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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 km^2, while females maintain territories between 10 and 30 km^2 (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 km^2 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).