Can tigers survive in human-dominated landscapes?

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An adult female tiger. Female tigers play an important role in a reintroduction program by producing and raising the cubs needed to build the population.

4 New insights into the factors influencing movements and spatial distribution of reintroduced Bengal tigers (*Panthera tigris tigris*) in the human-dominated buffer zone of Panna Tiger Reserve, India

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Abstract

The influence of tiger-specific (sex, age group), environmental (seasons, photoperiod) and anthropogenic (human use regimes) factors on the movements and spatial distribution of tigers using the human-dominated buffer zone of the Panna Tiger Reserve, India was studied. Generalised linear mixed models were used to test the significance of the relationships between the covariates influencing tiger presence. We report that tiger-specific factors – age group (generation) and sex – and environmental factors – seasons and day/night – significantly explain the observed variations in tiger use of the human-dominated buffer zone. For instance, second-generation tigers (sub- adults) spent 40% of their time in the human-use areas, compared to 10% spent by first-generation tigers (adult). When in human-use areas, sub-adult tigers approached areas near villages and spent 30% less time in areas close to water than adult tigers. Our study concludes that, in addition to tiger-specific factors, human factors, including livestock practices and peoples' activities, influence tiger behaviour and their use of shared spaces. These unchecked human practices may lead to increased negative tiger-human interactions and restrict tigers from exploiting the resources in multiple-use areas.

Keywords: Central India; human-carnivore interactions; multiple-use forests; reintroduced tigers.

4.1 Introduction

In many countries, large carnivores persist in relatively small protected areas that are surrounded by multiple-use forests and human-dominated landscapes (De Fries *et al.*, 2005, Boitani *et al.*, 2007, Chundawat *et al.*, 2016, Santini *et al.*, 2016). Animals living in such environments frequently move beyond the protected boundaries to search for prey, to establish new territories, or to look for mates (Boitani and Powell, 2012). This inevitably results in contact with human communities and increased predation by carnivores on domestic livestock or attacks (Woodroffe and Ginsberg, 1998, Dickman *et al.*, 2013, Miller *et al.*, 2016). When people experience such losses, they retaliate (Woodroffe and Ginsberg, 1998, De Fries *et al.*, 2005, Wikramanayake *et al.*, 2011, Santini *et al.*, 2016). It is well established that human factors, including human-carnivore conflicts, contribute significantly to the decline of carnivore species outside the protected areas (Wikramanayake *et al.*, 2004, De Fries *et al.*, 2005, Boitani *et al.*, 2007, Dickman *et al.*, 2013). The tiger is a conservation priority and there are several approaches to recovering tiger populations across the world (Johnsingh and Madhusudan, 2009, Walston *et al.*, 2010). India's National Tiger Conservation Authority has established 48 tiger reserves or genetic source pools across the subcontinent (http://projecttiger.nic.in). Projects like this secure breeding sub-populations and create networks of source pools (Hanski, 1998, Wikramanayake *et al.*, 2004, Johnsingh and Madhusudan, 2009).

The Panna Tiger Reserve (PTR) in India is one such genetic source pool. The state Forest Department initiated a tiger reintroduction programme in 2009 after local tigers became extinct due to poaching (Gopal *et al.*, 2009, Sarkar *et al.*, 2016). Following successful breeding, tiger numbers in PTR increased from six founder animals to over 30 individuals between 2009 and 2014 (Sarkar *et al.*, 2016). Currently, the Forest Department aims to create and strengthen safe areas across the larger landscape and secure the tiger species outside the reserves (Gopal *et al.*, 2009, Wikramanayake *et al.*, 2011).

Like most tiger reserves, the PTR is an isolated, protected area surrounded by multiple-use forests and human-dominated landscapes. In the PTR, the home ranges of male and female tigers are larger than the average ranges in other parts of India (Chundawat *et al.*, 2016, Sarkar *et al.*, 2016). These large ranges and the relatively small size of the protected area lead to a mismatch between the space needed for tigers and the available protected area (Chundawat *et al.*, 2016). Consequently, tigers, including the breeding females, which are vital to the survival of the source pool, frequently move outside the protected area (Chundawat *et al.*, 2016, Sarkar *et al.*, 2016). Moreover, new tigers also enter the PTR and sometimes dispersing males, unable to find suitable habitat outside, also return to the PTR (Chundawat *et al.*, 2016), shifting tiger territories and changing their social organisation. These new insights into the factors shaping tiger territoriality show that tiger territoriality is very flexible. The dynamic territories of tigers, the protected area-home range (hereafter, PA-home range) mismatch, the frequently changing social organisation and the increasing numbers of tigers within the PTR, all suggest that some portion of the current PTR tiger population will recurrently move and use areas outside the reserve. This finding compels tiger researchers and conservation managers to find ways to ensure tigers' persistence in shared spaces outside protected areas (Carter and Linnell 2016). In this article, we expand further on the subject of tigers and humans sharing a landscape and examine a case of very high frequency (VHF)-radio-collared tigers from the PTR tiger reintroduction programme using the human-dominated buffer zone.

The current understanding of tigers in India is based on protected areas, where human activity is restricted (Athreya *et al.*, 2014). Knowledge of how tigers use areas outside the protected areas is not available and creates uncertainty regarding the tigers' use of forests with human presence and activity. For example, it is not clear whether tigers will approach areas near to the villages or avoid them. There is evidence in a study of African lions by Oriol-Cotterill *et al.*, (2015) in Laikipia, Kenya that they show avoidance behaviour towards human settlements and roads. Moreover, it is not certain, how tigers will respond to human activity near shared water bodies that are important both for tigers and the local communities, or whether all tigers respond similarly or if the use of space varies among tigers. My study addresses the knowledge gap on tigers' responses to shared landscapes. Such understanding could lead to improved management of multiple-use landscapes both for the benefit of the tiger and the people using the areas.

In this study, we focus on tiger space utilisation in areas with known human activity and identify variations in use among tigers. We have defined two main research questions:

1. Do tigers use multiple-use buffer zones differently from core areas, in particular human settlements, waterholes?
2. How does the presence of tigers in multiple-use areas change over time?

The VHF data from radio-collared tigers was grouped into sex and age categories and estimates the percentage use of spaces with known human activity. Next, we examined how space use varies with changes in tiger sex, age group, seasons, day and night, near water and in time.

4.2 Materials and methods

4.2.1 Study area

This research was carried out in the PTR located in north central Madhya Pradesh, India. The reserve has a surface area of 1645 km^2 and is divided into two management units: a core zone (550 km^2) and a multiple-use buffer zone (1095 km^2) (Figure 1). Human activity and natural resource extraction are restricted in the core area. In the buffer zone, 43 villages with over 40,000 people and 42,000 livestock live and depend on the forest resources (Kolipaka *et al.*, 2015).

The tiger reserve is in the western Vindhya Hill ranges, which is part of a broken chain of narrow but elongated highlands and plateau escarpments and multiple-use forests that extend to the north and to the south. The tiger reserve is approximately 30 km at its widest (range 10-30 km) and approximately 100 km long.

The terrain is hilly with flat plateaus and undulating plains (Karanth *et al.*, 2004). The vegetation is predominantly savannah-type woodland-grassland habitat and mixed forests. Bamboo grows on the slopes.

Rainwater from the hills flows through numerous streams that cut through the open areas and eventually flow into the Ken River, the largest water source in the area. Due to the hilly topography, rapid drainage and the short rainy season, the availability of surface water is limited during the summer (Gopal *et al.*, 2009).

4.2.2 Tiger reintroduction programme

In 2009, two adult female tigers, T1 and T2, were introduced into the Panna Tiger Reserve, followed by a male tiger T3 in November 2009. Subsequently, three more female tigers T4, T5, and T6 were phased into the reserve. Table 1 and Sarkar *et al.*, (2016) provide details of the founder tigers (hereafter referred to as first-generation tigers) and their descendants.

4.2.3 Tiger location fixes

All first-generation tigers introduced into the PTR are mature adults (Table 1) fitted with radio collars. Sarkar *et al.*, (2016) published detailed information on the collars and collaring procedure used at PTR. Teams comprising three to six trained monitoring staff, working in 8 h shifts, monitored the collared tigers with handheld VHF receivers. They recorded and reported the data to the manager to facilitate decision-making. Radio collars were subsequently fitted to the second-generation sub adult tigers aged between 18 and 24 months. More generations of tigers had been born in PTR by the end of our study but not all tigers were radio-collared (Figure 2). In this article, the word generation refers to sub-adult tigers.

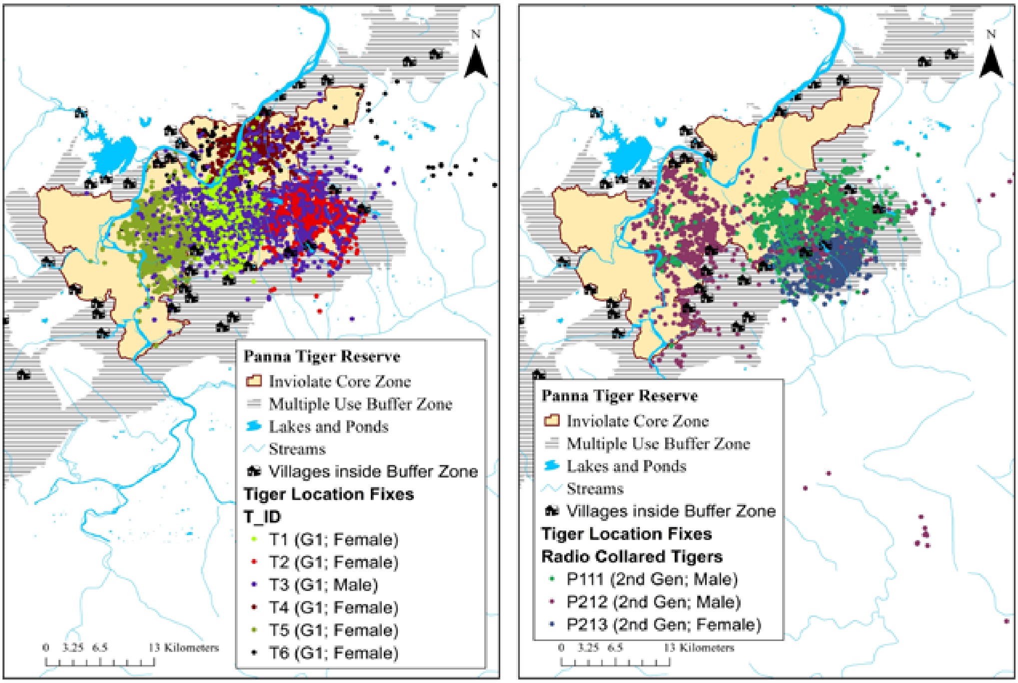

Figure 4.1 VHF radio collar location fixes of six Generation 1 (left) and three Generation 2 tigers (right) for the year 2013 in the Panna Tiger Reserve.

Table 4.1: Histories of the nine radio collared tigers from the Panna tiger reintroduction program that are included in this study.

TIGER ID	SEX	GENERATION	LITTERS BORN AS OF 2014	ORIGIN	YEAR BORN (B) OR REINTRODUCED (RE)	AGE WHEN FIRST COLLARED	TOTAL GPS FIXES (IN YEARS)	STATUS AS OF JANUARY 2016 ANALYSED
T1	♀	1	3	Bandhavgadh National Park	2009 Re	C. 7	31487	Alive
T2	♀	1	4	Kanha National Park	2009 Re	C. 7	18922	Alive
T3	♂	1	NA	Pench National Park	2009 Re	C. 7	35835	Alive
T4	♀	1	2	Kanha National Park	2011 Re	C. 7	19333	Dead
T5	♀	1	1	Kanha National Park	2011 Re	C. 7	18985	Dead
T6	♀	1	1	Pench National Park	2011 Re	C. 7	1590	Alive
P212	♂	2	NA	Born in Panna	2010 B	C. 1.8	15146	Dead
P213	♀	2	1	Born in Panna	2010 B	C. 1.8	15809	Alive
P111	♂	2	NA	Born in Panna	2010 B	C. 1.8	18933	Alive

Generation 1, adult tigers when introduced; Generation 2, sub-adults when introduced; NA, not applicable.

4.2.4 Human use of buffer zone forests

Residents access forests daily to graze their livestock, collect fuel wood and extract non-timber forest products both for subsistence and as a source of income. Livestock rearing is common and consists mainly of cows, buffalos and goats (Kolipaka *et al.*, 2015).

4.2.5 Three distinctive human-use areas

We identified regions with high human activity within the buffer zone and examined tiger use and variations in tiger presence within three areas (Kolipaka *et al.*, 2015).

4.2.6 Human-dominated buffer zone

The tiger reserve area has two management zones, a core zone and a multiple-use buffer zone (Figure 1). The core zone is an inviolate area within the tiger reserve, where human presence and activities are strictly regulated. This zone is fully secured against wildlife and approximately 15% is open for non-consumptive, vehicle-based tourism. The buffer zone, on the other hand, includes villages and accommodates peoples' activities. We examined tiger use of the buffer zone and hypothesised that some tigers – probably sub-adult tigers – most likely influenced by the territoriality of the dominant adults in the core zone and the PA-home range mismatch (Chundawat *et al.*, 2016), will use the human-dominated buffer zone more.

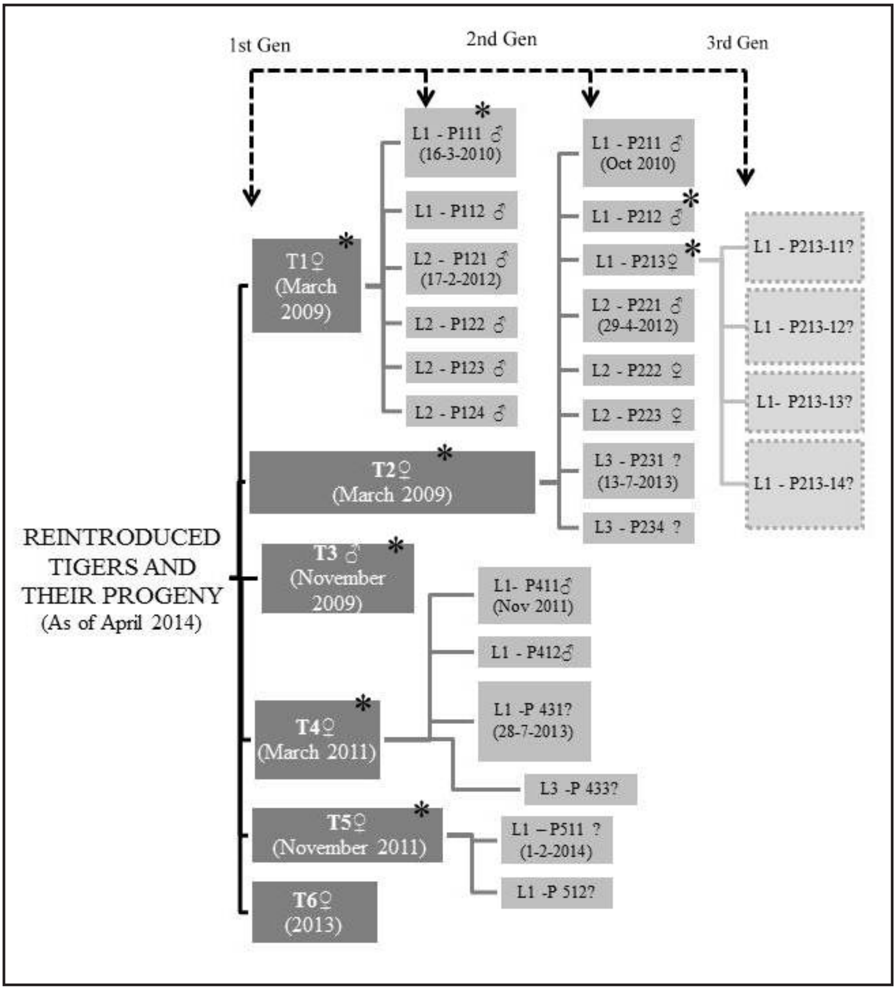

Figure 4.2 The first generation of reintroduced tigers T1, T2, T3, T4, T5 and T6 and the progeny born subsequently in the Panna Tiger Reserve as of April 2014. The dates indicate reintroduction and dates of birth. L, litter number; (?), sex unknown; (*), collared tigers and VHF location data included in this study.

4.2.7 Near villages

In an earlier study, we estimated that during daytime (7:00 h–17:00 h), people of all age groups actively move and use areas within a 2 km radius of villages (Kolipaka *et al.*, 2015) to conduct their daily activities and for resource collection. We examined tiger presence and use of areas near villages located in the buffer zone to gain an understanding of how tigers respond to such human activity. We hypothesise that tigers avoid areas close to the villages due to the high human presence and activity.

4.2.8 Near water bodies

The availability of water in the buffer zone varies greatly across the seasons. In an earlier study, we recorded that, during daytime, herders and their livestock frequently access water bodies and habitually stay close to water (Kolipaka *et al.*, 2015). Their presence and activity were high within 250 m on either side of the water bodies. We hypothesised that tigers failed to utilise resources in areas where human presence and livestock activity is high. We therefore examined tiger presence near water in the human-use areas.

4.2.9 Statistical analysis

We conducted our final analysis on nine radio-collared tigers (three and six animals) and analysed 5 years of tiger VHF locations between 2010 and 2014 (see Table 1). We examined tiger presence in the three distinctive human-use areas and compared the percentage of tiger presence in these regions with the human-dominated buffer zone and the core area. Within the buffer zone, we examined the 2 km distances from villages and 250 m on either side of the water bodies. Since the high human-use areas are equivalent in size to the areas outside, it is possible to make a comparison between the two. The decision to measure presence inside or outside human-use areas necessitated the use of binary response variables in the analysis. We expected that tiger presence in the human-use areas would vary in relation to tiger-biological and ecological attributes treated as independent variables. For the first analysis, we included generation (first generation = adults and second generation = sub-adults), sex (male/female), seasons (summer, rainy, winter), day (7 am–6 pm)/night (6 pm–7 am) and year (2010–2014, continuous). We included two additional independent variables in the 2nd and 3rd analysis: zone (core/buffer) and livestock grazing areas (inside/5 km outside the village). Hourly tiger location fixes are naturally correlated, i.e. the spatial location of a tiger at a point in time is related to the spatial location in the next 1 h. We arbitrarily selected two location fixes for each day to create a random element to the data, as suggested by Oriol- Cotterill *et al.*, (2015). We randomly picked a daytime location fixed (5 am–5 pm) and one fix for night-time locations (6 pm - 6 am). All analyses were performed using SPSS ver. 23 (IBM Corp 2014) with the proportion of tiger fixes within the three predefined human-use areas as dependent (response) binary variables, using generalised linear mixed models (GLMM) with binomial logistic regression link function. Since we restricted data to nine tigers (30% of the population), we treated individual tigers as a random effect. That is, we treated the effects of this random variable as a random sample of the effects of all the tigers in the PTR. In the mixed-effects model (GLMM), sex, age group (generation), season, day/night, year (continuous), zone and 5 km buffer were treated as main effects and as two-way interactions. To examine trends (over time) in tiger presence, we used “year” as a continuous predictor. Adequate model fits ensure stepwise removal of non-significant ($p < 0.05$) two-way interactions and we optimised the model based on all main effects and only those two-way interactions that were significant (see Supplemental Appendices 1, 2 and 3 for coefficients and the model selection procedure). We present Akaike Information Criterion (AIC) of our final model fits to explain suitability of the best fit model.

4.3 Results

4.3.1 Presence of tigers in human-dominated buffer zone

Variations in the presence of tigers in the core zone and the human-dominated buffer zone are presented in the regression Table 2. In the best fit model (AIC 84,042.759, accuracy 81.8%), four out of five main effects and six two-way interactions are significant (Table 2; see also Supplemental Appendix 1 for regression coefficients). The important interactions are described below.

Table 4.2: Binomial logistic regressions of variables (main effects) and interactions between variables explaining tiger presence in the multiple use buffer zone of the Panna Tiger Reserve.

VARIABLES AND INTERACTIONS	F	DF1	DF2	SIG
Corrected model	18.276	14	16,452	P<0.000
Generation	14.159	1	16,452	P<0.000
Sex	1.450	1	16,452	P=0.229
Season	28.170	2	16,452	P<0.001
Day/ Night	85.085	1	16,452	P<0.001
Year	46.608	1	16,452	P<0.001
Generation & Day/Night	26.191	1	16.452	P<0.001
Generation & Year	26.732	1	16,452	P<0.001
Sex & Day/Night	6.937	1	16,452	P=0.008
Sex & Year	24.815	1	16,452	P<0.001
Seasons & day/night	3.743	2	16,452	P=0.024
Seasons & year	20.203	2	16,452	P<0.001
Significance is determined at p < 0.050; greater values are not considered significant.				

The presence in the buffer zone of second-generation tigers is 40%, which is about four times higher than for first-generation tigers. In this area, all tigers showed a higher nocturnal presence compared to the diurnal presence (temporal variation in presence). However, the nocturnal presence was twice as high as the diurnal presence among first-generation tigers and less pronounced in the sub-adult second-generation tigers (interaction: generation * day/night, p < 0.001, Table 2; Supplemental Appendix 4A). There is also a significant interaction between variables sex and day/night (Table 2). Male and female tigers showed no variation in their nocturnal presence in the buffer zone. However, during the daytime, female tiger presence was higher in the buffer zone than male tiger presence (interaction: sex * day/night, p = 0.008, Supplemental Appendix 4B).

Tiger presence in the buffer zone varied seasonally, with a significantly higher presence during the rainy and winter seasons and significantly lower presence in the summer. During the rainy and winter seasons, temporal variation in tiger presence (nocturnal to the diurnal difference in presence) was also low. In the summer, overall tiger presence in the buffer zone was low, but tigers maintained a higher temporal variation. Their night-time presence was greater than during the day (interaction: season * day/night, $p = 0.024$, Supplemental Appendix 4C). Over a period of 5 years, all tigers showed a decreasing trend, over time, in terms of presence in the buffer zone (Figure 3D, coeff: −0.307, $p < 0.001$). This decrease is much stronger among second-generation tigers (coeff: −0.281, $p < 0.001$) than among first-generation tigers. Between sexes, male tigers show a continuing trend in terms of presence (coeff: −0.242, $p < 0.001$), unlike female tigers. There were no significant changes in tiger presence between seasons, with a higher tiger presence in the winter and rainy seasons than during the summer months (coeff: 0.339, $p < 0.001$; Table 2).

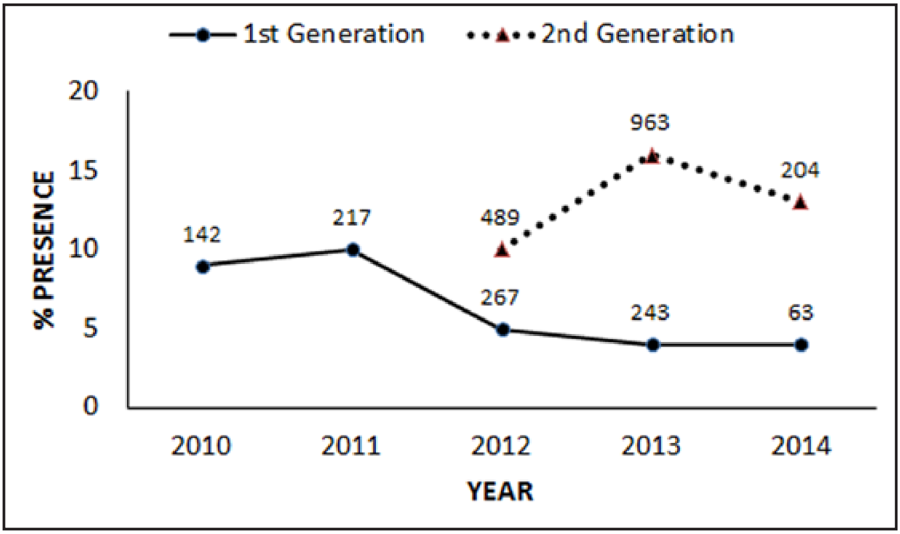

Figure 4.3 The change in first- and second-generation tiger presence near villages that transpired over a 5-year period between 2010 and 2014 in PTR. (N, randomly sampled tiger VHF location fixes).

4.3.2 Presence near villages

Table 3 presents the results of the statistical analysis of the presence of tigers near villages. This analysis focuses on the tiger use of areas where human presence and activity is very high. In the best fit final model (AIC 87.393,131, accuracy 84.5%), three out of the six main effects and eight two-way interactions are significant (Table 3, see also Supplemental Appendix 2 for regression coefficients). The important interactions are described below.

Table 3: Binomial logistic regression of variables (main effects) and interactions between variables explaining tiger presence within 2 km of the villages located in the buffer zone of the Panna Tiger Reserve.

VARIABLES AND INTERACTIONS	F	DF1	DF2	SIG
Corrected model	43.542	18	16,448	P<0.001
Generation	1.104	1	16,448	P=0.293
Sex	2.849	1	16,448	P=0.091
Seasons	19.755	2	16,448	P<0.001
Day/Night	0.939	1	16,448	P=0.333
Year	16.843	1	16,448	P<0.001
Zone-cl	5.585	1	16,448	P=0.018
Gen & Seasons	3.658	2	16,448	P=0.026
Gen & Year	57.214	1	16,448	P<0.001
Gen & Zone_cl	243.769	1	16,448	P<0.001
Sex & Season	3.389	2	16,448	P=0.034
Sex & Year	19.150	1	16,448	P<0.001
Sex & Zone_cl	56.145	1	16,448	P<0.001
Season & Year	10.416	2	16,448	P<0.001
Year & Zone_cl	10.574	1	16,448	P=0.001

Three out of the six variables are not significant on their own but significant as interactions. Significance is determined at $p < 0.050$; values greater are not significant. The variables generation and sex interact significantly with seasons (Table 3). Second-generation tiger presence near villages is considerably higher than the presence of first-generation tigers (interaction: generation * zone, $p < 0.001$, see Table 3; Supplemental Appendix 4D). The presence of sub-adult tigers near villages was consistently greater than that of first-generation tigers in all three seasons and throughout the study period. Between sexes, male and female tigers were equally present near villages and did not show any sex-biased difference in their presence (interaction: sex * zone, $p < 0.001$, see Table 3; Supplemental Appendix 4E). The difference between males and females was in the location of their presence. Female tiger presence was higher near those villages that are very close to the core zone, while male tiger presence was also high near villages that were far from the core area. Moreover, this difference in presence between the sexes was consistent and significant for all the three seasons (Table 3). Second-generation tigers and male tigers showed significantly higher presence near villages during the rainy season; this decreased marginally during the winter months and was least in the summer season (interactions generation * season, $p = 0.026$; Table 3; Supplemental Appendix 4F); (interactions sex * season, $p = 0.034$; Table 3; Supplemental Appendix 4G). The tiger presence near villages changed gradually over the 5-year study period. The first-generation tiger presence near the villages decreased further but the decline in second-generation tiger presence was very gradual and continued to be higher than the first-generation tigers (coeff: 0.467, $p < 0.001$). Between sexes, male tigers showed a stronger declining trend than females in terms of presence over time near the villages (Male: coeff: −0.254; $p < 0.001$; Figure 4). Within seasons, tigers continued to show a significantly higher presence near villages during the rainy and winter seasons and this presence decreased to the lowest levels during the summer months (summer: coeff: 0.316, $p < 0.001$; Figure 5).

4.3.3 Presence near water bodies

Table 4 presents the results of the statistical analysis of the presence of tigers near water bodies. This analysis focuses on tiger presence near water bodies used by people and livestock. In the best fit final model (AIC 80,937.956, accuracy 83.6%), three out of seven main effects and seven two-way interactions are significant (Table 4, see also Supplemental Appendix 3 for regression coefficients). The important interactions are described below.

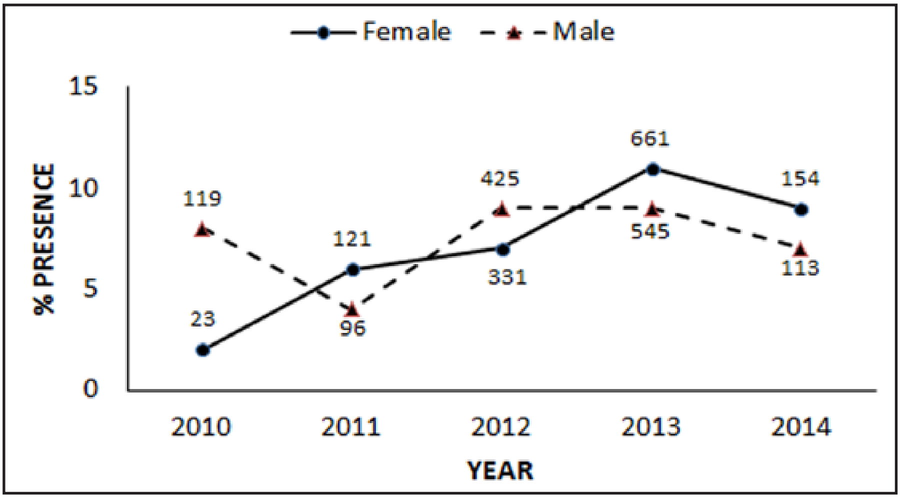

Figure 4.4 The change in the male and female tiger presence near the villages that transpired over a 5-year period between 2010 and 2014 in PTR. (N, randomly sampled tiger VHF location fixes).

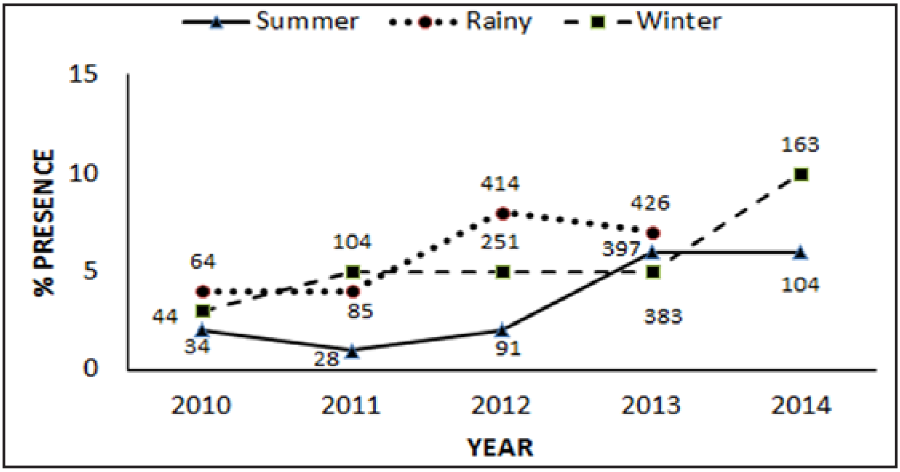

Figure 4.5 The seasonal change in tiger presence near the villages that transpired over a 5-year period between 2010 and 2014 in PTR. (N, randomly sampled tiger VHF location fixes).

Table 4.4: Binomial logistic regression of variables (main effects) and interactions between variables explaining tiger presence within 250 m of water bodies and in livestock herding areas.

VARIABLES AND INTERACTIONS	F	DF1	DF2	SIG
Corrected model	11.587	18	16,449	P<0.001
Generation	1.842	1	16,449	P=0.175
Sex	1.386	1	16,449	P=0.239
Season	8.547	2	16,449	P<0.001
Day/Night	3.403	1	16,449	P=0.065
Year	0.837	1	16,449	P=0.360
Zone_cl	4.461	1	16,449	P=0.035
Points_in_ 5k_buffer	7.736	1	16,449	P=0.005
Gen & Seasons	14.278	2	16,449	P<0.001
Gen & Year	7.226	1	16,449	P=0.007
Sex & Season	6.379	2	16,449	P=0.002
Sex & Year	14.158	1	16,449	P<0.001
Sex & Zone	11.370	1	16,449	P=0.001
Sex & Points in 5km buffer	10.049	1	16,449	P=0.002
Seasons & Zone	3.032	2	16,449	P=0.048

Seasons (as the main effect) and six interacting variables significantly explain tiger presence near water and livestock grazing areas. Significance is determined at $p < 0.050$; greater values are not significant.

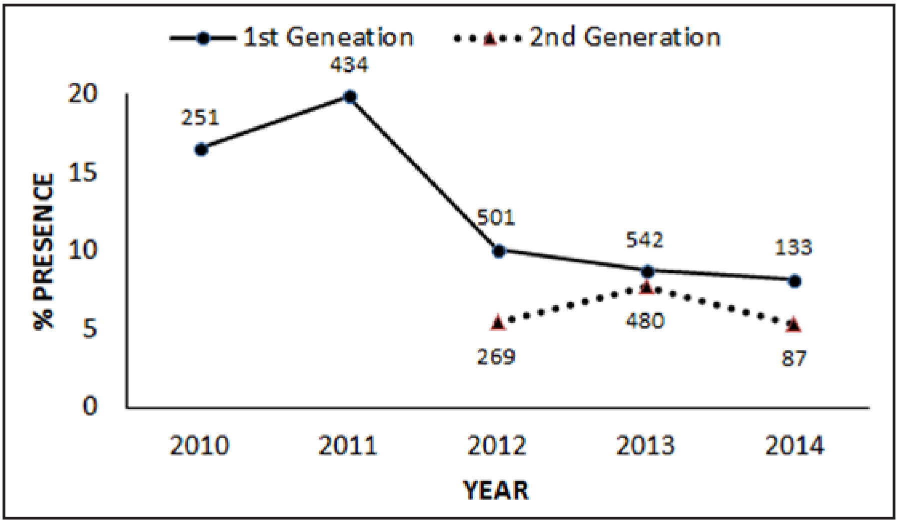

Figure 4.6 The seasonal change in the first- and second-generation tiger presence near water bodies that transpired over a 5-year period in PTR between 2010 and 2014. (N, randomly sampled tiger VHF location fixes).

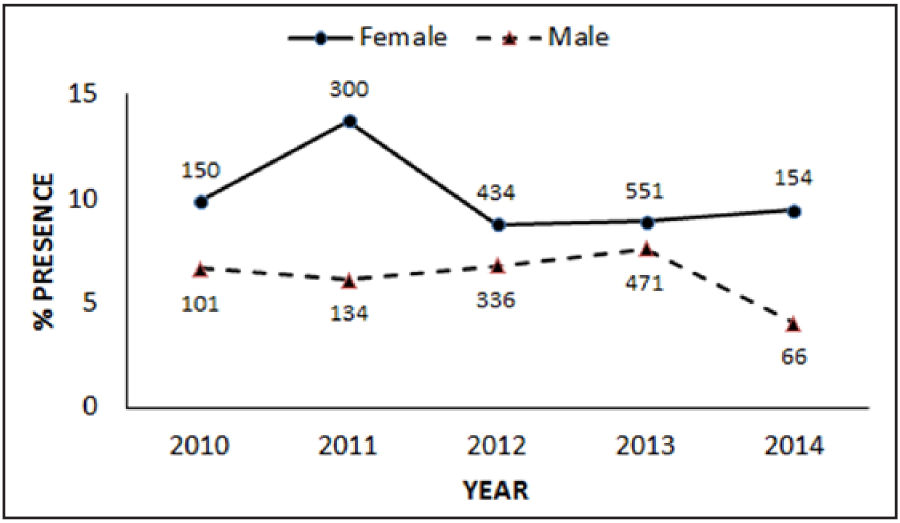

Figure 4.7 The change in the male and female tiger presence near the water bodies that transpired over a 5-year period in PTR between 2010 and 2014. (N, randomly sampled tiger VHF location fixes).

VHF-radio-collared tigers spent 25% of their time at locations close to water. Tiger presence near water was the highest during the summer months and declined over the rainy and winter seasons. This seasonal difference in presence near water did not change while tigers were in the core zone or the buffer zone (Supplemental Appendix 4L). However, we observed age related differences among tigers and their presence near water. Male and female second generation tigers that used the buffer zone spent considerably less time near water during the summer (interactions generation * season; $p < 0.001$; Table 4; Supplemental Appendix 4H) and (interactions sex * season; $p = 0.001$; Table 4; Supplemental Appendix 4K) this reduced presence of tigers near water while in the buffer zone did not change over the 5-year study period ($p = 0.007$; Figure 6). When tigers used livestock grazing areas, at a 5 km distance around the villages, their presence near water was also low (interaction sex * 5 km circle; $p = 0.002$; Table 4; Supplemental Appendix 4J).

4.4 Discussion

We examined variations in tiger presence in areas with high human presence and activity. We discussed the observed variations and focussed on the implications for tiger conservation in human-use areas. Our analysis shows that between 2009 and 2014, as tiger numbers grew in the Panna Tiger Reserve from six founder animals to over 30 animals, tiger presence also increased in the adjacent human-dominated buffer zone. The increase was most pronounced in second-generation tigers or sub-adults in comparison to first-generation adult tigers. This outward expansion of sub-adult tigers from the protected core zone of the PTR into the adjacent human-use areas is most likely because of intraspecific competition with the dominant tigers and the need for younger tigers to disperse from their natal areas and establish their territories (Goodrich *et al.*, 2010). These are naturally occurring tiger behaviours and when they occur in a small-sized protected area like the PTR, where tiger home ranges are relatively larger than the available space within the protected area (Chundawat *et al.*, 2016), tigers inevitably move into the adjacent buffer zones and the unprotected landscape beyond the PTR. We found remarkable differences between groups of tigers in the use of the shared spaces. The group of sub adult tigers used the shared spaces both during the day, when human and livestock activity was high and at night, when such activity was low. In comparison, the group of adult, first-generation tigers revealed a higher nocturnal presence, showing temporal variation in their use (Supplemental Appendix 4A). Temporal partitioning by tigers while using human-use areas is reported by Carter *et al.*, (2012) from their studies in Nepal. Such use of shared spaces when human activity is low may decrease confrontation with people. However, our analysis demonstrates that some, but not all tigers have the opportunity for temporal partitioning. In the PTR, it is the dominant adult tigers that show greater temporal partitioning while using human-use areas compared to sub-adult second generation tigers.

We also noticed that tigers dispersing through the human-dominated landscapes rested close to the villages during the day, most likely because they did not have other options. Both male and female sub-adult tigers approached areas near the villages much more than adult tigers. People conduct their daily activities near villages and village cows congregate unguarded in these areas at night (Kolipaka *et al.*, 2015). There is also an abundance of unguarded domestic prey in the PTR as a result of domestic cow management practises (Srivastava 2014, Kolipaka *et al.*, 2015). As a result, tigers are increasingly killing livestock (Kolipaka *et al.*, 2017b). Moreover, the forced removal of a sub-adult third-generation tigress from a village in the buffer zone in 2016, as evidenced by newspaper reports (TOI, 2016), demonstrate the negative consequences of sub-adult tigers engaging in livestock raids close to the villages. The sub-adult tiger presence near the villages peaked to 16% during 2012 and showed a slow decline in 2013. We cannot comment on whether their presence further declined as we only have 2 years of data on sub-adult tigers. We can speculate that the initial increase in presence near the villages may be a result of chance encounters of sub-adult tigers with villages while establishing new territories. Further, lenient local grazing practices (Srivastava 2014, Kolipaka *et al.*, 2015) and the seasonally changing vegetation near the villages may provide the cover tigers need when hunting for prey near villages without being detected. Our studies on tiger diet in the buffer zone of the PTR reveal that sub-adult tigers and adult male tigers kill greater numbers of domestic prey animals, even in areas where wild prey is available (Kolipaka *et al.*, 2017a). However, our studies do not reveal any significant increase of tiger kills in the neighbouring villages. In fact, tigers are known to be wary of people and avoid encounters with humans (Karanth and Gopal 2005).

We also offer an alternative explanation for the sub-adult tiger presence near villages using the “concept of naivety” amongst young carnivores (Kojola *et al.*, 2016). Kojola *et al.*, (2016) observed that young, sub-adult wolves approached areas close to human settlements much more frequently than adults during the initial dispersal periods from the natal pack. However, with age, they changed this behaviour and avoided villages. The initial increase and subsequent decrease in sub-adult tiger presence near villages, especially among younger male tigers, may be due to the “naivety” of the sub-adult tigers. This decrease, however, should not be confused with the natural decrease that comes with the readjustment of home ranges as tigers age. Future research should focus on this “naivety hypothesis” in young tigers as they could become vulnerable to conflicts while in human-use areas. The reduced conflicts as a result of complete, partial, or even temporal avoidance of areas close to villages can have positive consequences for tiger survival. We see the decrease in tiger presence, over time, near villages in the PTR as a positive sign. While we know the risks to livestock from tigers using the areas near villages, the risks to human life and safety from tigers cannot be ascertained in this study because there have been no reported tiger attacks on people in the PTR. The low number of human attacks may also be a result of the high awareness amongst residents about carnivores and the prevailing traditional norms that regulate the presence of people (not domestic cows) in the forests of PTR after dark (Kolipaka *et al.*, 2015). In contrast, tiger attacks leading to injuries and even deaths of people are frequent in the buffer zone of the Bandhavgarh Tiger Reserve, which is just 300 km away from the PTR (Pers Comm: R. Sreenivasa Murthy). This difference is most likely as a result of people’s awareness about tigers and people’s use of shared areas. We hypothesise that a combination of factors, including peoples’ practices, environmental factors, distribution of prey in the areas and the individual characteristics of tigers (sub-adult/adult, male or female) are better predictors of tiger presence near villages than one single factor. Overall tiger presence in the buffer zone also decreased during our 5-year study period. The observed initial increase and subsequent decrease in overall tiger presence in human-use areas are most likely because of dynamic shifts in individual tiger territories. As sub-adult tigers grow in age, some of them may reclaim territory and readjust their home ranges (Goodrich *et al.*, 2010, Chundawat *et al.*, 2016) and use less of the buffer zone. However, this change did not last long in PTR. A new, third generation of tigers was added to the population and new, sub-adult tigers moved into the human-use buffer zone and continued using areas near villages (TOI, 2016).

4.4.1 Tiger presence near shared water bodies

As expected, tiger presence near water bodies in the PTR was significantly higher in the hot summer months than during the winter and rainy seasons. Overall, tigers spent a quarter of their time in areas near water. Their prominence near water suggests the importance of this habitat to tigers. Recent ex-situ studies on tigers indicate that tigers benefit in several ways from access to water, including improved self-grooming, biological functioning through immersion, affiliative behaviours, ability to hide and beneficial interactions with their surroundings (Biolatti *et al.*, 2016). Tigers using the buffer zone spent less time near water during the summers than tigers using the core area. Tigers also spent less time near water when they were present in the livestock grazing areas. This situation did not improve during the study period (Figure 7). Tigers that moved further away from the periphery of the core zone are affected more than those that remained close, in this case, mostly sub-adult tigers and male tigers. We understand from the studies on African lions that human and livestock activities in shared areas restrict lions from exploiting the resources in these places (Oriol-Cotterill *et al.*, 2015). We suspect that tigers in the PTR are also impacted by such human factors while using areas with human activity.

4.5 Concluding remarks and recommendations

In tiger reserves like the PTR, which are surrounded by human-dominated landscapes, the likelihood of sub-adult tigers and dispersing tigers using human-use areas is high. It is encouraging that adult tigers that breed and add offspring to the source pool – vital from a conservation perspective – show temporal partitioning while using human-use areas. However, sub-adults tend to approach villages readily, creating challenges for management. Over time, there was a decline in this behaviour. Second-generation tigers also reorganised their territories, and there was an overall decline in tiger presence in the buffer zone during our study period. However, a third generation of tigers was born in the PTR and they recolonised the human-use areas. This recurring pattern of new, sub-adult tigers moving into human-use areas is likely to continue. At this stage, it is unclear whether the presence of tigers in human-use areas increases risks to human safety or tiger survival, but higher livestock losses do occur. We give due warning in this regard that, left unaddressed, this situation has the potential to increase conflict between humans and tigers. To manage tigers in source pools like the PTR, which are surrounded by human-use landscapes, managers must invest in long-term conservation programmes aimed at encouraging changes to people's practices in such landscapes. This includes the use of corrals for cows, discouraging free grazing and dumping dead animal carcasses within designated areas and not in forests. The abovementioned activities are not compatible with multiple-use and will encourage tigers to kill unguarded livestock and approach the villages. By regulating people's use of the forests, the risks to people and livestock from tigers can decrease. Further, it will allow tigers to use water and feral cows within shared landscapes to their advantage. Finally, monitoring of sub-adult tigers that readily use areas near villages and marginal lands will be integral to tiger survival in human-use areas.

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