

Elevated potential for intraspecific competition in territorial carnivores occupying fragmented landscapes

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ABSTRACT

The distribution of mammals is determined by a suite of endogenous and exogenous factors. In territorial, polygynous species like tigers (*Panthera tigris*), males often center their space-use around female territories, repelling competitors from these areas. Competition among males for females leads to increased mortality of both sexes and infanticide of unrelated cubs, which can lead to population declines. We hypothesized that increased territorial overlap among adult male tigers and elevated levels of inter and intra-sex competition would be manifest in populations with male-biased adult sex ratios (ASR). We also assessed whether inter-sex variation in adult survival or degree of habitat connectivity resulted in skewed ASR. We evaluated these hypotheses using camera trap data from three tiger populations occupying habitat patches with varying levels of connectivity and ASRs. Data were analyzed using multi-state occupancy models, where states were defined as habitat use by one or more male tigers in sites with and without female use. As predicted, in populations with male-biased or even ASR we found evidence for increased spatial overlap between male tigers, particularly pronounced in areas adjacent to female territories. Given parity in adult survival, habitat fragmentation likely caused male-biased ASR. Our results suggest that the persistence of small tiger populations in habitat patches with male-biased ASR may be significantly compromised by behavior-mediated endogenous demographic processes that are often overlooked. In habitat fragments with pronounced male biased ASR, population recovery of territorial carnivores may require timely supplementation of individuals to compensate for population losses from intraspecific competition.

1. Introduction

Adult sex ratio (ASR, male:female) is an important demographic parameter that influences both individual behavior and population dynamics (Caswell, 2001; Haridas et al., 2014; Le Galliard et al., 2005; Székely et al., 2014). Skewed or uneven sex ratios in animal populations can occur for a variety of reasons, including sex differences in survival due to disproportionate costs of reproduction for females and sex-biased immigration or emigration by males (Veran and Beissinger, 2009). It has been hypothesized that ASR in many species may also be an artifact of intrasexual competition which can result in increased mortality or dispersal of the sex with higher frequency in a population (Clutton-Brock et al., 2002; López-Sepulcre et al., 2009). Male-biased sex ratios may result in increased aggression by males towards females, resulting in a decline in their fecundity and survival with negative effects on population growth and persistence (Barrientos, 2015; Grayson et al.,

2014; Le Galliard et al., 2005).

In polygamous species, adult male territories often encompass the territories of multiple females. Skewed ASR's may have pronounced impacts on the behavior and demography of carnivores—for example, intraspecific predation has been documented in at least 14 large carnivore species (Polis, 1981). Territorial disputes may result in the killing of immature animals by adult males and has the potential to substantially reduce population size (Polis, 1981). When first acquiring a female territory, adult male carnivores are known to seek out and kill non-related juveniles to increase their reproductive fitness (Barlow et al., 2009; Hrdy, 1979; Persson et al., 2003). Additive mortality from intraspecific competition and infanticide may be especially detrimental for small populations of several terrestrial carnivores that are already vulnerable to extinction (Chapron et al., 2008).

Worldwide, large carnivores face high extinction risks, in part because of their extensive area requirements, extensive and accelerating

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Table 1

Five occupancy states for male tigers and associated patterns of habitat-use, and specific predictions in relation to ASR.

Occupancy state for male tigers		Probability of fine-scale habitat use by male tigers		Specific hypotheses
		Category 1	Category 2	
State 1 (1- Ψ - Ψ)	No male use	Very High (+ +)	Very Low (– –)	High probability that large areas of available habitat may go unused by male tigers in sites with male-biased ASR, because males hone in on female territories.
State 2 Ψ (1-f)	Use by single male tiger and no female use	High (+)	Low (–)	A few dominant males are expected to secure and restrict access to females in sites with male-biased ASR. Thus, higher likelihood of male tiger use outside of female territories is expected.
State 3 Ψ (f)	Use by single male tiger and female use	Low (–)	High (+)	In sites with male-biased ASR, males with compete fiercely for access to females. In sites with female-biased ASR, there is a higher probability that every male tiger in the population will have access to one or more female(s).
State 4 Ψ' (1-f)	Use by multiple male tigers and no female use	Very High (+ +)	Low (–)	High probability of shared habitat use by multiple male tigers in sites with male-biased ASR because of increased intraspecific competition for mates. Shared use of sites expected in the vicinity of female home-range boundaries.
State 5 Ψ' (f)	Use by multiple male tigers and female use	High (+)	Low (–)	High probability of shared habitat use by multiple male tigers in sites with male-biased ASR because of increased intraspecific competition for mates. Territorial behavior may reduce shared use of locations, relative to sites with no female use.

Footnotes:

Category 1 sites (i.e. Dudhwa National Park and Katerniaghat Wildlife Sanctuary) have the following characteristics: poor habitat connectivity, male-biased/even ASR and lower adult survival rates (expected).

Category 2 (i.e. Kishanpur Wildlife Sanctuary) has the following characteristics: good habitat connectivity, female-biased ASR and higher adult survival rates.

habitat loss and real or perceived conflicts with humans (Ripple et al., 2014). Tiger (*Panthera tigris*) populations are especially at risk because of illegal global trade in their pelts and other body parts. As a consequence, as few as 3900 individuals may currently exist in the wild (WWF, 2016) and remnant populations are small with fewer than 20 populations > 50 individuals. While the risk of local extinction is primarily driven by illegal hunting and habitat loss and fragmentation, several endogenous behavioral factors may exacerbate extinction risks of small populations. For example, aggressive behaviors arising from territorial disputes may be an additive source of mortality. Intraspecific competition and aggression, especially in areas with male-biased ASR, can increase the extinction risk for small populations (Barlow et al., 2009). Adult male tigers fiercely defend their territories from competing males in order to retain access to breeding females (Horev et al., 2012; Sunquist, 1981). If a dominant territorial male is displaced by a rival, the outcome is often infanticide of the former's cubs by the later (Barlow et al., 2009; Smith and McDougal, 1991). Loss of their original mate results in females more quickly becoming reproductively accessible to the new dominant male. The harem size of male tigers and degree to which breeding males are able to maintain stable territory sizes can profoundly impact population dynamics and extinction rates (Horev et al., 2012).

Several aspects of the social behavior of tigers, including a polygynous mating system, territoriality and dispersal, are relevant to demography, behavior and space-use. Female tigers select territories to secure access to adequate resources to protect and raise young (e.g., sufficient prey, cover and water), and males compete for territorial dominance of one or more females (Goodrich et al., 2008; Smith, 1993; Smith and McDougal, 1991; Sunquist, 1981). In South Asia, male tiger territory size is usually > 100 km², while females maintain territories between 10 and 30 km² (Sunquist, 1981). Dispersal is also typically male-biased: adult females tolerate their female offspring establishing territories in close proximity to their own, but male offspring are driven away. Young males in search of new territories often disperse over large distances and commonly experience aggressive interactions with other males (Reddy et al., 2016; Smith, 1993). Although published information is sparse, ASR (males:females) between 1:2 and 1:3 have generally been reported from South Asia (Majumder et al., 2017; Sunquist, 1981). Some studies in India, however, have revealed that densities and sex ratios of adult tigers can vary widely (Sadhu et al., 2017), and may even be male-biased (Chanchani et al., 2014a).

Considering the social and population biology of tigers raise several

questions relevant to tiger spatial ecology, especially in fragmented landscapes with small populations. Foremost is whether there is a high potential for intraspecific competition, infanticide and antagonism among tigers due to high levels of habitat use (i.e., site occupancy) by multiple male tigers, with and without female tigers. Second, does variation in ASR affect patterns of fine-scale habitat use by male tigers, such that we might expect higher potential intraspecific competition in local populations with male-biased ASR? Lastly, what are the relative contributions of sex-biased emigration, limited habitat connectivity, or differences in sex-specific adult survival rates to inter-site variations in ASR?

To evaluate these hypotheses, we analyzed an extensive camera trap dataset for a tiger population in the Dudhwa Tiger Reserve (DTR) – a 1200 km² protected area within the Central Terai Landscape (CTL) in North India. DTR consists of three disjoint protected areas (subsequently referred to as, 'sites'). Sites are characterized by pronounced differences in tiger density, habitat connectivity and variation in ASR—ranging from high connectivity, high density and female-biased ASR to isolated, low density and male-biased ASR (Chanchani, 2016). Given the polygynous mating-system in tigers, sites with an even sex ratio, or those with more adult males than females were deemed as having male-biased ASR. We tested the null hypothesis that the probability of habitat use (fine-scale occupancy) by one or more male tigers would be unrelated to a site's ASR. Alternatively, we proposed two hypotheses about changes in fine-scale space-use patterns by male tigers occupying sites with male-biased ASR. First, we hypothesized that otherwise suitable habitat areas distant from female territories would infrequently be used by male tigers (hypothesis 1, Table 1). Second, we hypothesized that pronounced competition among males for access to females lead to the following space-use patterns: (a) high male-use in locations along the margins of female territories (hypotheses 2 and 4, Table 1); and (b) a high probability that multiple male tigers would "use" female territories (hypotheses 3 and 5, Table 1). Our hypotheses are based on the expectation that harem sizes are smaller in areas with male-biased ASR, and multiple males are thus expected to compete intensively for access to each female (Table 1). Finally, to investigate factors contributing to male-biased ASR in isolated sites, we assessed if male distribution was related to inter-sex differences in movement probabilities, a consequence of differences in dispersal behavior or the effects of habitat fragmentation (Smith, 1993).

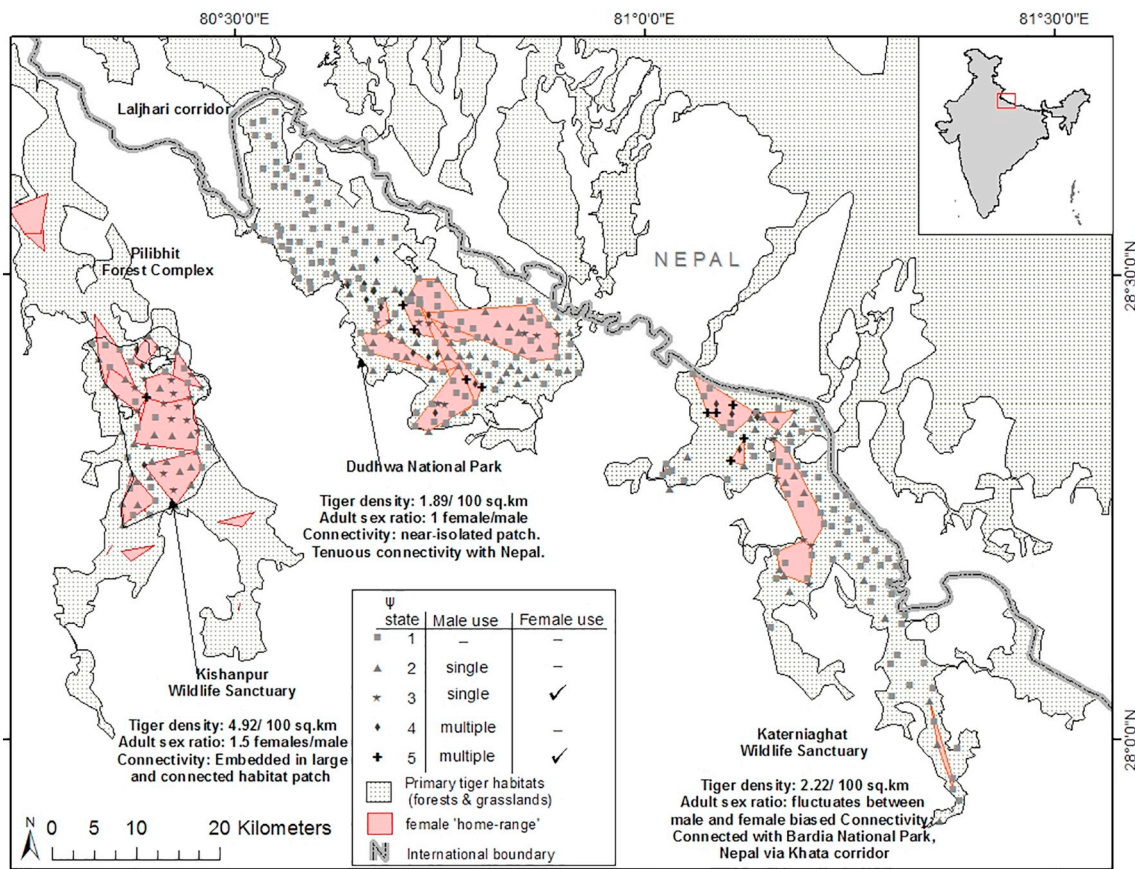


Fig. 1. Map of the Central Terai Landscape depicting female home range locations, and state-wise photo-capture locations of male tigers (in 2013). The approximate 'home ranges' of females tigers (defined by minimum convex polygons around capture locations) are delineated in pale red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2. Materials and methods

2.1. Description of study area

Dudhwa Tiger Reserve is located in the Terai-Duar savannas and grasslands ecoregion that extends to areas in Nepal, India, Bhutan and Bangladesh (Olson and Dinerstein, 1998; Fig. 1). DTR includes Dudhwa National Park (~700 km²), Katarniaghat Wildlife Sanctuary (~450 km²) and Kishanpur WLS (~200 km²), established in 1977, 1975 and 1972 respectively. DTR's productive wildlife habitats, grasslands and wetlands, comprise approximately 18% of the overall area. Other habitats include dry deciduous sal (*Shorea robusta*) forests, and mixed-dry deciduous forests and teak (*Tectonia grandis*) plantations. Within India, the last remnant patches of once-extensive grassland-wetland habitats that characterize the CTL are now restricted to small, fragmented areas in and around DTR. Management of the Reserve has undergone drastic changes over the past 150 years. Through the 19th century and until about 1960, large forest tracts were designated hunting areas for India's colonial administrators and Indian royalty. Other areas within DTR were intensively managed for sal timber production (Strahorn, 2009).

The three protected areas (PAs) of DTR vary in connectedness with other tiger habitats in India and Nepal. Kishanpur Wildlife Sanctuary is embedded within a large area of suitable tiger habitat (~1400 km² Pilibhit forest complex in India) and connected with Shuklaphanta Wildlife Sanctuary in Nepal via the Sharda River corridor. Katarniaghat WLS is connected to the 968 km² Bardia National Park via the 40 km Khata corridor (along the Karnali River). In recent decades, connectivity between Dudhwa National Park and Laljhari and Basanta community forests in Nepal has been severely degraded due to land use

change and expanding human settlements (Chanchani et al., 2014b; Joshi et al., 2016; Kanagaraj et al., 2013). Finally, tiger density and ASR in DTR's three PAs vary extensively. The highest tiger density (4.66 and 4.92 tigers/100 km²) and most female-biased ASR (adult males = 29% of population) were recorded from Kishanpur WLS in 2013 (Chanchani et al., 2014a; Table 2). In contrast, tiger densities were lower in Katarniaghat WLS (4.72 and 2.22 tigers/100 km², 61% and 33% males in 2012 and 2013 respectively) and Dudhwa National Park (1.05 and 1.89 tigers/100 km², 58% and 47% males in 2012 and 2013) (Jhala et al., 2015; Chanchani, 2016; Table 2). Adult sex-ratio estimates are precisely known because they are based on a near-census of the target populations (Appendix A).

2.2. Camera trap sampling

Between November 2011 and June 2013, we conducted extensive camera-trap surveys to assess the status of tigers in the CTL (Fig. 1). We used a grid-based sampling design and positioned pairs of cameras at intervals of approximately 2 km within tiger habitats. Pairs of camera traps were placed along animal movement routes (forest trails or drainages) to maximize detection probability. Surveys were completed in ≤ 60 days to meet the closure assumption of occupancy and capture recapture models (Karanth et al., 2002). At each location, cameras were operated from 14 to 56 days. Overall, 304 locations were sampled with camera traps from November 2011–May 2012, and 380 locations were sampled from November–June 2013 (Table 2).

2.3. Data processing, model formulation and analysis

To evaluate our a priori hypotheses, we fit multi-state occupancy

Table 2

Details of camera trap effort in DTR's three protected areas. p_{mix} is the estimated proportion of males in the population based on a spatially-explicit, capture-recapture model. DNP and Katerniaghat have male-biased/even sex ratios and relatively poor habitat connectivity. Kishanpur has female-biased sex ratios and good habitat connectivity.

Site	Year	No. of cameras	Effort (trap nights)	No. of unique individuals detected	Total captures	No. of females	No. of female captures	No. of males	No. of male captures	Males/female ^a	Estimated tiger density/100 km ^{2b}
DNP	2012	159	2626	14	126	5	42	9	84	1.80	2.05 (0.38)
DNP	2013	202	4861	14	274	7	92	7	182	1.00	1.89 (0.34)
Katerniaghat	2012	82	2190	18	88	7	35	11	53	1.57	4.72 (0.92)
Katerniaghat	2013	111	3663	17	207	11	106	7	101	0.636	2.22 (0.40)
Kishanpur	2012	63	2648	16	264	11	119	8	145	0.727	4.66 (0.67)
Kishanpur	2013	67	2655	15	254	9	151	6	103	0.667	4.92 (0.88)
Totals		684	18,643	94	1213	50	545	48	668		

^a Adult sex ratio, calculated as the number of males/female. Measures of uncertainty are not included because mark-recapture analyses indicated we censused the population.

^b Density estimates from Bayesian spatially capture-recapture analyses reported in Chanchani et al. (2014a).

models to the camera trap data (Nichols et al., 2007). Such data have been traditionally analyzed in a mark-recapture framework to estimate abundance and/or survival, but these data are increasingly being used to also estimate of patch occupancy and species co-occurrence (O'Connell and Bailey, 2011). We applied multi-state occupancy models to test hypotheses about tiger distribution in the context of variable habitat connectivity (Johnsingh et al., 2004; Kanagaraj et al., 2013; Wikramanayake et al., 2004; Nichols et al., 2007) and ASR within habitat patches in our study area.

Photo-captured adult tigers were individually identified by three independent observers and by using pattern recognition software (Hiby et al., 2009). The sex of all tigers was discernible from the photos, allowing us to assign habitat-use states by sex and individual. We defined a sampling occasion as a 14-day period corresponding to the duration over which tiger spray scent (used for territorial marking) remains detectable (Smith et al., 1989). At each camera trap location and sampling occasion, male tiger captures were assigned to one of five habitat-use states. These states indicated probability of use of locations by single (ψ) or multiple (ψ') male tigers, in the context of female use (presence/absence) (f ; Table 1). Tiger habitat use states were defined as: State 1, no male use ($1 - \psi - \psi'$); State 2, location use by a single male and no female use ($\psi \times (1 - f)$); State 3, use by single male, and any female ($\psi \times f$); State 4, use by multiple males and no female use ($\psi' \times (1 - f)$); and State 5, use by multiple males, and female use ($\psi' \times f$). Notations in parentheses are mathematical probability statements uniquely identifying each state. We accounted for state-uncertainty by estimating misclassification probabilities – for example, we might record the presence of a male tiger during a 14-day occasion (observe state 2) even though females were also present (true state 3); the probability of this misclassification is $p_{3,2}$ (Fig. 2). We estimated model parameters using a hierarchical Bayesian multi-state occupancy model (Kery and Schaub, 2012; Royle and Dorazio, 2008). The true (latent) state of each location (trap station), z , can take on values equal to 1, 2, 3, 4 or 5, corresponding to the five habitat use states. Latent occurrence, z , is modeled by estimating Ω_i , the state vector describing the probability that site i is in one of the five states. The observation process describes how the true state z is linked with the observations, y_{ij} , the observed states of tiger habitat use at site i on occasion j . The conditional relationship between y_{ij} and z is described by a categorical distribution with the θ_z representing the observation matrix (Fig. 2). Elements of the observation matrix are the probabilities of observing tiger use in each of the five states. Diagonal elements are the probabilities of correct classification and off-diagonals elements are the probabilities of misclassification. Probabilities in each row of the observation matrix sum to 1. Detection probabilities were allowed to vary among survey occasions (2 week-long periods).

Because sex-specific fine-scale habitat use by tigers was unknown, we specified vague logit normal priors for ψ and ψ' (Fig. 2). The prior for f was modeled as a beta distribution, implying a uniform probability

between 0 and 1. We used Dirchlet priors to describe the distribution of elements within the rows of the observation matrix ($p_{n,k}$: $p_{1,k}$, $p_{2,k}$, $p_{3,k}$, $p_{4,k}$, and $p_{5,k}$), where n represents the true state of a site and k represents the observed state. The Dirchlet distribution satisfies the requirement that the elements of each row of the observation array sum to 1 (Hobbs and Hooten, 2015; Kery and Schaub, 2012). We fit the Bayesian model using Markov chain Monte Carlo (MCMC) algorithms implemented in program JAGS (Plummer, 2003) linked to R (R Development Core Team). We separately analyzed data for three PAs in DTR in each of the two survey years, unless there were fewer than 2 sampling occasions. Data-sets were all fit using three chains (to assess parameter convergence), each with 100,000 MCMC iterations, and a burn-in value of 10,000.

2.4. Model support and evaluation

To assess departures from similarity for posterior distributions of estimated parameters we used a one-sided test based on Bayesian p values. This allowed us to test whether a given prediction was supported — for example, that probability of multiple-male tigers using a location would be higher at sites with male-biased ASR ($\psi'_{site2} \times f_{site2}$) than in sites with female-biased ASR ($\psi'_{site1} \times f_{site1}$) — we derived:

$$\sum_{i=1}^{n.mcmc} ((\psi'_{site2} \times f_{site2}) - (\psi'_{site1} \times f_{site1})) > 0/n.mcmc,$$

where $n.mcmc$ is the number of MCMC iterations. If the posterior distributions were identical, we expect a value of 0.5 (i.e., given any value from $(\psi' \times f)_{site2}$ compared to $(\psi' \times f)_{site1}$, 50% will be greater). Values > 0.5 indicate support for the hypothesis. In a scenario where all samples in $(\psi' \times f)_{site2} > (\psi' \times f)_{site1}$, we expected a Bayesian p value of 1.

We assessed model fit via a posterior predictive check where simulated datasets for each site/year were compared to the original datasets (Gelman and Hill, 2007). We examined whether the probabilities of the observed data were more extreme than the simulated data. These checks revealed no evidence of lack of fit (Appendix B).

2.5. Estimating survival

We used Cormack-Jolly-Seber (CJS) models to estimate apparent annual survival rates for adult tigers (Lebreton et al., 1992). We refer to 'apparent' survival because mortality cannot be discriminated from permanent emigration and survival for at least one year (Karanth et al., 2006). Data on tiger survival were available from a four-year (2010–2014) capture-recapture dataset. To assemble capture histories for open population models, we used data from two separate sources. Data for 2012 and 2013 came from our camera trap studies. For the years 2010 and 2014, we identified individual tigers from published photo databases of individual tigers captured in DTR (Jhala et al., 2011,

Observation Process:

$$y_{i,j} | z_i \sim \text{Categorical}(\theta[z_i(s), j])$$

	Observation state						True state
	State 1	State 2	State 3	State 4	State 5		
$\theta z_i(s), j =$	1	0	0	0	0		State 1
	$1 - p_{.2,j}$	$p_{.2,j}$	0	0	0		State 2
	$p_{.3,1,j}$	$p_{.3,2,j}$	$1 - p_{.3,1,j} - p_{.3,2,j}$	0	0		State 3
	$p_{.4,1,j}$	$p_{.4,2,j}$	0	$1 - p_{.4,1,j} - p_{.4,2,j}$	0		State 4
	$p_{.5,1,j}$	$p_{.5,2,j}$	$p_{.5,3,j}$	$p_{.5,4,j}$	$1 - \sum (p_{.5,1,j}, p_{.5,2,j}, p_{.5,3,j}, p_{.5,4,j})$		State 5

Ecological Process:

$$z_i \sim \text{Categorical}(\Omega_i)$$

$$\Omega_i = \begin{bmatrix} 1 - \psi - \psi' & \text{State 1} \\ \psi \times (1 - f) & \text{State 2} \\ \psi \times f & \text{State 3} \\ \psi' \times (1 - f) & \text{State 4} \\ \psi' \times f & \text{State 5} \end{bmatrix}$$

Occupancy state priors:

$$lpsi \sim \text{Normal}(0, 2), \psi' \sim \text{Normal}(0, 2), f \sim \text{Beta}(1, 1)$$

To constrain the parameters ψ and ψ' of the state matrix such that their sum was ≤ 1 , we used a logit transformation.

$$\psi = \frac{e^{lpsi}}{1 + e^{lpsi} + e^{lpsi'}}, \text{ and } \psi' = \frac{e^{lpsi'}}{1 + e^{lpsi} + e^{lpsi'}}$$

Joint posterior distribution:

$$[\Omega, \theta | y] \propto \prod_{i=1}^N \prod_{j=1}^J [y_i | \Omega \times \theta][\Omega | \psi, \psi', f][\theta | p_{.2,j}, p_{.3,1,j}, p_{.3,2,j}, p_{.4,1,j}, p_{.4,2,j}, p_{.5,1,j}, p_{.5,2,j}, p_{.5,3,j}, p_{.5,4,j}][\psi][\psi'][f][p_{.2}][p_{.3,1}][p_{.3,2}][p_{.4,1}][p_{.4,2}][p_{.5,1}][p_{.5,2}][p_{.5,3}][p_{.5,4}]$$

Fig. 2. Bayesian, multi state occupancy model used to test hypothesis about habitat use and intra-specific completion among male tigers. The five true (latent) habitat use states are State 1: no male use; State 2: location use by single male tiger and no female use; State 3: habitat use by a single male tiger and female use; State 4: habitat use by multiple male tigers and no female use; State 5: habitat use by multiple male tigers, and female use. The observation matrix (θ) details the observation process associated the detection of tigers in each of the five habitat use states (s) at site (i) and sampling occasion (j). The diagonal elements are the probabilities of correct classification and the all off-diagonals are probabilities of mis-classification of a state. The probabilities in each row of the matrix sum to 1. All p_{ij} are vectors of detection parameters that vary by time.

2015). We separately estimated probabilities of apparent survival (ϕ) and recapture probabilities (p) for the three PAs allowing for ϕ and p to be constant, vary by sex or year, or both.

3. Results

Over the two-year study period, with a cumulative sampling effort of 18,643 trap-nights, we photo-captured 62 unique adult tigers (> 2 years in age). Of these, 29 (47%) were female and 33 (53%) male (Table 2). We were unable to estimate multi-state occurrence parameters for Dudhwa National Park in 2012 because a large numbers of locations only had one sampling occasion (14 days). The relative proportions of tiger records in each of the five states varied across our study sites.

We generally found that habitat use in the five states varied within and among sites (Fig. 3). Notably, the probability that a habitat area went unused by male tigers (State 1; $(1 - \psi - \psi')$) was as high as 0.65 (medians) at Katerniaghat WLS and 0.56 (median) at Dudhwa NP. The lowest probability of habitat use by male tigers occurred at the site with the highest female-biased sex ratio and habitat connectivity (0.24,

median, Kishanpur WLS). Our results did not support the null hypothesis that habitat use by male tigers would be unrelated to male ASR (Table 3). The probability of habitat use by a single male tiger and no female tigers (State 2; $(\psi \times (1 - f))$) was fairly similar across sites; parameter uncertainty was relatively large and thus difficult to provide clear evidence of any differences.

Given a tiger population occurring in habitat with sufficient prey resources, and stable territories and social dynamics, we would expect that most habitat use would be described by State 3 ($\psi \times f$), a single male tiger with ≥ 1 females present. However, we found the highest median probabilities of habitat use in State 3 were only 0.38 and 0.4, occurring at Kishanpur WLS. Nevertheless, these probabilities were still higher than at other sites with lower habitat connectivity and higher male-biased/even ASR, thus supporting our hypothesis.

We found empirical support of potential intraspecific competition among tigers in areas with relatively high habitat use by multiple male tigers in the presence of females (State 5; $(\psi' \times f)$) or without females (State 4; $(\psi' \times (1 - f))$). The probability of a location being in state 4 or 5 varied across sites from 0.03 to 0.2 (medians). Furthermore, model estimates also provided support for our hypotheses of increased

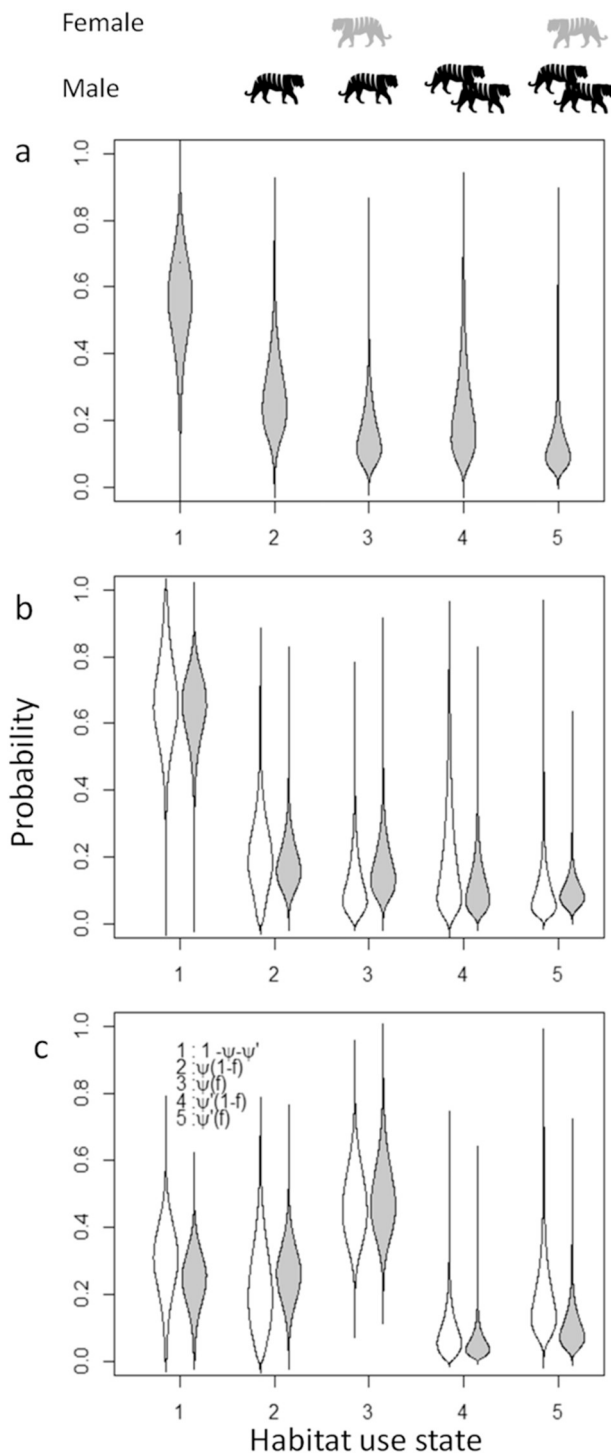


Fig. 3. Posterior distributions for parameters linked to the five habitat use states for three PAs in DTR ((a) Dudhwa NP, (b) Katerniaghat WLS and (c) Kishanpur WLS) over the two study-years (white: 2012 and gray: 2013). These PAs span gradients of habitat connectivity and ASR (male-biased to female-biased). The width of the strip in these plots is proportional to the density. Tiger silhouettes at the top of the figure indicate habitat use states, i.e., use by 0, 1 or > 1 males, with (1 or more) and without female use.

potential for intraspecific competition in sites with male-biased/even ASR. Median estimates of habitat use in state 4 were 1.5–2 times higher in sites with male-biased/even ASR compared to Kishanpur, a site with a female-biased ASR (Table 3; Fig. 3). However, we note that ASR was male-biased in Katerniaghat WLS in 2012 but female-biased in 2013. In

Table 3

Bayesian *p* values to test hypotheses about differences in fine scale occupancy of tigers across gradients of adult sex ratios and habitat connectivity. When distributions were exactly the same, the Bayesian *p* values would be 0.5. Values > 0.5 indicate that our hypothesis (indicated by > sign) was supported, while values < 0.5 signified our hypotheses was not supported. Probabilities near 1 indicate the strongest support possible.

Year	State	Hypothesis about occupancy ^a & Bayesian <i>p</i> values		
		DNP > KPUR (MBI > FBC)	KGHAT > KPUR (MBSC > FBC)	DNP > KGHAT (MBI > MBSC)
2012	1 (1- Ψ - Ψ')		0.99	
2013	1 (1- Ψ - Ψ')	0.95	1.00	0.03
2012	2 Ψ (1- <i>f</i>)		0.45	
2013	2 Ψ (1- <i>f</i>)	0.31	0.21	0.55
2012	3 Ψ (<i>f</i>) ^b		0.01	
2013	3 Ψ (<i>f</i>) ^b	0.01	0.01	0.43
2012	4 Ψ' (1- <i>f</i>)		0.66	
2013	4 Ψ' (1- <i>f</i>)	0.97	0.79	0.92
2012	5 Ψ' (<i>f</i>)		0.28	
2013	5 Ψ' (<i>f</i>)	0.67	0.40	0.74

^a Dudhwa National Park (DNP) had even/male-biased sex ratios and poor habitat connectivity. Kishanpur Wildlife Sanctuary (KPUR) had female-biased adult sex ratios and good habitat connectivity. Adult sex ratios in Katerniaghat Wildlife sanctuary (KGHAT) fluctuated between strongly male-biased and female-biased over the study period this site is connected to a PA in Nepal via a forest corridor. MBI - male-biased and isolated; FBC - female-biased and well connected; MBSC - male-biased, connected via a single corridor.

^b Note that hypotheses about State 3 are that higher male-biased ASR's and lower connectivity will lead to lower habitat use in State 3 (Table 1), thus low Bayesian *p*-values are predicted.

general, probabilities of fine-scale habitat use by multiple male tigers and females (State 5 ($\Psi' \times f$)), appeared to be generally low and similar across sites, regardless of ASR, suggesting that dominant males may be highly effective in deterring territorial intrusions by rivals. However, parameter uncertainty makes it difficult to statistically differentiate possible differences.

3.1. Survival estimates

Apparent survival for adult male and female tigers were similar in the three sites, suggesting that differential survival of adult male and female tigers is unlikely to be the key factor underlying among-site variation in ASR (Fig. 4). Point estimates of female survival were highest in Kishanpur WLS ($\Phi = 0.85$, SE = 0.06) and 10–15% lower in two other study sites with lower habitat connectivity. However,

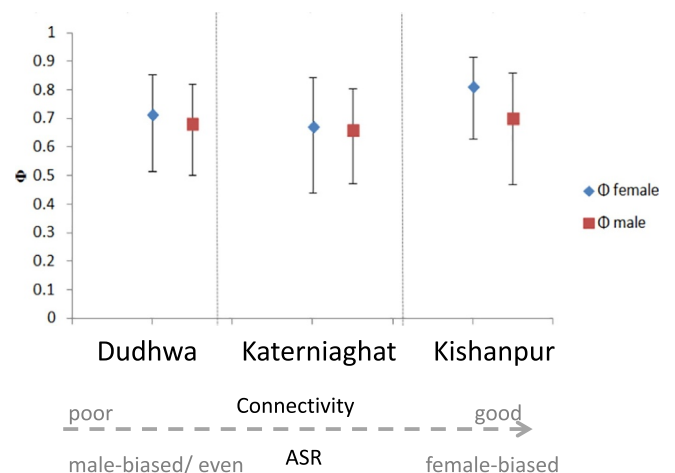


Fig. 4. Model averaged estimates of apparent survival probability of male and female tigers in DTR's three protected areas.

confidence intervals overlapped across sites providing no clear statistical evidence of a difference. Estimates of male survival were similar in all three sites ($\Phi = 0.65$). Overall, models with sex-specific differences in survival were weakly supported relative to other models that assumed constant survival probabilities for males and females. (Appendix C).

4. Discussion

Our study highlights several patterns of variation in fine-scale habitat use (ψ) that appear to be linked to territorial behavior. First, large areas of suitable habitat may not be used by male tigers if these areas are not used by females. Second, in the populations we surveyed, only a relatively small proportion locations were associated with the socially stable state 3 (use by female and only a single male). Third, the finding that a substantial area of habitat is simultaneously used by multiple males (independent of female use) suggests the potential for unstable social dynamics. If this is a common occurrence, it has the potential to adversely affect population growth rates as a consequence of infanticide, inter and intra-sex aggression. Finally, our results also indicate that tiger space use and co-occurrence of males at fine spatial scales varied across the three study sites, and may be a consequence of two inter-related factors: ASR interacting with the degree of habitat connectivity or isolation – and not variation in adult survival.

We think it likely that adult sex ratios profoundly influence fine scale space use and co-occurrence of male tigers. In populations with even or near-even sex ratios (i.e. Dudhwa and Katerniaghat) we estimated a higher probability of non-use of available habitat areas by male tigers. A related finding was that sites with more males per female appear to have lower likelihood of stable space use (one male per female territory), and instead found some evidence for ‘heaping’ of overlapping male territories around female territories.

Further, our working hypothesis that sites with limited connectivity would likely be associated with male-biased sex ratios appears to be valid, with both Dudhwa and Katerniaghat being associated with even or male: biased sex ratios. Thus, fragmentation not only has the potential to influence landscape-scale tiger occupancy (Chanchani et al., 2016), but also fine-scale space use. Our finding of similar probabilities of apparent survival for adult male and female tigers in the three study sites lends support to the idea that habitat fragmentation, rather than variation in adult survival, may underlie skew in ASR. While habitat fragmentation has previously been associated with population declines and loss of genetic heterozygosity (Mondol et al., 2013; Thatte et al., 2018), the ‘indirect’ impacts of fragmentation on space use, behavior and individual fitness have received less attention.

We think it likely that increased territorial overlap (unstable states 4 and 5), whether driven by fragmentation or other factors, will likely impact population structure and demography. Intensified competition for mates in populations with male-biased ASR will likely have deleterious effects on survival of males, females and juveniles, with negative feedbacks on population growth. It is evident that many tiger populations may exist below the ecological carrying capacity as a consequence of poaching, habitat fragmentation and intraspecific competition (Barlow et al., 2009; Carter et al., 2015). When poaching is combined with skewed (male-biased) ASR, increased intraspecific competition and Allee effects can have a synergistic negative effect on the populations (Lande, 1998; Stephens and Sutherland, 1999). In territorial species with skewed sex ratios, models of equilibrium occupancy predict that mate finding difficulties may lead to Allee effects (Stephens and Sutherland, 1999). For tigers, we are referring specifically to depensation – a decrease in the size of the breeding population leading to reduced reproduction and lower population growth rates (Lande, 1987).

In the CTL, we speculate that male-biased ASR may result in reduced probabilities of encountering mates as a consequence of both low population density and increased competition for females (Rankin

et al., 2011; Wadekind, 2012). Difficulty in encountering potential mates because of fierce competition may be compounded by the occasional emigration of female tigers. For example, we have documented multiple females that have raised litters in farmlands away from their primary habitats. Such strategies may be a response to the risk of infanticide from displacement of a dominant male (Ebensperger, 1998; Singh et al., 2014; Swenson, 2003). Our results also highlight that variation in ASR is temporally dynamic, and that skewed ASR may be reversed by sex-biased mortality or immigration/emigration of a few individuals from or into small populations (Robinson et al., 2008; Sweanor et al., 2000).

Finally, we recognize that overlapping space use by tigers as inferred from camera trap data, is at best an indirect measure of the potential for intraspecific conflict. Our analyses neither provide probabilities of actual conflict and associated demographic impacts, nor do they establish causal relationships with ASR or fragmentation. Moreover our sample size is small ($n = 3$ sites). Nonetheless, we have compared these sites in the context of known variability (ASR, habitat connectivity) and based on our findings, there is generally consistent evidence supporting our hypothesis of possible influence of ASR and connectivity on tiger occurrence. We expect that these results will encourage others to explore how environment, animal behavior and other endogenous factors collectively influence carnivore space-use and demography, which will add support to or help refine our ideas.

4.1. Conservation and management implications

In many areas across the extant range of large carnivores, the lack of effective protection from poaching has led to large habitat tracts that support very low tiger densities (Hilborn et al., 2006; Liberg et al., 2012). The terai’s tiger populations face multiple threats. Estimates of apparent survival for adult tigers in our study area were ~10–15% lower than in larger and better connected habitats elsewhere in India and SE Asia (Duangchantrasiri et al., 2016; Karanth et al., 2006; Majumder et al., 2017; Sadhu et al., 2017). We speculate that small population sizes and low survival rates are due to poaching, among other factors, in part, a consequence of the proximity of our sites to the international border with Nepal (Chanchani et al., 2016). Threats to small populations may be exacerbated by imbalances in the sex ratios. Our study suggests that in the CTL there may be less than the assumed three adult females per male in many tiger populations, even in areas with good habitat connectivity. Similar skews in sex ratios may also exist among other large carnivore species (Palomares et al., 2012). Our results also suggest that in fragmented habitats, small populations with skewed sex-ratios may exhibit unstable dynamics, which may make them more vulnerable to extinction from poaching and stochastic factors.

In such scenarios, wildlife corridors are central to enabling population recovery and persistence (Wikramanayake et al., 2010; Thapa et al., 2017). However, rapid land use change in the Terai has degraded key corridors and limited the potential for animal dispersal (Harihar and Pandav, 2012; Joshi et al., 2016; Chanchani et al., 2016). The maintenance and restoration of vital wildlife corridors often have little political support, especially if they involve land acquisition or removal of encroachments or barriers. Even as key corridors are eroded, it is increasingly being recognized that the agricultural matrix around PAs may support large carnivore presence and dispersal (Athreya et al., 2013; Joshi et al., 2013). For the matrix to function as a corridor, policies must be developed to minimize human-wildlife conflict, increase human tolerance of tigers (and prey) and limit large-scale land use change. The success of these and other conservation measures requires not only political will and funding, but also societal support for conservation (Rastogi et al., 2012).

Finally, our study underscores that small populations in habitat fragments may be associated with unstable sex-ratios which have the potential to suppress population growth. Managers must therefore

routinely monitor sex-ratios, reproduction and survival in addition to population size. In situations where corridors are no longer viable, or will require decades for restoration, the recovery of carnivore populations with severely skewed ASR and low abundance may well depend on the timely supplementation or reintroduction of breeding-age individuals (Lambertucci et al., 2013; Reddy et al., 2016). As tiger populations continue to decline in many areas, this is increasingly being recognized as an essential and viable strategy to repopulate habitat tracts or stave the species away from extinction (Sankar et al., 2010; Gray et al., 2017; Kolipaka et al., 2017; Harihar et al., 2018).

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Appendices. Supplementary data

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