. Since most cells were either agricultural land or river beds, substrate quality was consistently high except during the monsoon season. We additionally ensured independence of sign surveys by walking transects that did not overlap GPS tracks associated with transects from previous temporal occasions.

Camera surveys (CS) were conducted in a randomly selected subset of the sign survey cells (47). We placed a single motion-activated Cuddeback Attack 5.0-megapixel Trail Camera (Cuddeback Digital, Green Bay, Wisconsin, USA) within
a cell for 30–40 d during a given season. Detections of large mammals generated over this period formed an additional source of certain detections for all species (i.e., no species misidentification). Within a cell, camera placement targeted areas with higher likelihood of animal movements such as natural drainages. In the subsequent analysis, we treated each five-day

Fig. 1. Study area and sampling design. The study area is the agricultural matrix separating Pilibhit Tiger Reserve (PTR), Kishanpur Wildlife Sanctuary (KWS), and Dudhwa National Park (DNP). In the winter season, a total of 94 randomly selected 2.6-km² cells were surveyed. A subset of these cells was surveyed in the summer (91 cells) and monsoon seasons (85 cells). Cell colors indicate the survey methods applied during each sampling season (FS, farmer surveys; SS, sign surveys; CS, camera surveys). The black and white dashed lines represent the international border between India and Nepal, and features in blue represent water bodies associated with the Sharada River system. Yellow polygons in the background are outlines of settlements.
period the camera was active as a survey occasion. Since tigers can be individually identified based on their coat patterns, we tallied the total number of individual tigers detected in the study area by comparing the stripe patterns of photo-captured individuals. We then compared these images with the tiger ID database maintained for nearby PAs (Dudhwa tiger reserve and Pilibhit tiger reserve) to identify the source populations these individuals belonged to.

In each season, we first deployed camera traps in cells, followed by SS. Efforts were made to conduct FS toward the end of each season to limit tiger detections to the given season.

**Statistical analyses**

Our goal was to estimate factors influencing the probability and the relative frequency of cell use by tigers and the seasonal dynamics of use. We estimated model parameters (Table 2) by fitting dynamic occupancy models that account for false-positive errors. The false-positive model (Miller et al. 2013, MacKenzie et al. 2017) extends the traditional dynamic occupancy model (MacKenzie et al. 2003) to allow the estimation of false-positive detection rates by exploiting data from both certain and uncertain detection methods. In our study, FS, the more extensively applied survey method, was the source of uncertain detections, whereas CS and SS were the sources of certain tiger detections.

Based on the landscape of coexistence concept (Oriol-Cotterill et al. 2015), we developed a priori hypotheses about the drivers of habitat use and identified candidate covariates (Table 3) for inclusion in our models. The concept posits that spatiotemporal patterns of carnivore occurrence in human-altered landscapes are governed

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### Table 1. Seasonal characteristics (mean temperature, mean precipitation, and plant cover), sampling effort, and tiger detections for three survey methods: farmer surveys (FS), sign surveys (SS), and camera surveys (CS).

| Seasons | Max temp (°C) | Mean precip (mm) | Cover | No. cells | No. cells with tigers | No. cells | No. cells with tigers | No. cells | No. cells with tigers |
|---------|---------------|------------------|-------|-----------|-----------------------|-----------|-----------------------|-----------|-----------------------|
| Winter  | 22            | 19.1             | VH    | 94 (1–12) | 58                    | 69 (1–4)  | 13                    | 47 (9–39) | 4                      |
| Summer  | 38            | 5.8              | L     | 91 (1–12) | 55                    | 56 (1–6)  | 3                     | 43 (8–39) | 3                      |
| Monsoon | 33.8          | 277              | H     | 85 (1–10) | 22                    | 26 (1)†   | 1                     | 32 (4–36) | 2                      |

Notes: Season durations were winter, 15 December–15 February; summer, 15 March–15 May; and monsoon, 15 July–15 August. Cover abbreviations are VH, very high; L, low; and H, high. Values in parentheses are the min-max range of number of surveys per cell. Values in parenthesis indicate minimum and maximum surveys per cell.† In the monsoon season, sign surveys were conducted only on a single occasion due to inclement weather conditions.

### Table 2. Name, notation, and definitions for parameters in the false-positive dynamic occupancy model.

| Parameters (Symbol) | Definitions |
|---------------------|-------------|
| Probability of use in winter \( (P_{u,w}) \) | Probability that a cell was used by tigers in the first season of the study (winter) |
| Extinction probability \( (e_t) \) | Probability that a used cell in season \( t \) will not be used in the subsequent season \( t + 1 \) |
| Colonization probability \( (\gamma_t) \) | Probability that an unused cell in season \( t \) will be used in the subsequent season \( t + 1 \) |
| False-positive detection probability, \( (p_{fi}^{FS}) \) | Probability that a species will be incorrectly detected during a given survey in an unused cell. This probability is nonzero for farmer surveys (FS) only. The probability was fixed to zero for sign and camera trap surveys \( (p_{fi}^{SS} = p_{fi}^{CS} = 0) \) |
| True detection probability, \( (p_{fi}^{FS}) \), \( (p_{fi}^{SS}) \), \( (p_{fi}^{CS}) \) | Probability of detecting tigers on a survey occasion given the cell was used by tigers during the survey season. True detection probability varied among the three survey types (FS, SS, and CS) |
| Probability of certain detection \( (b^{FS}), (b^{SS}), (b^{CS}) \) | Probability that a detection can be designated as certain given that a cell was used by tigers and the species was detected. This probability was fixed to zero for farmer surveys \( (b^{FS} = 0) \) and to 1 for camera and sign surveys \( (b^{SS} = b^{CS} = 1) \) |

**Note:** The first entry of the detection probability subscript designates the detection state \( (1 = \text{detected}) \), while the second entry designates the true occupancy (use) state, \( 0 \) if the cell was truly not used by tigers and \( 1 \) if the cell was truly used.
The availability of permanent water sources will positively influence use in the summer (dry) season (i.e., lower local extinction probability) and negatively in the monsoon season (flooding).

The availability of wild prey will positively influence spatiotemporal space-use patterns (Abbreya et al. 2014, Gehr et al. 2017).

The probability of use should be higher for cells that experience a net increase in prey availability between seasons.

We modeled the probability of initial tiger use within a cell (winter, $\Psi_w$) as a function of six covariates: median NDVI values (NDVI_W), prey availability index (Prey_W; Appendix S2), distance to PA, length of natural drainages (Drain), percent tree canopy cover (Tree), and proportion of settlement (Sett). Changes in cell use between seasons were modeled via two dynamic processes, local extinction and colonization. Local extinction probability ($\epsilon_t$) is the probability that a cell used in one season ($t$) is not used in season ($t+1$); $\gamma_t$ probability that an unused cell in season ($t$) will be used in season ($t+1$). $\epsilon_t$ probability that a surveyed farmer will report a tiger as present in a cell that is truly unused; probability of detecting tigers using farmer surveys ($p_{FS}^{\text{f}}$), sign surveys ($p_{SS}^{\text{s}}$), and camera surveys ($p_{CS}^{\text{c}}$).

Table 3. Covariates and their a priori hypothesized and estimated relationships with model parameters.

| Hypotheses | Covariates | $\beta_{\text{hypothesized}}$ $\dagger$ | $\beta_{\text{estimated}}$ $\ddagger$ (standard error) |
|------------|------------|----------------------------------------|--------------------------------------------------------|
| Seasonal tiger use and false-positive detection probability for farmer surveys will be higher in cells proximate to protected area boundaries (Karanth 2016) | Protected area (PA): minimum Euclidean distance (km) between cell center and protected area boundary | $\Psi_{w}$ (−) | $\Psi_{w_{\text{PA}}}$: −0.42 (0.14) |
| Winter tiger use and true detection probability using farmer surveys (FS), sign surveys (SS), and camera surveys (CS) will increase in a linear or quadratic manner with cover availability | NDVI_W, NDVI_S, NDVI_M: cell-specific median NDVI values for each season (index of cover availability) | $\Psi_{w}$ (+)/quadratic | $\Psi_{w_{\text{NDVI_W}}}$: 42.72 (20.77); $\Psi_{w_{\text{NDVI_M}}}$: −53.78 (24.72) |

$\dagger$ Hypothesized direction of relationship between covariates and model parameters: $\Psi_{w}$, probability of cell use in winter; $\epsilon_t$, probability that a cell used in season $t$ will not be used in season $t+1$; $\gamma_t$, probability that an unused cell in season $t$ will be used in season $t+1$; $p_{FS}^{\text{f}}$, probability that a surveyed farmer will report a tiger as present in a cell that is truly unused; probability of detecting tigers using farmer surveys ($p_{FS}^{\text{f}}$), sign surveys ($p_{SS}^{\text{s}}$), and camera surveys ($p_{CS}^{\text{c}}$).

$\ddagger$ Estimated relationship between model parameters and covariate based on best supported model in the overall model set (see Appendices).
in the subsequent season \((t + 1)\). We expected local \(e_t\) to vary across seasons and cells primarily as a function of two covariates: water availability (Water) and cover availability in the subsequent season \((\text{NDVI}_S, \text{NDVI}_M)\). Local colonization probability \(\gamma_t\), the probability that an unused cell in season \(t\) will be used in the subsequent season \((t + 1)\), was modeled as a function of three covariates: median NDVI values in the subsequent season \((\text{NDVI}_S, \text{NDVI}_M)\), prey availability in the subsequent season \((\text{Prey}_S, \text{Prey}_M)\), and change in prey availability between successive seasons \((\text{Prey}_WS, \text{Prey}_SM)\).

We modeled two types of detection probabilities: true detection probability \((p_{t1})\) or the probability of detecting species’ use when the cell was truly used and false-positive detection probability \((p_{10})\), the probability of falsely reporting use. The parameter \(p_{t1}\) was modeled as a function of survey method (Method), season (Season), an index of season-specific cover availability \((\text{NDVI}_W, \text{NDVI}_S, \text{NDVI}_M)\), and the proportion of settlement within a cell (Sett). Survey effort (spatial coverage) of FS was higher than CS and SS; therefore, we expected detection probabilities for all seasons to be highest for FS and lowest for CS \((p_{t1}^{FS} > p_{t1}^{SS} > p_{t1}^{CS})\). Since false-positive detections were possible for farmer surveys \((p_{10}^{PA})\), we modeled this parameter as a function of season and distance to protected area boundary (PA). We expected farmers living further from PA boundaries to be less familiar with tiger signs and hence more likely to falsely report use. We hypothesized that the probability of false positive reporting of tigers would be highest in the winter. Extensive engagement with farmers in the study area revealed that farmers in the region believe that tigers (and other species) occur extensively in the matrix in the winter season and return to the forests in the summer and monsoon seasons.

We evaluated the above hypotheses using the false-positive, robust design occupancy model in Program MARK (White and Burnham 1999). Models within a set were ranked according to Akaike’s information criteria (AIC; Burnham and Anderson 2003). Employing a sequential approach to model building, we compared alternative models to identify the best supported covariate structure (lowest AIC) for detection probabilities \((p_{t1}^{FS}, p_{t1}^{SS}, p_{t1}^{CS}, p_{10}^{FS})\) while retaining a global structure (i.e., all covariate of interest) on initial tiger use \((\Psi_w)\) and associated vital rates (local extinction and colonization). We retained the best supported structure for detection probabilities and a global structure on the vital rates, to identify the model that best explains initial space-use probabilities. Finally, for retaining the best supported model structures for detection probabilities and initial use probabilities, we identified the best supported model for \(\gamma_t\) and \(e_t\) (Appendix S2: Tables S1–S3).

For comparison, in the final model set we included (1) a model where all parameters were modeled without covariates (i.e., the null model) and (2) a model with identical covariate structure to the best supported model but assumed no false-positive errors \((p_{10} = 0\) for all survey types; Appendix S4: Table S1). Finally, using parameter estimates from the best supported model, we derived estimates of \(\psi_t\) for summer and monsoon seasons using the recursive equation (Eq. 1; MacKenzie et al. 2017). Specifically, we derived estimates of \(\psi_t\) and associated vital rates \((\gamma_t\) and \(e_t\) in one season \((t)\) to estimate tiger use in the subsequent season \((t + 1)\).

\[
\psi_{t+1} = \psi_t \times (1 - e_t) + (1 - \psi_t) \times \gamma_t
\]

**RESULTS**

**Survey effort, species detections, and naive use estimates**

We interviewed 1495 farmers, conducted 322 sign surveys, and obtained photo-captures of tigers and prey species over 3449 trap nights. Using CS, we detected 15 mammal species including tigers and locally rare species such as the Indian wolf \((\text{Canis lupus pallipes})\) and fishing cat \((\text{Prionailurus viverrinus})\). Tigers were detected in all seasons using all survey methods. Detections were highest in the winter season for all three methods and the lowest in the monsoon season (Table 1). We obtained 11 tiger photo-captures, over the three survey seasons belonging to at least seven distinct individuals, including a female with a cub. Two individuals were previously photo-captured within Dudhwa National Park (DNP), and the tigress with the cub had been photo-captured within Kishanpur Wildlife Sanctuary in 2013. Within the study area, two of
the seven individuals were captured in single cell adjoining the DNP boundary and the other five individuals were captured at cells ranging from 0.5 to 3 km from a PA boundary. Tiger sign was detected in cells ranging up to 8 km from PA boundaries.

**Covariate relationships and parameter estimates**

We fit a total of 79 models (Appendix S4: Table S1) estimating the effects of covariates on the parameters of interest, including intercept-only models and a version of the best supported model that assumed no false-positive detections ($p_{10} = 0$ for all survey methods). Variation in true detection probability ($p_{11}$) was best explained by an additive combination of season and method (Appendix S3: Table S1). The parameter $p_{11}$ was highest for FS followed by SS and CS (Fig. 2). For all survey types, true detection probability was highest during the winter season and declined in the summer and monsoon seasons. The best supported model for false-positive detection probability for farmer surveys ($p_{FS10}$) included the covariates season and distance to PAs. As expected, the probability of a false-positive detection increased with increasing distance to a PA boundary (Table 3) and was highest in the winter season and lowest in the monsoon season. On average, the probability of a false-positive tiger detection from a farmer survey was 0.09 in the winter season (standard error [SE] 0.02), 0.06 in the summer season (SE 0.01), and 0.01 in the monsoon season (SE 0.01).

Initial probability of tiger use in winter ($\Psi_w$) was a function of distance to PAs, length of drainages and proportion of settlements within a cell, and a quadratic relationship with median NDVI values in winter (NDVI_W). This model had nearly three times more weight than the next best supported model, which included the additional covariate mean percent tree cover (Appendix S3: Table S2). Tiger use in winter decreased with distance from protected areas and proportion of settlements in the cell and increased with increasing length of drainages within a cell (Table 3, Fig. 3). Tiger use had a quadratic relationship with winter cover availability (NDVI_W; Fig. 3). Models that included prey availability as a covariate were not strongly supported.

The probability of local extinction ($e_t$) was best explained by models that included seasonal variation, water availability, and distance to PA.

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**Fig. 2.** True detection probability estimates ($p_{11}$) by season and method (farmer surveys [FS], sign surveys [SS], and camera surveys [CS]) with associated 95% confidence intervals. Estimates are based on the best supported model in the overall model set (Table 3; see Appendix S4: Table S1).
While there was considerable model uncertainty, the season covariate was included in seven of the top-supported models, with a cumulative model weight of 80%. The covariates Water and PA were also important and were included in six of the top models. Consistent with our predictions, local extinction probability increased with increasing distance to PAs (Table 3, Fig. 4). Availability of permanent water sources within a cell increased the probability of extinction in both the winter–summer and summer–monsoon transitions. Local extinction probability was higher in the summer–monsoon transition as compared to the winter–summer transition (Table 3, Fig. 4).

The best supported colonization probability ($\gamma_c$) structure suggested that no new cells were used in the summer and monsoon seasons (Appendix S3: Table S4). This model was 2.5 times more likely than the next best supported model and suggests that tiger use of the matrix is highest during the winter, with declining use throughout the remainder of the year (Fig. 5). The model assuming no false-positive detections performed poorly ($\Delta AIC_c = 132.58$) compared to the best supported model (Appendix S4: Table S1) and overestimated mean tiger-use probabilities for all seasons (Fig. 5). The intercept-only model was the least supported model in our overall model set ($\Delta AIC_c = 291.07$).

**DISCUSSION**

We quantified space-use patterns of tigers in agricultural areas of the Central Terai Landscape (CTL), one of the most densely populated landscapes in the tiger’s range. Using dynamic occupancy models that correct for false-positive detections, we found that tigers used agricultural areas extensively, with seasonal variation in the...
extent of use. Agricultural areas were primarily composed of annual croplands, remnant riparian habitats, and human settlements. Tigers selected areas with high vegetation cover while avoiding areas with large human settlements. Use probability was highest in the winter season when vegetation cover provided by sugarcane crops and riparian grasslands was most extensive. Tigers showed a preference for areas dominated by intermediate cover availability and avoided areas with very sparse and very dense cover. In our study area, intermediate cover availability often occurred in areas where sugarcane crop merges into native riparian habitats. In human-dominated landscapes, the availability of cover helps large carnivores modulate their exposure to anthropogenic risks (Oriol-Cotterill et al. 2015, Llaneza et al. 2016). Since we do not have movement data on tigers from our study area, it is unclear whether moderate to high vegetative cover provides refugia from human disturbance or if these areas offer enhanced foraging opportunities.

Probability of use declined with increasing distance to PAs; however, areas up to six kilometers from PA boundaries experienced high use by tigers during the winter season. Similar declines in the use of human-modified areas with increasing distance to PA boundaries have been noted for other threatened and endangered large carnivore species such as jaguars (Boron et al. 2016, Petracca et al. 2018). Our results thus further support the observation of Ferreira et al. (2018) that agroecosystems are more likely to support large carnivores if they retain patches of native habitats within them. These results strongly

Fig. 4. Covariate relationships with probability of local extinction (e) between winter–summer and summer–monsoon seasons. Relationships are based on coefficient estimates from the best supported model in the overall model set (Table 3; see Appendices) using mean values for covariates that are not graphed. Water availability: mean index of water availability within a cell. Values range from no water (0) to presence of permanent water sources (100).
contradict the findings of Kanagaraj et al. (2011) that deemed the agricultural matrix of the CTL as unsuitable habitats for tigers. We found that cells including natural drainages were used with higher probability by tigers. Drainages may function both as a source of cover and as movement routes for tiger and prey species to travel between patches of native habitats. Contrary to our expectations and findings from recent studies on other large carnivore species (Filla et al. 2017, Gehr et al. 2017), the availability of wild prey, as measured in our study, was not a strong predictor of local tiger space-use probabilities. We believe that tigers using agricultural areas subsist largely on wild prey since reports of livestock depredation in the matrix are very rare, despite a strong incentive for livestock owners to report these losses (Chatterjee et al. 2018).

In human-dominated landscapes, seasonality in habitat use may result from trade-offs made by large carnivores in accessing resources while avoiding human disturbance (Ordiz et al. 2017). We found that space-use probabilities declined from the winter (high use) season as reflected in low (no) local colonization probabilities ($\gamma_i$) and high local extinction probabilities ($\epsilon_i$; Figs. 4, 5). Cells with more perennial water sources and further away from PAs experienced higher local extinction probabilities. This dynamic may be a consequence of increased human disturbances near perennial water sources in the summer and a high likelihood that these areas are inundated during the monsoon season. It also indicates that areas closer to PA boundaries experience more sustained use by tigers. Our results thus underscore the highly variable nature of habitat availability in landscapes dominated by annual croplands. Discounting this dynamism can lead to an incorrect inference regarding the value of human-modified lands to large carnivores, leading to inappropriate conservation actions (Hansen and DeFries 2007).

Our results also highlight the prevalence of false-positive errors in interview-based detection...
data, despite precautions taken during the data collection process to minimize such errors. This probability varied both spatially and seasonally, suggesting the cautious interpretation of occupancy and use probabilities estimated using interview data. Discounting false-positive errors resulted in an overestimation of use probabilities in all three seasons. Detection probabilities were higher with FS than SS and CS. At sites used by tigers, our methodology was unable to distinguish a true-positive detection from a false-positive detection generated using farmer surveys. For example, farmers interviewed at a site that is indeed used by tigers may falsely claim to have seen a tiger (or its signs), thus inflating the true detection probability. We recommend that studies involving interview-based detection data incorporate at least one other survey method that is free of false-positive errors, at least at a subset of the sample sites, or incorporate other measures to verify responses to correct this bias (Pillay et al. 2014).

In a recent review, Ferreira et al. (2018) note the conspicuous paucity of studies examining the use of annual croplands by threatened large carnivores and the causal factors underlying this use. We believe our study is the first to comprehensively document the seasonal space-use patterns of tigers within an agricultural matrix, comprised largely of annual croplands. During our study, we obtained photographs of multiple tigers, including a tigress with a cub, previously photographed within the boundaries of Kishanpur Wildlife Sanctuary during a camera trap-based population study in 2013. The presence of tigresses with cubs has been reported on multiple occasions both within the study area and in the larger landscape (WWF-India, personal communication). In 2016, camera trapping in PAs in the landscape documented the first known successful dispersal of a tiger from Kishanpur Wildlife Sanctuary into Dudhwa National Park (WWF-India, personal communication). Our results and these observations together suggest that the agricultural areas of the CTL, despite high human densities, serve not only as dispersal routes, but also as breeding areas for tigers. Previous studies assessing connectivity in the landscape, relying on expert-opinion-based classification of landscape resistance, have tended to classify agricultural areas as offering high resistance to movements (Kanagaraj et al. 2013). In their connectivity model for the CTL and adjoining areas, Wikramanayake et al. (2004) assumed that tigers can move unimpeded through sugarcane farmlands. Our results support this assumption, with the caveat that vegetative cover characteristics, season, and large human settlements may influence the degree to which these movements are facilitated.

Acknowledging the role of the agricultural matrix in supporting local tiger populations in the CTL emphasizes the need to regulate accelerating changes in land use and human population growth. Human populations are projected to increase across most tiger landscapes including the CTL. The consequent increase in the rates of urbanization is predicted to significantly impact tiger persistence probabilities (Joshi et al. 2013, Sanderson et al. 2019). In the CTL, cells with >15% of their area under human settlements were not used by tigers. This suggests that even minor increases in the extent of human settlement in the matrix may cause sharp declines in the net available habitat for tigers and further reduce connectivity. As a first step toward regulating land-use change in the CTL, we recommend the establishment of an ESZ around protected areas that extend at least 8 km beyond the boundaries of PAs. In addition, promoting land-sharing conservation measures such as incentivizing the cultivation of cover providing crops, the restoration of native riparian grassland habitats currently threatened by livestock grazing, and establishment of long-term conservation easements can help enhance the role the matrix plays in supporting tiger populations in India (Kinnaird and O’Brien 2012).

In addition, our study provides a much-needed spatiotemporal context to understanding human-tiger conflicts both within the CTL and in other tiger landscapes. Even though tigers overlap with humans and livestock over a large portion of the study area, attacks on humans and livestock have been recorded primarily within or near PA boundaries in the winter season (Chatterjee et al. 2018) where our study shows persistent use by tigers. This suggests that mere spatial overlap between tigers, humans, and their livestock is not a sufficient condition to precipitate conflicts and that there may be other factors that
determine the risk of conflict with tigers. This has been shown for leopards (Athreya et al. 2013) and tigers (Carter et al. 2012) using human-dominated landscapes. Further, as the apex predator in the system tigers may impose a “landscape of fear” on other carnivores such as leopards and wolves, meso-predators such as jackals (Canis aureus), and ungulates that occur in the study area. This may influence the spatial and temporal patterns of conflicts between these species and local communities (Thinley et al. 2018).

The continuing loss of unprotected critical habitats is predicted to exacerbate the rate of decline of many large carnivore populations (Di Minin et al. 2016). Results from our study expand our current understanding of these critical habitats to include annual croplands such as sugarcane (Ferreira et al. 2018). In India, as in many tropical nations that support large carnivores, agroecosystems are comprised primarily of smallholder and subsistence agriculture. These systems are characterized by high vulnerability to climate change (Morton 2007). High temperatures and variable rainfall driven by climate change could trigger a decline in agricultural productivity and rapid shifts in agricultural practices, resulting in accelerated land-use change or land-use regime shifts (Ramankutty and Coomes 2016). Such changes in agroecosystems with large carnivores can have far-reaching impacts on connectivity and patterns of human–carnivore conflicts. The role of large carnivores in buffering the impacts of climate change on other wildlife species has been discussed (Ripple et al. 2014), but little is known about the direct impacts of climate change on large carnivore populations. Based on our results, we hypothesize that in agricultural landscapes with large carnivore populations, climate change impacts on large carnivore persistence may be mediated by its effects on subsistence agriculture. Within agroecosystems, we recommend that, large carnivore conservation should better integrate existing PA-based measures with broader land-sharing approaches. Such an approach, while acknowledging the primacy of native habitats in the conservation process, would also acknowledge the contribution of agricultural lands to the success of large carnivore conservation efforts.

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