

2018

Elevated potential for intraspecific competition in territorial carnivores occupying fragmented landscapes

Pranav Chanchani

Brian D. Gerber

University of Rhode Island, bgerber@uri.edu

See next page for additional authors

Follow this and additional works at: https://digitalcommons.uri.edu/nrs_facpubs

**The University of Rhode Island Faculty have made this article openly available.
Please let us know how Open Access to this research benefits you.**

This is a pre-publication author manuscript of the final, published article.

Terms of Use

This article is made available under the terms and conditions applicable towards Open Access Policy Articles, as set forth in our [Terms of Use](#).

Citation/Publisher Attribution

Chanchani, P., Gerber, B. D., & Noon, B. R. (2018). Elevated potential for intraspecific competition in territorial carnivores occupying fragmented landscapes. *Biological Conservation*, 227, 275-283. doi: 10.1016/j.biocon.2018.08.017

Available at: <https://doi.org/10.1016/j.biocon.2018.08.017>

This Article is brought to you for free and open access by the Natural Resources Science at DigitalCommons@URI. It has been accepted for inclusion in Natural Resources Science Faculty Publications by an authorized administrator of DigitalCommons@URI. For more information, please contact digitalcommons@etal.uri.edu.

Authors

Pranav Chanchani, Brian D. Gerber, and Barry R. Noon

Elevated potential for intraspecific competition in territorial carnivores occupying fragmented landscapes

Authors:

Pranav Chanchani^{1,2,3*}, Brian D. Gerber⁴, Barry R. Noon^{1,2}

¹Department of Fish, Wildlife and Conservation Biology, Colorado State University,
Fort Collins, 80523, USA.

²Graduate Degree Program in Ecology, Colorado State University, Fort Collins, 80523, USA

³Current affiliation: World Wide Fund for Nature, 172-B Lodi Estate, New Delhi, 110003, India.

⁴ Department of Natural Resources Science, University of Rhode Island, Kingston,
Rhode Island, 02881, USA.

* Corresponding author's email:

Pranav Chanchani: pranav.chanchani@gmail.com

1 **Abstract**

2

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

22 **Keywords:** carnivores; intra-specific competition; fragmentation; multi-state occupancy; sex
23 ratio; survival

24 **1. Introduction**

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

36 In polygamous species, adult male territories often encompass the territories of multiple
37 females. Skewed ASR's have especially pronounced impact on the behavior and demography of
38 carnivores—for example, intraspecific predation has been documented in at least 14 large
39 carnivore species (Polis, 1981). This typically involves infanticide or killing of younger and
40 immature animals and cubs by adults, typically on account of territorial disputes, and has been
41 shown to substantially reduce population size (Polis, 1981). When first acquiring a female
42 territory, adult male carnivores are known to seek out and kill non-related juveniles to increase
43 their reproductive fitness (Barlow et al., 2009; Hrdy, 1979; Persson et al., 2003). Additive
44 mortality from intraspecific competition and infanticide may be especially detrimental for small
45 populations of several terrestrial carnivores that are already vulnerable to extinction (Chapron et
46 al., 2008).

47 Large carnivores worldwide face high extinction risks, in part because of their extensive
48 area requirements, habitat loss and real or perceived conflicts with humans (Ripple et al., 2014).
49 Tiger (*Panthera tigris*) populations are especially at risk because of a lucrative illegal global
50 trade in their pelts and other body parts -- as few as 3900 individuals may now exist in the wild
51 (WWF 2016) and remnant populations are small -- there are now probably fewer than 20
52 populations >50 individuals. While the risk of local extinction is primarily driven by illegal
53 hunting and habitat loss and fragmentation, several endogenous factors may exacerbate
54 extinction risks of small populations. For example, strong territorial behavior can aggravate the
55 demographic issues of small and fractured populations. Intraspecific competition and aggression,
56 especially in areas with male-biased ASR can increase the extinction risks of small populations
57 (Barlow et al., 2009). Adult male tigers fiercely defend their territories from competing males to
58 retain access to breeding females (Horev et al., 2012; Sunquist, 1981). If a dominant territorial
59 male is displaced by a rival, the outcome is often infanticide of the former's cubs by the later
60 (Barlow et al., 2009; Smith and McDougal, 1991); this enables females to become receptive
61 mates more quickly to the new dominant male. The harem size of male tigers and degree to
62 which breeding males are able to maintain stable territory sizes can profoundly impact
63 population dynamics and extinction rates (Horev et al., 2012).

64 Several aspects of the social behavior of tigers, including a polygynous mating system,
65 territoriality and dispersal, are relevant to demography, behavior and space-use. Female tigers
66 select territories to secure access to adequate resources to protect and raise young (e.g., sufficient
67 prey, cover and water), and males compete for territorial dominance of one or more female
68 territories (Goodrich et al., 2008; Smith, 1993; Smith and McDougal, 1991; Sunquist, 1981). In
69 South Asia, male tiger territory size is usually >100 km², while females maintain territories

70 between 10-30 km² (Sunquist, 1981). Dispersal is also typically male-biased: adult females
71 tolerate their female offspring establishing territories in close proximity to their own, but male
72 offspring are driven away. Young males in search of new territories often disperse over large
73 distances and commonly experience aggressive interactions with other males (Reddy et al., 2016;
74 Smith, 1993). Although published information is sparse, ASR (Males:Females) between 1:2 and
75 1:3 have generally been reported from South Asia (Majumder et al., 2017; Sunquist, 1981).
76 Some studies in India, however, have revealed that densities and sex ratios of adult tigers can
77 vary widely (Sadhu et al., 2017), and may even be male-biased (Chanchani et al., 2014a).

78 Considering the social and population biology of tigers raise several questions relevant to
79 tiger spatial ecology, especially in fragmented landscapes with small populations. Foremost is
80 whether there is a high potential for intraspecific competition, infanticide and antagonism among
81 tigers due to high levels of habitat use (i.e., site occupancy) by multiple male tigers, with and
82 without female tigers. Second, does variation in ASR help understand patterns of fine-scale
83 habitat use by male tigers, such that we might expect higher potential intraspecific competition in
84 local populations with male-biased ASR? Lastly, can inter-site variations in ASR for tiger
85 populations be attributed to sex-biased emigration, limited habitat connectivity, or to differences
86 in sex-specific adult survival rates?

87 To evaluate these hypotheses, we analyze an extensive capture-recapture dataset for a
88 tiger population in the Dudhwa Tiger Reserve (DTR) – a 1,200 km² protected area within the
89 Central Terai Landscape (CTL) in North India. DTR consists of three disjoint protected areas
90 (subsequently referred to as, ‘sites’). Sites are characterized by strong gradients in tiger density,
91 habitat connectivity and variation in ASR—ranging from highly connectivity, high density and
92 female-biased ASR—to isolated, low density and male-biased ASR (Chanchani, 2016). Given

93 the polygynous mating-system in tigers, sites with an even sex ratio, or those with more adult
94 males than females were deemed as having male-biased ASR. We tested the null hypothesis that
95 the probability of habitat use (fine-scale occupancy) by one or more male tigers would be
96 similar, regardless of a site's ASR. Alternatively, we had two general predictions about the fine-
97 scale space-use by male tigers in sites with male-biased ASR. First, we predicted lower overall
98 male habitat use, i.e., extensive habitat areas that are distant from female territories will not used
99 by male tigers (hypothesis 1 in Table 1). Second, we predicted high competition among males to
100 secure access to female territories would be manifest in the following space-use patterns: (a) high
101 male-use of tigers in locations with no female use (specifically along the margins of female
102 territories; hypotheses 2 and 4, Table 1); and (b) high probability of multiple rather than single
103 male-use in locations with female-use (hypotheses 3 and 5, Table 1). This is expected because
104 harem sizes are smaller in areas with male-biased ASR, and multiple males are thus expected to
105 compete intensively for access to each female (Table 1). Finally, to investigate the factors
106 contributing to male-biased ASR in sites with limited connectivity, we also assessed if male
107 distribution was affected by inter-sex differences in movement probabilities (stemming from
108 differences in dispersal behavior and habitat fragmentation). When adult survival is similar for
109 both sexes, or when female survival $>$ male survival -- male-biased ASR in populations can be
110 an artifact of high rates of female emigration, and/or differential male immigration from
111 surrounding populations (Smith, 1993).

112

113

114

115

116

117 **2. Materials and Methods**

118

119

120 *2.1 Description of study area*

121 Dudhwa Tiger Reserve is located in the Terai-Duar savannas and grasslands ecoregion that spans
122 areas of Nepal, India, Bhutan and Bangladesh (Olson et al., 1998; Fig. 1). DTR is comprised of
123 Dudhwa National Park (~700 km²), Katerniaghat Wildlife Sanctuary (WLS; ~450 km²) and
124 Kishanpur WLS (~200 km²), established in 1977, 1975 and 1972 respectively. DTR's most
125 productive wildlife habitats, grasslands and wetlands, comprise approximately 18% of the overall
126 area. Other habitats include dry deciduous Sal (*Shorea robusta*) forests, and mixed-dry deciduous
127 forests and teak (*Tectonia grandis*) plantations. Within India, the last remnant patches of the once-
128 extensive grassland-wetland mosaics that characterize the CTL are now restricted to small areas in
129 and around DTR. The reserve's management has undergone drastic changes over the past 150
130 years. Through the 19th century and until about 1960, large forest tracts were exclusive hunting
131 blocks for India's colonial administrators and Indian royalty. Other areas were intensively managed
132 to supply high-grade sal (*Shorea robusta*) timber (Strahorn, 2009).

133 The three protected areas (PAs) of DTR vary in their degree of connectedness with other
134 tiger habitats in India and Nepal. Kishanpur Wildlife Sanctuary is embedded within a larger tiger
135 habitat patch (~1400 km² Pilibhit forest complex in India) and connected with Shuklaphanta
136 Wildlife Sanctuary in Nepal, via the Sharda River corridor. Katerniaghat WLS is connected to the
137 968 km² Bardia National Park via the 40 km long Khata corridor (along the Karnali River).
138 Connectivity between Dudhwa National Park and Laljhari and Basanta community forests in Nepal
139 has been severely degraded due to land use change and expanding human settlements in recent
140 decades (Chanchani et al., 2014b; Joshi et al., 2016; Kanagaraj et al., 2013). Finally, tiger density

141 and ASR in DTR's three PA's vary extensively. The highest tiger density (4.66 and 4.92 tigers/
142 100 km²) and most female-biased ASR (adult males = 29% of population) were recorded from
143 Kishanpur WLS in 2013 (Chanchani et al., 2014a; Table 2). In contrast, tiger densities were lower
144 in Katarniaghat WLS (4.72 and 2.22 tigers/100 km², (61% and 33% males in 2012 and 2013
145 respectively) and Dudhwa National Park (1.05 and 1.89 tigers/100 km², 58% and 47% males in
146 2012 and 2013) (Jhala et al. 2015; Chanchani 2016; Table 2). There is negligible uncertainty
147 associated with adult sex-ratios because estimates come from a near-census of the target
148 populations (Appendix A).

149 *2.2 Camera Trap Sampling*

150 Between November 2011 and June 2013, we conducted extensive camera-trap surveys to
151 assess the status of tigers in the CTL (Fig. 1). We used a grid-based sampling design and
152 positioned pairs of cameras at intervals of approximately 2 km within tiger habitats. Camera traps
153 were placed along forest trails or water courses to maximize detection probability. These surveys
154 were completed in ≤ 60 days to meet the demographic closure assumption of occupancy and
155 capture recapture models (Karanth et al., 2002). At each location, cameras were operated from 14-
156 56 days. Overall, 304 locations were sampled with camera traps from November 2011- May 2012,
157 and 380 locations were sampled from November - June 2013 (Table 2).

158

159 *2.3 Data Processing, Model Formulation and Analysis*

160 To evaluate our *a priori* hypotheses, we fit multi-state occupancy models to our camera
161 trap data (Nichols et al., 2007). Camera trapping data have been traditionally analyzed in a mark-
162 recapture framework to estimate demographic parameters (such as abundance and survival), but
163 recent extensions of these methods allow estimates of patch occupancy and species co-occurrence

164 (Nichols et al., 2007; O’Connell and Bailey, 2011). We apply multi-state occupancy models to
165 test hypotheses about tiger distribution in the context of variable habitat connectivity (Johnsingh
166 et al., 2004; Kanagaraj et al., 2013; Wikramanayake et al., 2004) and ASR within habitat patches
167 in our study area.

168 Photo-captured adult tigers were individually identified from photos by three independent
169 observers and by using pattern recognition software (Hiby et al., 2009). The sex of all tigers was
170 discernible from the photos which allowed us to assign habitat-use states by sex and individual. We
171 defined a sampling occasion as a 14-day period corresponding to the duration over which tiger
172 spray scent (used for territorial marking) remains detectable (Smith et al., 1989). At each camera
173 trap location and on every sampling occasion, male tiger captures were assigned to one of five
174 habitat-use states. These states indicated probability of use of locations by single (ψ) or multiple
175 (ψ') male tigers, in the context of female use (presence/absence) (f ; Table 1). Tiger habitat use
176 states were defined as: State 1, no male use ($1 - \psi - \psi'$); State 2, location use by a single male
177 and no female use ($\psi \times (1 - f)$); State 3, location use by single male, and any female ($\psi \times f$);
178 State 4, use of location by multiple males and no female use ($\psi' \times (1 - f)$); and State 5, use by
179 multiple males, and female use ($\psi' \times f$). Notations in parentheses are mathematical probability
180 statements uniquely identifying each state. Multi-state occupancy models allow for state
181 uncertainty. We accounted for non-detection of male tigers by estimating misclassification
182 probabilities – for example, we might record the presence of a male tiger during a 14-day occasion
183 (observe state 2) even though females were also present (true state 3); the probability of this
184 misclassification is p_{-3_2} (Fig. 2). We estimated model parameters using a hierarchical Bayesian
185 multi-state occupancy model (Kery and Schaub, 2012; Royle and Dorazio, 2008). The true (latent)
186 state of each location (trap station), z , can take on state values equal to 1, 2, 3, 4 or 5,

187 corresponding to the five habitat use states. Latent occurrence, z , is modeled by estimating Ω_i , the
188 state vector describing the probability that site i is in one of the five states. The observation process
189 describes how the true state z is linked with the observations, y_{ij} , the observed states of tiger habitat
190 use at site i and occasion j . The conditional relationship between y_{ij} and z is described by a
191 categorical distribution with the θ_z , representing the observation matrix (Fig. 2). The elements of
192 the observation matrix are the probabilities of observing tiger use in each of the five states.
193 Diagonal elements are the probabilities of correct classification and off-diagonals elements are the
194 probabilities of misclassification. The probabilities in each row of the observation matrix sum to 1.
195 Detection probabilities were allowed to vary among survey occasions (2 week-long periods).

196 Because sex-specific fine-scale habitat use by tigers was unknown, we specified vague
197 logit normal priors for ψ and ψ' (Fig. 2). The prior for f was modeled using a beta distribution
198 prior, implying a uniform probability between 0 and 1. We used Dirchlet priors to describe the
199 distribution of elements within observation array rows ($p_{n,k}$: $p_{1,k}$, $p_{2,k}$, $p_{3,k}$, $p_{4,k}$, and p_{5k}), where n
200 represents the true state of a site and k represents the observed state. The Dirchlet distribution
201 satisfies the requirement that the elements of each row of the observation array sum to 1 (Hobbs
202 and Hooten, 2015; Kery and Schaub, 2012). We fit our Bayesian model using Markov chain
203 Monte Carlo (MCMC) algorithms implemented in program JAGS (Plummer, 2003) linked to R (R
204 Development Core Team). We separately analyzed data for three PA's in DTR in each of the two
205 survey years, with the exception of Dudhwa National Park, (2012), where the survey period was
206 short (14 days). Each data-set was fit using three chains (to assess parameter convergence), each
207 with 100,000 MCMC iterations, and a burn-in value of 10,000.

208

209 *2.4 Model Support and Evaluation*

210 To assess departures from similarity for posterior distributions of estimated parameters
211 and model support, we used a one-sided test based on Bayesian p values. Specifically, to test
212 whether a given prediction was supported — for example, that probability of multiple-male
213 tigers using a location would be higher at sites with male-biased ASR ($\psi'_{site\ 2} \times f_{site2}$) than in sites
214 with female-biased ASR ($\psi'_{site\ 1} \times f_{site1}$) — we derived:

215

$$216 \sum_{i=1}^{n.mcmc} ((\psi'_{site2} \times f_{site2}) - (\psi'_{site1} \times f_{site1})) > 0 / n.mcmc,$$

217

218 where $n.mcmc$ is the number of MCMC iterations. If the posterior distributions were exactly the
219 same, we expect a value of 0.5 (i.e., given any value from $(\psi' \times f)_{site2}$ compared to $(\psi' \times f)_{site1}$
220 , 50% will be greater). Values >0.5 indicate support for the hypothesis. In a scenario where all
221 samples in $(\psi' \times f)_{site2} > (\psi' \times f)_{site1}$, we expected a Bayesian p value of 1.

222 We assessed model fit via a posterior predictive check where simulated data sets for each
223 site/year are compared with the original data sets (Gelman and Hill, 2007). We examined
224 whether the probabilities of the observed data were more extreme relative to the simulated data.
225 Posterior predictive checks revealed no evidence of lack of fit because test statistics based on the
226 observed data were not more extreme than test statistics calculated from the simulated data
227 (Appendix B).

228

229 *2.5 Estimating Survival*

230 We used Cormack-Jolly-Seber (CJS) models to estimate apparent annual survival rates for
231 adult tigers (Lebreton et al., 1992). We refer to ‘apparent’ survival because mortality cannot be
232 discriminated from permanent emigration and survival for at least one year (Karanth et al., 2006).

233 Data on tiger survival were available from a four-year (2010-2014) capture-recapture data set. To
234 assemble capture histories for open population models, we used data from two separate sources.
235 Data for 2012 and 2013 came from our camera trap studies. For the years 2010 and 2014, we
236 identified individual tigers from published photo databases of individual tigers captured in DTR
237 (Jhala et al., 2015, 2011). We separately estimated probabilities of apparent survival (Φ) and
238 recapture probabilities (p) for the three PA's allowing for Φ and p to be constant, vary by sex or
239 year, or both.

240
241

242 **3. Results**

243

244 Over the two-year study period, with a cumulative sampling effort of 18,643 trap-nights,
245 we photo-captured 62 unique adult tigers (>2 years in age). Of these, 29 (47%) were female and 33
246 (53%) male (Table 2). We were unable to estimate multi-state occurrence parameters for Dudhwa
247 National Park in 2012 because a large numbers of locations only had one sampling occasion (14
248 days). The relative proportions of tiger records in each of the five states varied across our study
249 sites.

250 We generally found that habitat use in the five different states varied within and among
251 sites (Figure 3). Notably, the probability habitat went unused by male tigers (State 1; $(1 - \psi - \psi')$)
252 was as high as 0.65 (medians) at Katerniaghat WLS and 0.56 (median) at Dudhwa NP. The lowest
253 probability of habitat being unused by male tigers occurred at the site with the highest female-
254 biased sex ratio and habitat connectivity (0.24, median, Kishanpur WLS). As such, we did not find
255 support for the null hypothesis that habitat use by male tigers would be similar in sites with and
256 without male-biased ASR (Table 3) Interestingly, the probability of habitat use by a single male

257 tiger and no female tigers (State 2; $(\psi \times (I-f))$) was fairly similar; parameter uncertainty was
258 relatively large and thus difficult to provide clear evidence of any differences.

259 Given a tiger population occurs in relatively good habitat with the necessary resources and
260 stable territories and social dynamics, we would generally expect that most habitat use could be
261 described as State 3 ($\psi \times f$), a single male tiger with one or more females present. As such, it is
262 interesting that we found the highest median probabilities of habitat use in State 3 were only 0.38
263 and 0.4, occurring at Kishapur WLS. However, these probabilities are still higher than those from
264 the other sites, which had lower habitat connectivity and higher male-biased/even ASR, thus
265 supporting our hypothesis..

266 We found empirical support of potential intraspecific competition, infanticide, and
267 antagonism among tigers with relatively high habitat use by multiple male tigers with females
268 (State 5; $(\psi' \times (f))$) or without females (State 4; $\psi' \times (I-f)$). The probability of a location being in
269 state 4 or 5 ranged across sites from 0.03 to 0.2 (medians). Furthermore, model estimates also
270 indicated support for our hypotheses about increased potential for intraspecific competition in sites
271 with male-biased/even ASR. Median estimates of habitat use in state 4 were 1.5-2 times higher in
272 sites with male-biased/even ASR, than in Kishanpur, a site with a female-biased ASR (Table 3;
273 Fig. 3). However, we note that ASR was male-biased in Katarniaghat WLS in 2012 but female-
274 biased in 2013. In general, probabilities of fine-scale habitat use by multiple male tigers and
275 females (State 5 ($\psi' \times (f)$)), appeared to be generally low and similar across sites, regardless of
276 ASR, suggesting that dominant males may be highly effective in warding off territorial intrusions
277 by rivals. However, parameter uncertainty makes it difficult to statistically differentiate possible
278 differences.

279

280 3.1 Survival Estimates

281 Apparent survival for adult male and female tigers were similar in the three sites,
282 suggesting that differential survival of adult male and female tigers is unlikely to be the key factor
283 underlying variation in ASR in these sites. Estimates of male and female survival were very similar
284 in two of our three study sites (Fig. 4). Point estimates of female survival was highest in
285 Kishanpur WLS ($\Phi=0.85$, $SE=0.06$) and were 10-15% lower in our two other study sites with
286 lower habitat connectivity. However, the confidence intervals overlapped across sites providing no
287 clear statistical evidence of a difference. Estimates of male survival were similar in all three sites
288 ($\Phi=0.65$). Overall, models with sex-specific differences in survival were weakly supported
289 relative to other models that assumed constant survival probabilities for males and females.
290 (Appendix C).

291 4. Discussion

292 Our study casts light on how space use of a territorial carnivore is influenced by the species
293 territorial behavior and intra-specific interactions. By modeling shared space use by tigers at point
294 locations (camera trap stations), we are also able to investigate how heterogeneity in species
295 occurrence may also be influenced by endogenous factors, in addition exogenous variables (for
296 example abundance, vegetation attributes, and human presence) that are typically used to explain
297 species occurrence (Barber-Meyer et al., 2013; Sunarto et al., 2012). We highlight three patterns in
298 inter-site variations in fine-scale habitat use (ψ) that appear to be linked to territorial behaviour.
299 First, large areas of suitable habitat may not be used by male tigers, likely because these areas are
300 not used by females. Second, in the populations we surveyed, only a relatively small proportion of
301 sites was associated with the socially stable state 3 (use by female and only a single male). Lastly,
302 the finding that a non-negligible amount of habitat is used by multiple males (regardless of female
303
304

305 use) suggests potentially unstable social dynamics, in which male behavior may disrupt potential
306 population growth. This could arise from infanticide and associated inter-sex aggression, as well
307 as intra-sex competition to secure mates and increase harem sizes.

308 Our analyses also suggest that these inter-site variations in the probability of shared space
309 use by male tigers may be attributed to, at least in part, by two inter-related factors: ASR and
310 degree of habitat connectivity or isolation. In the following sections, we (a) interpret our results
311 about linkages between ASR variation and probability of shared space use; (b) examine how
312 habitat connectivity and isolation may have some influence on ASR and population structure, and
313 thereby indirectly influence space use; (c) delve into potential demographic consequences of
314 shared space use (and ensuing intraspecific competition) on small populations of territorial
315 carnivores; and (d) elucidate the relevance of our study for conservation and management of tiger
316 populations in fragmented landscapes. First, we found that the considerable variation in co-
317 occurrence of tigers may be an artifact of adult sex ratios. A previous study noted that expansive
318 areas of habitat within some PAs (Dudhwa and Katerniaghat in our study) were associated with
319 low tiger use (Chanchani et al., 2016). Our results confirm that these sites had even or near-even
320 sex ratios (as many males as females) and were associated with higher probability of use at camera
321 trap locations (areas of the PA) with no use by male tigers, than a site with female-biased ASR. A
322 related finding was that sites with males per female, appear to have lower likelihood of stable
323 space use (one male per female territory), and instead found some evidence for 'heaping' of
324 overlapping male territories in areas used by females, which potentially depresses population
325 growth rates.

326

327 (b)

328 Second, we evaluate support for our prediction that the degree of overlapping space use in
329 populations would be indirectly influenced by the degree of habitat connectivity or isolation. Our
330 working hypothesis was that sites with poor connectivity would likely be associated with male-
331 biased sex ratios. This prediction appears to be supported: Dudhwa and Katarniaghat both have
332 poorer habitat connectivity with other tiger occupied areas than Kishanpur, and were also
333 associated with even adult sex ratios, and associated patterns of fine-scale space use. A previous
334 study established that habitat connectivity influences tiger occupancy (Chanchani et al., 2016).
335 While we have not explicitly modeled the relationship between habitat connectivity and ASR in
336 this study, we think it may be a critical factor driving variation in adult sex ratios in our study area.
337 Our finding of similar probabilities of apparent survival for adult male and female tigers in the
338 three study sites, lends support to the idea that habitat fragmentation, rather than variation in adult
339 survival, may underlie skew in ASR and associated patterns of habitat use. While habitat
340 fragmentation has previously been associated with population declines and loss of genetic
341 heterozygosity (Mondol, et al. 2013), the ‘indirect’ impacts of fragmentation on population
342 demography and individual fitness have received less attention, even though is recognize that the
343 omission of spatial structure can undermine analysis of population vulnerability (Gilpin, 1987).

344 Third, we speculate that increased territorial overlap may have local effects on demography
345 and population structure. Specifically, we suggest that this will be on account of two factors. First,
346 male tigers in sites with male-biased ASR are likely to compete intensely for access to female
347 territories. Second, intensified competition between males may have deleterious effects on survival
348 of males, females and juveniles, with negative feedbacks on population growth. Reproductive
349 success, cub survival and population growth may be depressed for several reasons. Models of
350 equilibrium occupancy for territorial species predict that mate finding difficulties may lead to Allee

351 effects (Stephens et al. 1999). For tigers, we are referring specifically to depensation—a decrease
352 in the size of the breeding population leading to reduced reproduction and lower population growth
353 rates (Lande, 1987).

354 We believe small tiger populations may exist below the ecological carrying capacity of
355 these sites as a consequence of a skewed ASR, among other factors .Recent population declines
356 populations in recent decades may have been accelerated by poor recruitment, survival and low
357 immigration of individuals, a result of poaching, habitat fragmentation and intraspecific
358 competition (Barlow et al., 2009; Carter et al., 2015). Further, Many tiger populations in habitat
359 fragments across the species range remain vulnerable to extinction because isolation reduces
360 genetic heterozygosity (Thatte et al., 2017). Extant habitats may only support small tiger
361 populations with elevated risk of patch -level extinction (Noon and McKelvey, 1996; Thapa et
362 al., 2017).

363 We think it plausible that these and other factors have depressed tiger populations in some
364 PAs within our study area. estimated apparent survival probabilities for adult male and female
365 tigers were ~ 10 -15% lower in fragmented sites with male-biased ASR (Dudhwa and Katerniaght)
366 relative to larger and better connected habitats including Nagarhole in Southern India and Huai
367 Kha Khaeng Sanctuary in Thailand and PAs in Central and Western India (Duangchantrasiri et
368 al., 2016; Karanth et al., 2006; Majumder et al., 2017; Sadhu et al., 2017).

369 We attribute small population sizes and low survival rates primarily to poaching, in part, a
370 consequence of the proximity of our sites to the international border with Nepal (Chanchani et al.,
371 2016). However, when poaching is combined with skewed, male-biased ASR, the increased
372 intraspecific competition and Allee effects have a synergistic negative effect on the populations
373 (Lande, 1998; Stephens and Sutherland, 1999). In the CTL, we speculate that male-biased ASR

374 may result in reduced probabilities of encountering mates may be a consequence of both low
375 population density and increased competition among males to gain access to females (Rankin et
376 al., 2011; Wadekind, 2012). Difficulty in encountering potential mates may be compounded by
377 the occasional emigration of female tigers from protected areas. We documented two female tigers
378 raising cubs in sugarcane plantations away from primary habitats in PAs and Reserve Forests. Such
379 local movements, whether temporary or permanent, may be a response to the likelihood of
380 infanticide from a novel, but dominant male (Ebensperger, 1998; Singh et al., 2014; Swenson,
381 2003). Further mortality of sub-dominant (and often younger males) that arise from territorial
382 conflicts with established, dominant males may result in high rates of male mortality. One study in
383 Nepal ascribed 50% of mortality of young male tigers due to intra-sexual aggression (Smith,
384 1993), even though the ASR in Chitwan National Park (Nepal) was ~ 1:3. Finally, we note that
385 recovery may be a slow process in tiger populations with low adult survival (e.g., Katarniaghat and
386 Dudhwa), which are extinction-prone even if significant measures are implemented to increase
387 prey abundance Chapron et al (2008).

388 We are aware that overlapping space use by tigers, as inferred from camera trap data, is an
389 indirect measure of the potential for intra-specific conflict and does not provide probabilities or
390 frequencies of occurrence of actual conflict. Further, our results highlight that variation in ASR are
391 temporally dynamic, and that skewed ASR may be reversed by changing population vital rates
392 (related to Birth, Immigration, Death, Emigration. In our study, we recorded transitions in ASR
393 from male-biased to female-biased in one site, Katarniaghat WLS. Such switches may be triggered
394 by sex biased mortality or immigration/ emigration of a few individuals from or into small
395 populations (Robinson et al., 2008). We speculate that such reversals in ASR are more likely to
396 occur over shorter time intervals in sites with good habitat connectivity, than those with poor

397 connectivity. While our sample size is small ($n = 3$ sites), we are comparing these sites in the
398 context of known variability (ASR, habitat connectivity) and based on our findings, there is
399 generally consistent evidence supporting our hypothesis of possible influence of ASR and
400 connectivity among our three study sites. We expect that this study will encourage others to look
401 beyond population dynamics at behavioral and other endogenous factors that may profoundly
402 influence tiger space and demography, which will help add support to or refine ideas brought up in
403 this manuscript.

404 *4.1 Conservation and Management Implications*

405 The maintenance of viable carnivore metapopulations requires that functional habitat
406 connectivity be maintained and that all available habitats, regardless of PA designation, be
407 effectively protected (Wikramanayake et al., 2011) In many areas across the extant range of large
408 carnivores , the lack of effective protection from poaching has led to large habitat tracts that
409 support very low tiger densities (Hilborn et al., 2006; Liberg et al., 2012). For example, in the
410 Terai, extensive tracts of suitable habitat in Nepal, only 1-2 kilometers away from the northern
411 boundary of DNP, face high hunting pressure of both tigers and their prey. As a result, they rarely
412 sustain breeding females whose offspring may disperse into Dudhwa NP's productive riparian
413 habitats (Wikramanayake et al., 2010; Chanchani et al., 2014(b)). However, our finding of male-
414 biased ASR in DNP, despite lower male survival rates of resident males, suggests that males may
415 occasionally immigrate into the park from surrounding areas, as is observed in many large
416 carnivores (Sweanor et al., 2000).

417 However, rapid land use change is severely degrading wildlife corridors in human
418 dominated landscapes, and may severely limit the movement of large mammals through the matrix
419 (Joshi et al., 2016). The maintenance and restoration of vital wildlife corridors often have little

420 political support, especially if they involve land acquisition or displacement of people. In the
421 absence of formal corridors, we are increasingly documenting the use of the surrounding
422 agricultural matrix by large carnivores (Athreya et al., 2013; Joshi et al., 2013). If policies can be
423 developed to minimize human-wildlife conflict and increase human tolerance of tigers (and prey)
424 in the agricultural matrix, it may be possible to compensate to some extent for inadequate extent of
425 protected area and lack of law enforcement (Gosling, 2003). Our study suggests that in the CTL
426 there may be less than the assumed three adult females per male in many tiger populations, even in
427 areas with good habitat connectivity. Similar skews in sex ratios may also exist among other large
428 carnivore species (Palomares et al., 2012). The persistence of small populations of territorial
429 species requires protecting and increasing prey populations and maintaining high adult survival
430 rates (Chapron et al., 2008; Karanth and Stith, 1999). The success of these and other conservation
431 measures requires not only upon political will, but also societal involvement in, and support for
432 conservation (Oldekop et al., 2015; Rastogi et al., 2012). Finally, our study underscores that
433 poaching and habitat fragmentation often result in male-biased ASR with the potential to
434 accelerate rates of population decline. Managers must therefore routinely monitor sex-ratios,
435 reproduction and survival, in addition to population size.

436 Finally, for carnivore populations with severely skewed ASR and low abundance,
437 recovery and persistence may well depend on the timely implementation of mitigation measures
438 such as the supplementation of breeding-age individuals to compensate for skewed sex-ratios
439 (Lambertucci et al., 2013; Reddy et al., 2016). With population declines in various areas, this is
440 increasingly being viewed as an essential and viable strategy to achieve tiger population recovery
441 across the species range (Sankar et al., 2010; Gray et al., 2017; Kolipaka et al., 2017; Harihar et
442 al., 2018),

443 **Acknowledgements:**

444 The Uttar Pradesh Forest Department granted necessary permits and provided logistic support.
445 Fieldwork was facilitated by funding from the U.S Fish and Wildlife Service's Rhinoceros and
446 Tiger Conservation Award, WWF-India, and WWF's Kathryn Fuller Science for Nature
447 Fellowship (awarded to PC). We also gratefully acknowledge collaboration from K Ramesh and
448 B. Pandav at the Wildlife Institute of India, and M.Gupta, D. Ghose, J. Borah and J. Vattakaven
449 at WWF-India. A. Bista, S. Nair, R. Warriar, R. Ravi, M. D'Almeida, R Sharma and S.S Bisht
450 contributed spiritedly to fieldwork. N.T Hobbs, J. Tack, L.L Bailey and K. Crooks provided
451 helpful advice on analysis and edited this manuscript. Finally, this manuscript was considerably
452 strengthened based on the feedback of two anonymous reviewers.

453

References

- Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J., Karanth, U., 2013. Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. PLoS One 8, e57872. doi:10.1371/journal.pone.0057872
- Barber-Meyer, S.M., Jnawali, S.R., Karki, J.B., Khanal, P., Lohani, S., Long, B., Mackenzie, D.I., Pandav, B., Pradhan, N.M.B., Shrestha, R., Subedi, N., Thapa, G., Thapa, K., Wikramanayake, E., 2013. Influence of prey depletion and human disturbance on tiger occupancy in Nepal. J. Zool. 289, 10–18. doi:10.1111/j.1469-7998.2012.00956.x
- Barlow, A.C.D., McDougal, C., Smith, J.L.D., Gurung, B., Bhatta, S.R., Kumal, S., Mahato, B., Tamang, D.B., 2009. Temporal Variation in Tiger (*Panthera tigris*) Populations and its Implications for Monitoring. J. Mammal. 90, 472-478. doi.org/10.1644/07-MAMM-A-415.1.
- Barrientos, R., 2015. Adult sex-ratio distortion in the native European polecat is related to the expansion of the invasive American mink. Biol. Conserv. 186, 28–34. doi:10.1016/j.biocon.2015.02.030
- Carter, N., Levin, S., Barlow, A., Grimm, V., 2015. Modeling tiger population and territory dynamics using an agent-based approach. Ecol. Modell. 312, 347–362. doi:10.1016/j.ecolmodel.2015.06.008
- Caswell, H., 2001. Matrix populaion models: construction, analysis and interpretation. Sinauer Associates.
- Chanchani, P., Bista, A., Warriar, R.A., Nair, S., Sharma, R., Hassan, D., Gupta, M., 2014a. Status and conservation of tigers and their prey in the Uttar Pradesh terai. WWF-India, New Delhi.

- Chanchani, P., Lamichhane, B.R., Malla, S., Maurya, K., Bista, A., Warriar, R., Nair, S., Almeida, M., Ravi, R., Sharma, R., Dhakal, M., Yadav, S.P., Thapa, M., Jnawali, S.R., Pradhan, N.B., Subedi, N., Thapa, G., Yadav, H., Jhala, Y. V., Qureshi, Q., Vattakaven, J., Borah, J., 2014b. Tigers of the Transboundary Terai Arc Landscape: Status, distribution and movement in the Terai of India and Nepal. National Tiger Conservation Authority of India, New Delhi and Department of National Parks and Wildlife Conservation, Kathmandu.
- Chanchani, P., Noon, B.R., Bailey, L.L., Warriar, R.A., 2016. Conserving Tigers in working landscapes. *Conserv. Biol.* 30, 649–660. doi:10.1111/cobi.12633
- Chanchani, P., 2016. Spatial ecology and conservation of tigers and their prey in the central terai landscape, India. Colorado State University, Fort Collins.
- Chapron, G., Miquelle, D.G., Lambert, A., Goodrich, J.M., Legendre, S., Clobert, J., 2008. The impact on tigers of poaching versus prey depletion. *J. Appl. Ecol.* 45, 1667–1674. doi:10.1111/j.1365-2664.2008.01538.x
- Clutton-Brock, T.H., Coulson, T., Milner-Gulland, E.J., Thomson, D., Armstrong, H., 2002. Sex differences in emigration and mortality affect optimal management of deer populations. *Nature* 415, 633–637. doi:10.1038/415633a
- Duangchantrasiri, S., Umponjan, M., Simcharoen, S., Pattanavibool, A., Chaiwattana, S., Maneerat, S., Kumar, N.S., Jathanna, D., Srivathsa, A., Karanth, K.U., 2016. Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. *Conserv. Biol.* 30, 639–648. doi:10.1111/cobi.12655
- Ebensperger, L.A., 1998. Strategies and counterstrategies to infanticide in mammals. *Biol. Rev.* 73, 321–346.
- Gelman, A., Hill, J., 2007. *Data Analysis Using Regression and Multilevel/Hierarchical Models*.

Cambridge University Press, New York.

Gilpin, E., 1987. Spatial structure and population vulnerability, in: Soulé, M.E. (Ed.), *Viable Populations for Conservation*. Cambridge University Press, Cambridge, UK.

Goodrich, J.M., Kerley, L.L., Smirnov, E.N., Miquelle, D.G., McDonald, L., Quigley, H.B., Hornocker, M.G., McDonald, T., 2008. Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. *J. Zool.* 276, 323–329.
doi:10.1111/j.1469-7998.2008.00458.x

Gosling, L.M., 2003. Adaptive behavior and population viability, in: Festa-Bianchet, M., Apollonio, M. (Eds.), *Animal Behavior and Wildlife Conservation*. Island Press, Washington D.C., pp. 13–30.

Gray, T.N.E., Crouthers, R., Ramesh, K., Vattakaven, J., Borah, J., Pasha, M.K.S., Lim, T., Phan, C., Singh, R., Long, B., Chapman, S., Keo, O., Baltzer, M., 2017. A framework for assessing readiness for tiger *Panthera tigris* reintroduction : a case study from eastern Biodivers. Conserv. doi:10.1007/s10531-017-1365-1

Grayson, K.L., Mitchell, N.J., Monks, J.M., Keall, S.N., Wilson, J.N., Nelson, N.J., 2014. Sex Ratio Bias and Extinction Risk in an Isolated Population of Tuatara (*Sphenodon punctatus*). *PLoS One* 9, e94214. doi:10.1371/journal.pone.0094214

Haridas, C.V., Eager, E.A., Rebarber, R., Tenhumberg, B., 2014. Frequency-dependent population dynamics: Effect of sex ratio and mating system on the elasticity of population growth rate. *Theor. Popul. Biol.* 97, 49–56. doi:10.1016/j.tpb.2014.08.003

Harihar, A., Ghosh-Harihar, M., Macmillan, D.C., 2018. Losing time for the tiger *Panthera tigris*: Delayed action puts a globally threatened species at risk of local extinction. *Oryx* 52, 78–88. doi:10.1017/S0030605317001156

- Harihar, A., Pandav, B., 2012. Influence of connectivity, wild prey and disturbance on occupancy of tigers in the human-dominated western Terai Arc landscape. *PLoS One* 7, 1–10. doi:10.1371/journal.pone.0040105
- Hilborn, R., Arcese, P., Borner, M., Hando, J., Hopcraft, G., Loibooki, M., Mduma, S., Sinclair, A.R.E., 2006. Effective enforcement in a conservation area. *Science* 314, 1266. doi:10.1126/science.1132780
- Hobbs, T.N., Hooten, M.B., 2015. *Bayesian models: A statistical primer for ecologists*. Princeton University Press, Princeton, NJ.
- Horev, A., Yosef, R., Tryjanowski, P., Ovadia, O., 2012. Consequences of variation in male harem size to population persistence: Modeling poaching and extinction risk of Bengal tigers (*Panthera tigris*). *Biol. Conserv.* 147, 22–31. doi:10.1016/j.biocon.2012.01.012
- Hrdy, S.B., 1979. Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethol. Sociobiol.* 1, 13–40. doi:10.1016/0162-3095(79)90004-9
- Jhala, Y. V., Qureshi, Q., Gopal, R., (eds.) 2015. *Status of tigers, copredators and their prey in India, 2014*. Dehradun, India. National Tiger Conservation Authority of India, New Delhi.
- Jhala, Y. V., Qureshi, Q., Gopal, Sinha, P.R., 2011. *Status of tigers, co-predators and prey in India, 2010*. doi:TR 2011/003 pp-302. National Tiger Conservation Authority of India, New Delhi.
- Johnsingh, A.J.T., Ramesh, K., Qureshi, Q., David, A., Goyal, S.P., Rawat, G.S., Kanagaraj, R., Prasad, S., 2004. *Conservation Status of Tiger and Associated Species in the Terai Arc Landscape*, India. Wildlife Institute of India, Dehradun.
- Joshi, A., Vaidyanathan, S., Mondol, S., Edgaonkar, A., Ramakrishnan, U., 2013. *Connectivity*

- of Tiger (*Panthera tigris*) Populations in the Human-Influenced Forest Mosaic of Central India. *PLoS One* 8, e77980. doi:10.1371/journal.pone.0077980
- Joshi, A.R., Dinerstein, E., Wikramanayake, E., Anderson, M.L., Olson, D., Jones, B.S., Seidensticker, J., Lumpkin, S., Hansen, M.C., Sizer, N.C., Davis, C.L., Palminteri, S., Hahn, N.R., 2016. Tracking changes and preventing loss in critical tiger habitat. *Sci. Adv.* 2, e1501675–e1501675. doi:10.1126/sciadv.1501675
- Kanagaraj, R., Wiegand, T., Kramer-Schadt, S., Goyal, S.P., 2013. Using individual-based movement models to assess inter-patch connectivity for large carnivores in fragmented landscapes. *Biol. Conserv.* 167, 298–309. doi:10.1016/j.biocon.2013.08.030
- Karanth, K.U., Gopalaswamy, A.M., Kumar, N.S., Vaidyanathan, S., Nichols, J.D., Mackenzie, D.I., 2011. Monitoring carnivore populations at the landscape scale: Occupancy modelling of tigers from sign surveys. *J. Appl. Ecol.* 48, 1048–1056. doi:10.1111/j.1365-2664.2011.02002.x
- Karanth, K.U., Nichols, J.D., Kumar, N.S., Hines, J.E., 2006. Assessing tiger population dynamics using photographic capture-recapture sampling. *Ecology* 87, 2925–2937. doi:10.1890/0012-9658(2006)87[2925:ATPDUP]2.0.CO;2
- Karanth, K.U., Stith, B.M., 1999. "Prey depletion as a critical determinant of tiger population viability, in: *Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes*. Cambridge University Press, Cambridge.
- Karanth, U.K., Nichols, J.D., Kumar, N.S., 2002. Monitoring tigers and their prey: a manual for researchers, managers, and conservationists in tropical Asia, in: Karanth, U.K., Nichols, J.D. (Eds.), . Centre for Wildlife Studies., Bangalore.
- Kery, M., Schaub, M., 2012. Bayesian Population Analysis using WinBUGS: A hierarchical

- perspective. Academic Press, Waltham, MA.
- Kolipaka, S.S., Persoon, G.A., Iongh, H.H. De, 2017. 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. doi:10.1515/mammalia-2016-0126
- Lambertucci, S.A., Carrete, M., Speziale, K.L., Hiraldo, F., Donázar, J.A., 2013. Population Sex Ratios: Another Consideration in the Reintroduction - Reinforcement Debate? PLoS One 8, 1–7. doi:10.1371/journal.pone.0075821
- Lande, R., 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. Res. Popul. Ecol. (Kyoto). 40, 259–269. doi:10.1007/BF02763457
- Lande, R., 1987. Extinction Thresholds in Demographic Models of Territorial Populations. Am. Nat. 130, 624–635. doi.org/10.1086/284734
- Le Galliard, J.F., Fitze, P.S., Ferrière, R., Clobert, J., 2005. Sex ratio bias, male aggression, and population collapse in lizards. Ings Natl. Acad. Sci. United States Am. 102, 18231–18236. doi.org/10.1073/pnas.0505172102
- Lebreton, J.-D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling Survival and Testing Biological Hypotheses Using Marked Animals : A Unified Approach with Case Studies. Ecol. Monogr. 62, 67–118. doi.org/10.2307/2937171
- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T., Sand, H., 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proceedings. Biol. Sci. 279, 910–5. doi:10.1098/rspb.2011.1275
- López-Sepulcre, A., Norris, K., Kokko, H., 2009. Reproductive conflict delays the recovery of an endangered social species. J. Anim. Ecol. 78, 219–225. doi:10.1111/j.1365-

2656.2008.01475.x

- Majumder, A., Qureshi, Q., Sankar, K., Kumar, A., 2017. Long-term monitoring of a Bengal tiger (*Panthera tigris tigris*) population in a human-dominated landscape of Central India. *Eur. J. Wildl. Res.* 63, 1–11. doi:10.1007/s10344-016-1070-5
- Mondol, S., Bruford, M.W., Ramakrishnan, U., 2013. Demographic loss, genetic structure and the conservation implications for Indian tigers. *Proc. Biol. Sci.* 280, 20130496. doi:10.1098/rspb.2013.0496
- Nichols, J.D., Hines, J.E., Mackenzie, D.I., Seamans, M.E., Gutierrez, R.J., 2007. Occupancy estimation and modeling with multiple states and state uncertainty. *Ecology* 88, 1395–1400. doi:10.1890/06-1474
- Noon, B.R., McKelvey, K.S., 1996. A common framework for conservation planning: linking individual and metapopulation models, in: McCullough, D.R. (Ed.), *Metapopulations and Wildlife Conservation*. Island Press, Washington D.C.
- O’Connell, A.F., Bailey, L.L., 2011. Inference for occupancy and occupancy dynamics, in: O’Connell, A.F., Nichols, J.D., Karanth, U.K. (Eds.), *Camera Traps in Animal Ecology: Methods and Analyses*. Springer, New York, pp. 191–206.
- Oldekop, J.A., Holmes, G., Harris, W.E., Evans, K.L., 2015. A global assessment of the social and conservation outcomes of protected areas. *Conserv. Biol.* 30, 133–141. doi:10.1111/cobi.12568
- Palomares, F., Roques, S., Chavez, C., Silveira, L., Keller, C., Sollmann, R., do Prado, D.M., Torres, P.C., Adrados, B., Godoy, J.A., Jacomo, de A.A.T., Torres, N.M., Furtado, M.M., Lopez-Bao, J.V., 2012. High Proportion of Male Faeces in Jaguar Populations. *PLoS One* 7 e52923. doi:10.1371/journal.pone.0052923

- Persson, J., Willebrand, T., Landa, A., Andersen, R., Segerström, P., 2003. The role of intraspecific predation in the survival of juvenile wolverines *Gulo gulo*. *Wildlife Biol.* 9, 21–28.....
- Plummer, M., 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.
- Polis, G.A., 1981. The evolution and dynamics of intraspecific predation. *Annu. Rev. Ecol. Syst.* 12, 225–251. doi.org/10.1146/annurev.es.12.110181.001301
- Rankin, D.J., Dieckmann, U., Kokko, H., 2011. Sexual Conflict and the Tragedy of the Commons. *Am. Nat.* 177, 780–791. doi:10.1086/659947
- Rastogi, A., Hickey, G.M., Badola, R., Hussain, S.A., 2012. Saving the superstar: A review of the social factors affecting tiger conservation in India. *J. Environ. Manage.* 113, 328–340. doi:10.1016/j.jenvman.2012.10.003
- Reddy, A., Ramesh, K., Shekhar Sarkar, M., Srivastava, A., Bhavanishankar, M., Shivaji, S., 2016. Significance of mate selection and adult sex ratio in tiger reintroduction/reinforcement programs. *J. Zool.* 299, 132–141. doi:10.1111/jzo.12331
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world’s largest carnivores. *Science* 343, 1241484. doi:10.1126/science.1241484
- Robinson, H.S., Wielgus, R.B., Cooley, H.S., Cooley, S.W., 2008. Sink Populations in Carnivore Management : Cougar Demography and Immigration in a Hunted Population. *Ecol. Appl.* 18, 1028–1037. doi:10.1890/07-0352.1
- Royle, J.A., Dorazio, R.M., 2008. Hierarchical Modeling and Inference in Ecology. Academic

Press, London.

Sadhu, A., Jayam, P.P.C., Qureshi, Q., Shekhawat, R.S., Sharma, S., Jhala, Y.V., 2017.

Demography of a small, isolated tiger (*Panthera tigris tigris*) population in a semi-arid region of western India. *BMC Zool.* 2, 16. doi:10.1186/s40850-017-0025-y

Sankar, K., Qureshi, Q., Nigam, P., Malik, P.K., Sinha, P.R., Mehrotra, R.N., Gopal, R., Mondal,

K., Gupta, S., 2010. Monitoring of reintroduced tigers in Sariska Tiger Reserve , Western India : preliminary findings on home range , prey selection and food habits 3, 301–318.

Tropical Conservation Science. 3, 301–318. doi.org/10.1177/194008291000300305

Singh, R., Nigam, P., Qureshi, Q., Sankar, K., Krausman, P.R., Goyal, S.P., 2014. Strategy of

female tigers to avoid infanticide. *Curr. Sci.* 107, 1595–1597.

Smith, J., McDougal, C., Miquelle, D.G., 1989. Scent marking in free ranging tigers, *Panthera*

tigris. *Anim. Behav.* 37, 1–10. [doi.org/10.1016/0003-3472\(89\)90001-8](https://doi.org/10.1016/0003-3472(89)90001-8)

Smith, J.L.D., 1993. The Role of Dispersal in Structuring the Chitwan Tiger Population.

Behaviour 124, 165–195. doi:10.1163/156853993X00560

Smith, J.L.D., McDougal, C., 1991. The contribution of variance in lifetime reproduction to

effective population size in tigers. *Conserv. Biol.* 5, 484–490. doi:10.1111/j.1523-

1739.1991.tb00355.x

Stephens, P.A., Sutherland, W.J., 1999. Consequences of the Allee effect for behaviour, ecology

and conservation. *Trends Ecol. Evol.* 14, 401–405. doi:10.1016/S0169-5347(99)01684-5

Strahorn, E.A., 2009. An Environmental History of Postcolonial North India: The Himalayan

Tarai in Uttar Pradesh and Uttaranchal. Peter Lang, New York.

Sunarto, S., Kelly, M.J., Parakkasi, K., Klenzendorf, S., Septayuda, E., Kurniawan, H., 2012.

Tigers need cover: Multi-scale occupancy study of the big cat in Sumatran forest and

- plantation landscapes. PLoS One 7, e30859. doi:10.1371/journal.pone.0030859
- Sunquist, M.E., 1981. The social organization of tigers (*Panthera tigris*) in Royal Chitwan National Park, Nepal. *Smithson. Contrib. to Zool.* 336, 1–98.
- Sweanor, L.L., Logan, K.A., Hornocker, M.G., 2000. Cougar Dispersal Patterns, Metapopulation Dynamics, and Conservation. *Conserv. Biol.* 14, 798–808. doi:10.1046/j.1523-1739.2000.99079.x
- Swenson, J.E., 2003. Implications of sexually selected infanticide for the hunting of large carnivores, in: Festa-Bianchet, M., Apollonio, M. (Eds.), *Animal Behavior and Wildlife Conservation*. Island Press, Washington D.C.
- Székel, T., Weissing, F., Komdeur, J., 2014. Adult sex ratio variation: implications for breeding system evolution. *J. Evol. Biol.* 27, 1500–1512. doi.org/10.1111/jeb.12415
- Thapa, K., Wikramanayake, E., Malla, S., Acharya, K.P., Lamichhane, B.R., Subedi, N., Pokharel, C.P., Thapa, G.J., Dhakal, M., Bista, A. and Borah, J., 2017. Tigers in the Terai: Strong evidence for meta-population dynamics contributing to tiger recovery and conservation in the Terai Arc Landscape. *PloS one*, 12, p.e0177548.
- Thatte, P., Joshi, A., Vaidyanathan, S., Landguth, E. and Ramakrishnan, U., 2018. Maintaining tiger connectivity and minimizing extinction into the next century: Insights from landscape genetics and spatially-explicit simulations. *Biol. Conserv.*, 218, 181-191. doi.org/10.1016/j.biocon.2017.12.022
- Veran, S., Beissinger, S., 2009. Demographic origins of skewed operational and adult sex ratios: perturbation analyses of two-sex models. *Ecol. Lett.* 129–143. doi.org/10.1111/j.1461-0248.2008.01268.x

- Wadekind, C., 2012. Managing population sex ratios in conservation practice: how and why?, in: Povilitis, T. (Ed.), Topics in Conservation Biology. InTech, Rijeka, pp. 81–96.
- Wikramanayake, E., Dinerstein, E., Seidensticker, J., Lumpkin, S., Pandav, B., Shrestha, M., Mishra, H., Ballou, J., Johnsingh, A.J.T., Chestin, I., Sunarto, S., Thinley, P., Thapa, K., Jiang, G., Elagupillay, S., Kafley, H., Pradhan, N.M.B., Jigme, K., Teak, S., Cutter, P., Aziz, M.A., Than, U., 2011. A landscape-based conservation strategy to double the wild tiger population. *Conserv. Lett.* 4, 219–227. doi:10.1111/j.1755-263X.2010.00162.x
- Wikramanayake, E., McKnight, M., Dinerstein, E., Joshi, A., Gurung, B., Smith, D., 2004. Designing a conservation landscape for tigers in human-dominated environments. *Conserv. Biol.* 18, 839–844. doi:10.1111/j.1523-1739.2004.00145.x
- Wikramanayake, E., Manandhar, A., Bajimaya, S., Nepal, S., Thapa, G. and Thapa, K., 2010. The Terai Arc Landscape: A tiger conservation success story in a human-dominated landscape. In Nyhus, P.J and Tislon, R (eds) *Tigers of the World (Second Edition)* (pp. 163-173).

Figures

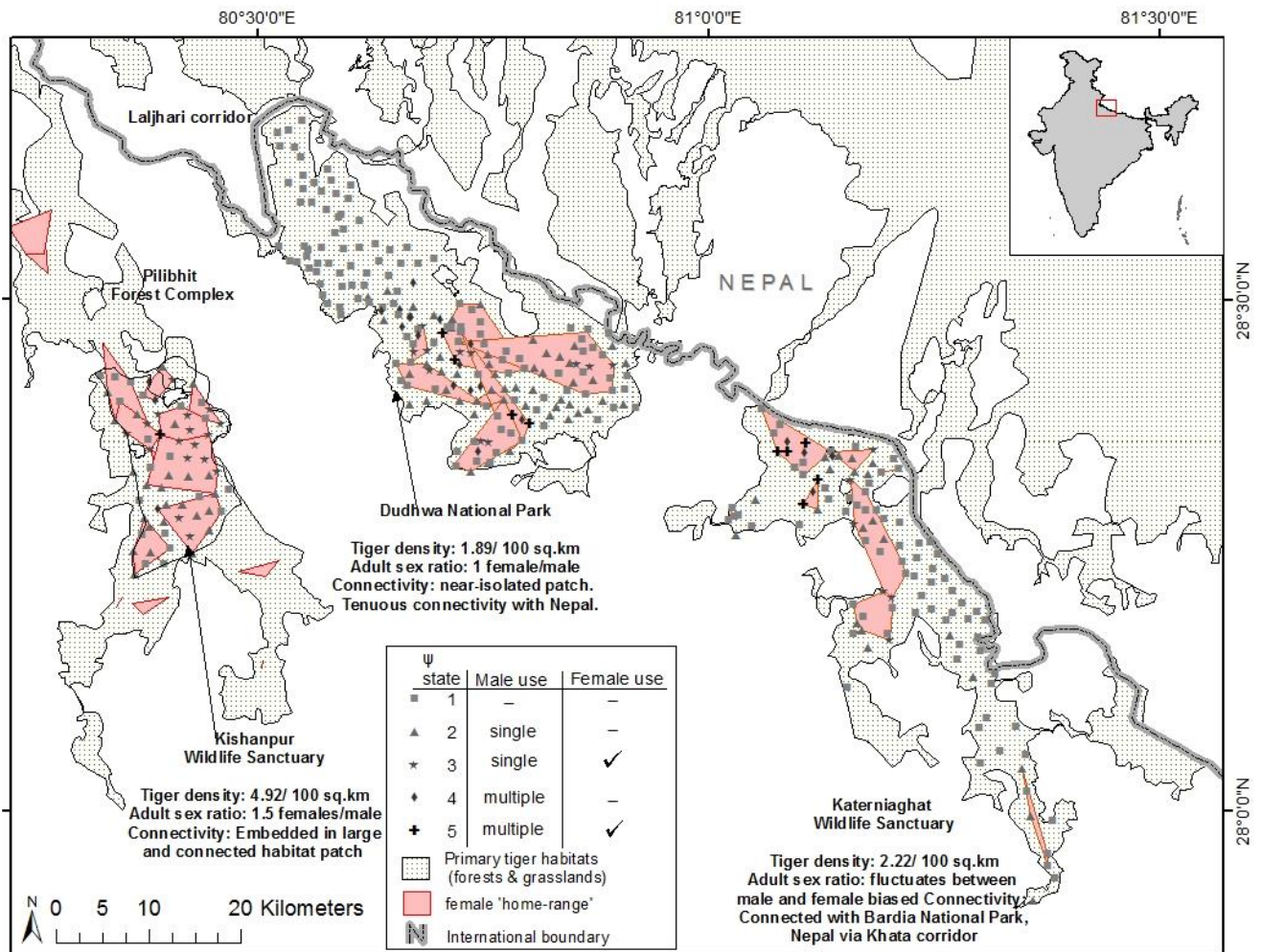


Figure 1. Map of the Central Terai Landscape depicting female home range locations, and state-wise 'photo-capture locations of male tigers (in 2013). The approximate 'home ranges' of females tigers (defined by minimum convex polygons around capture locations) are delineated in beige.

Figure 2

Ecological Process:

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

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

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	
$\theta_{i,j} =$	1	0	0	0	0	0	State 1
	$1 - p_{-2,j}$	$p_{-2,j}$	0	0	0	0	State 2
	$p_{-3-1,j}$	$p_{-3-2,j}$	$1 - p_{-3-1,j} - p_{-3-2,j}$	0	0	0	State 3
	$p_{-4-1,j}$	$p_{-4-2,j}$	0	$1 - p_{-4-1,j} - p_{-4-2,j}$	0	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

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:

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

Figure 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 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.

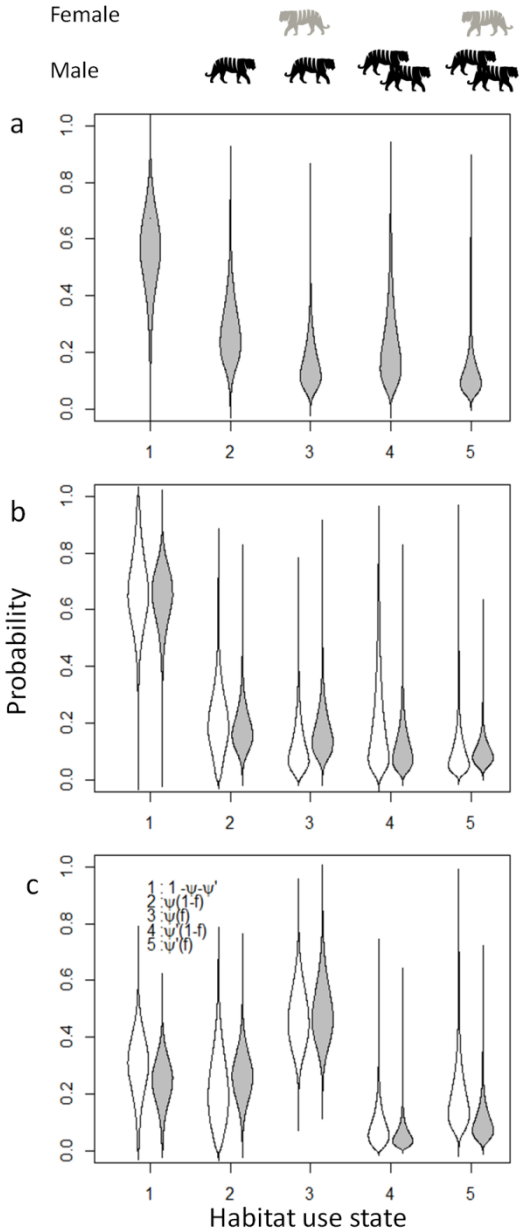


Figure 3: Posterior distributions for parameters linked to the five habitat use states for three PAs in DTR (a) Dudhwa NP, (b) Katerniaghat WLS and (c) Kishanpur WLS) over the two study-years (white: 2012 and grey: 2013). These PAs span gradients of habitat connectivity and ASR (male-biased to female-biased). 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.

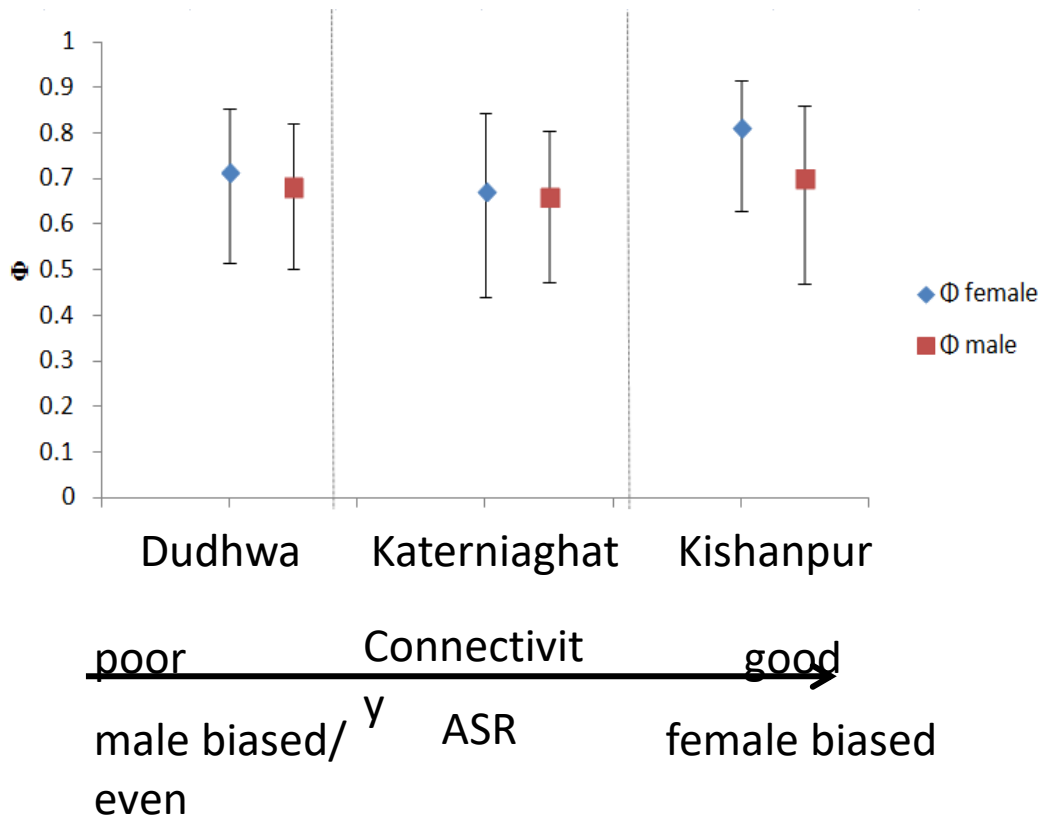


Figure 4. Model averaged estimates of apparent survival probability of male and female tigers in DTR's three protected areas over a 4-year period (2010-2014).

Tables

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	High (+ +)	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 will 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	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) have the following characteristics: poor habitat connectivity, male-biased/ even ASR and lower adult survival rates (expected)

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

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/100k m ² ^b
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	18643	94	1213	50	545	48	668		

Footnotes:

^a Adult sex ratio, calculated as the number of males/ female. Measures of uncertainty are no included because mark-recapture analyses indicated we censused the population.

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

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 p 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-f)		0.45	
2013	2 Ψ (1-f)	0.31	0.21	0.55
2012	3 Ψ (f) ^b		0.01	
2013	3 Ψ (f) ^b	0.01	0.01	0.43
2012	4 Ψ' (1-f)		0.66	
2013	4 Ψ' (1-f)	0.97	0.79	0.92
2012	5 Ψ' (f)		0.28	
2013	5 Ψ' (f)	0.67	0.40	0.74

^aDudhwa 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 Katarniaghat 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.

^bNote 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.

Electronic Supplementary Materials

Appendix A: Estimating abundance and p^* (probability that an individual is captured at least once)

Appendix B. Posterior predictive check plots showing distributions the of relative frequency of various values in a simulated data set, generated from the model.

Appendix C: Table of model selection results for open-population (CJS) models to estimate apparent survival for tigers.