

# Social networks of solitary carnivores: The case of endangered tigers and insights on their conservation

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## Abstract

Solitary carnivores are an ecologically important taxa and at a high risk of extinction worldwide. Interactions between conspecifics can influence fitness outcomes and may help these animals cope with environmental and anthropogenic disturbances. However, the structure and maintenance of these interactions in solitary carnivore species is underexplored. In this research, we leveraged existing camera trap data on tigers (*Panthera tigris*)—a globally endangered and solitary carnivore species—in Nepal's Chitwan National Park to examine for the first time their social networks over 8 years (2008–2017). These networks assume that the co-occurrence at camera trap locations represents an association between conspecifics. We found that tiger networks were fickle, remaining stable for about 3 years before dissolving. We also found that males were more likely than females to form bridges between other tigers, and resident tigers were more central in the networks than nonresidents. In addition, interactions between two animals were more frequent if they were of the opposite sex or were both residents. These insights have implications on disease transmission, population dynamics, and human-wildlife conflict. Combined with camera trap monitoring programs, collecting data on the conspecific interactions of solitary carnivores can advance our knowledge of animal ecology and improve conservation planning.

## KEYWORDS

camera trap, Nepal, network analysis, *Panthera tigris*

## 1 | INTRODUCTION

Interactions between animals influence a range of functional behaviors and can affect the dynamics of populations and communities. Through interactions with conspecifics, individuals can regulate conflicts, create affiliative bonds, cooperate, transmit information, and learn. These interactions also help individuals cope with ecological constraints specific to their living environment

(Sosa et al., 2021). With growing anthropogenic pressure on wildlife species worldwide, understanding the mechanisms underlying interactions with conspecifics can inform conservation planning. For instance, knowledge on the fine-scale structural dynamics of species can help us to understand their communication and reproductive strategies under environmental stress or for highlighting periods of individual and population vulnerability (Jacoby et al., 2016). Terrestrial carnivores—a group of

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ecologically important taxa—are among those species at most risk from extinction (Ripple et al., 2014), necessitating heightened attention to the behavioral processes that influence their vulnerability to environmental change. Approximately three-quarters of the ~250 carnivore species are solitary (Bekoff et al., 1984; Caro, 1989; Hunter, 2019; Sandell, 1989), indicating the ubiquity of this social organization in these taxa. However, despite the significance of conspecific interactions to animal survival and fitness, the structure and maintenance of these interactions in solitary carnivore species has received much less attention than social, gregarious, species. In this research we explore the social networks of tigers (*Panthera tigris*)—a globally endangered and solitary carnivore species—and discuss how insights on these networks may advance conservation science and practice.

Many solitary carnivore species live long lives in relatively stable territories, which may create opportunities for complex interactions to emerge among individuals through repeated interactions (Nowak, 2006). Investing in those interactions with conspecifics might improve one's mating success or access to food (Elbroch et al., 2016, 2017; Wilkinson et al., 2016). For example, tigers are highly territorial, with female tigers seeking to establish territories that maximize their access to prey resources, whereas males establish territories that overlap multiple females to maximize breeding opportunities. Like other solitary carnivores, tigers regularly use scent marks (chemical signals from urine or feces) to communicate their territorial boundaries to others and to determine whether conspecifics are neighbors, potential mates, or competitors (Allen et al., 2016; Gosling & Roberts, 2001; Smith et al., 1989). Based on previous research, we might also expect conspecific interactions in solitary carnivores to vary by individual characteristics, such as age, sex, life-history stage, or reproductive state (Kulahci & Quinn, 2019; Melzheimer et al., 2020; Sosa et al., 2021). Resident male tigers, for instance, may interact with the same group of neighbors over time, whereas a floater male (with no established territory) may interact with various new individuals while in search of a territory. Furthermore, interactions among solitary carnivores might be influenced by homophily, defined as the tendency for similar individuals to preferentially interact (Hirsch et al., 2013; McPherson et al., 2001). For example, resident male tigers may interact more often with females within their territory than with neighboring resident males. In contrast, dispersing males may more likely encounter other males than females as they challenge resident males for their territory. Interactions between conspecifics such as these are all important linkages between individual behavior and group-level dynamics. Understanding these links is highly germane to the conservation of solitary carnivores, for example, helping managers

predict impacts of poaching of certain individuals on group dynamics or the likelihood that translocating individuals to a region occupied by other interacting individuals will be successful. Insights on conspecific interactions can also help us better anticipate the effects of climate change or infectious disease on individuals and populations of solitary carnivores.

Social network theory provides a quantitative framework to study the link between individual behavior and group-level patterns and processes (Krause et al., 2007; Webber & Vander Wal, 2019). Networks consist of nodes connected by edges (Farine & Whitehead, 2015; Whitehead, 2008). Nodes are often individual animals, with individual characteristics such as age and sex. Edges represent how two nodes relate to one another, such as co-occurrence at a given site. Network analyses can then be used to assess network structure, including the presence and strength of conspecific interactions and the factors underlying those behaviors. This framework has greatly improved our understanding of behaviors in more gregarious species, yielding diverse insights ranging from mate choice to competition, from dispersal to predator avoidance, and from social learning to disease transmission, all with important implications for survival, population dynamics, and species evolution (Croft et al., 2016, 2008, 2011; Wey et al., 2008). However, despite compelling evidence of sociality, few attempts have been made to integrate this theoretical framework into behavioral models of solitary carnivores (Elbroch et al., 2017; Graw et al., 2019; Guilder et al., 2015; Quaglietta et al., 2014). The application of this framework to endangered solitary carnivore species is even more rare (Quaglietta et al., 2014; Sarmiento et al., 2019).

Here, we infer for the first time the social networks of tigers in Nepal's Chitwan National Park. We focus on Chitwan National Park, because it is part of a biodiversity hotspot and a tiger conservation priority area, with approximately 120 individuals (DNPWC, 2018). In addition, the park is home to a long-term tiger monitoring site, where information on individuals from an area with high tiger density has been recorded and maintained for over 20 years (McDougal et al., 2016). Starting in 2008 researchers at the site began systematically using digital camera traps to identify individuals and track them for a period of time each year. Information on individuals include important life-history events, such as whether they are a resident with established territory, a female accompanied by offspring, as well as when and how (if available) they died. We leveraged these camera trap data to construct tiger social networks from 2008 to 2017, a period of time in which the camera trap grid was largely located in the same area. Methods for examining social networks based on camera trap data have only recently been developed. These

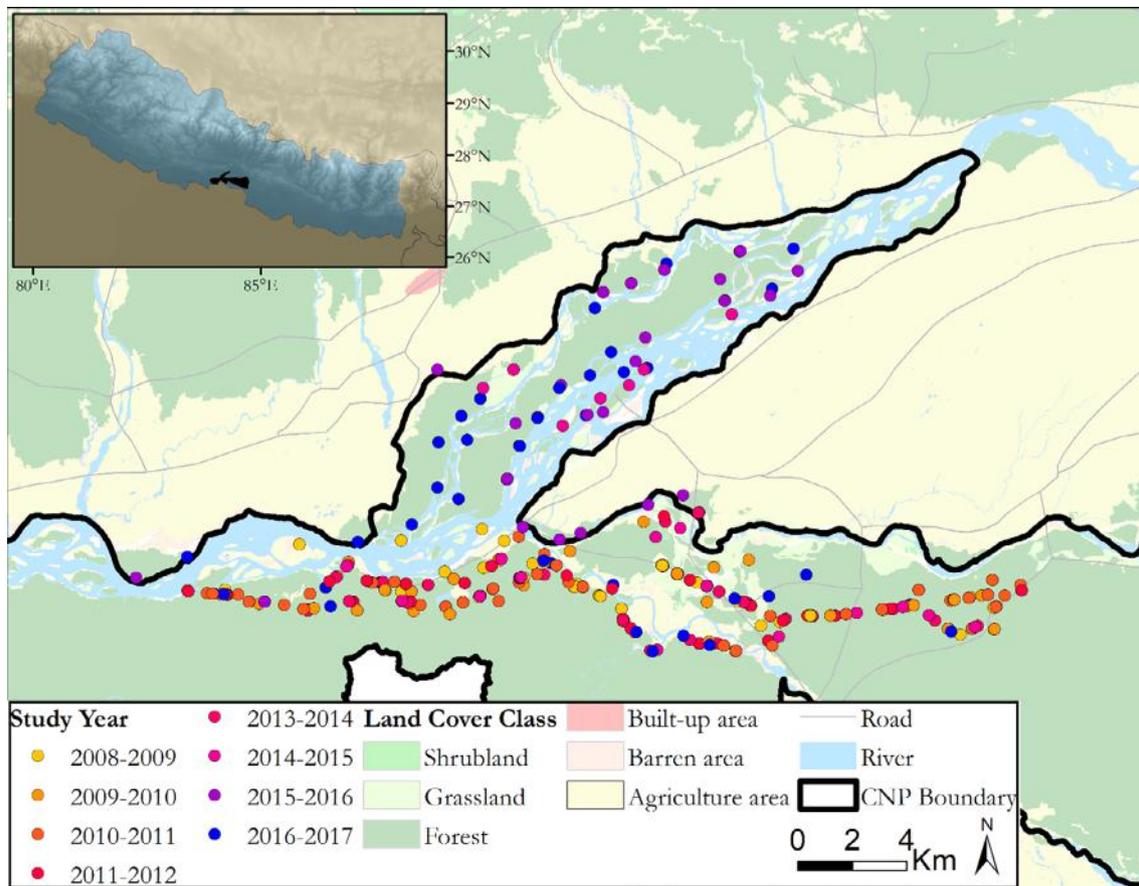


FIGURE 1 Placement of trail cameras between 2008–2017 in Chitwan National Park, Nepal. Inset photo shows the location of Chitwan within Nepal.

networks assume that the co-occurrence at camera trap locations represents an association between conspecifics, for example, tigers detecting and responding to the presence of other tigers. Although camera trap data do not provide detailed insights on conspecific interactions, given their growing ubiquity in ecological research and conservation, the application of social networks to these datasets open up exciting research directions that have hitherto been unexplored.

We had two objectives in this work: (1) construct annual networks to examine their dynamics over time and their relationships to life-history events; and (2) investigate whether tiger social network position and interactions between pairs (dyads) were affected by sex, residency status, and the reproductive status of females. We hypothesized that tigers, though considered “solitary” predators, have extensive interactions with conspecifics, but that interactions are modulated by intrinsic factors such as sex, residency, and reproductive status. We predicted that males would be more influential within networks (i.e., higher degree, eigencentrality, and betweenness) due to their larger home ranges and increased likelihood of encountering conspecifics and be more likely to associate with

females due to tiger mating systems (i.e., single males overlap several female territories). We predicted that residents would be more influential in networks due to interactions involved in the maintenance of territories and may have genetic or other relationships with individuals in adjoining territories, while nonresidents may avoid residents to avoid territorial conflict. Likewise, we predicted residents were more likely to interact with other residents through interactions along territorial edges. We also predicted that reproductive females would have lower values for social network metrics due to avoidance of conspecifics who may predate offspring. Finally, we synthesized insights to discuss the utility of explicitly integrating social network analyses into field monitoring programs and conservation plans.

## 2 | METHODS

### 2.1 | Data collection

We deployed digital passive infrared trail cameras (Moultrie, Moultrie Feeders, AL, USA) in Chitwan National Park (Figure 1) in south central Nepal during

September through July of 2008–2017, with the exception of 2012, as part of the long-term tiger monitoring (LTTM) project. We divided the study area into four blocks (17–29 km<sup>2</sup> in area) with 4–10 camera stations placed within each block. Additionally, we expanded the study area between 2014–2015 and 2016–2017 to include three additional survey blocks in the adjacent Bandarjhula Island region. We established camera stations by deploying two cameras along roads, trails, or other known tiger travel routes to simultaneously photograph tigers from both sides ensuring an accurate identification from stripe patterns. Camera stations were a minimum of 1 km apart and were active 1–3 trapping sessions per year and for 10–27 trap nights per session. GPS locations for each camera trapping site were recorded and each camera recorded metadata including trapping site name, date, and time so that each photo included this information. Individual tigers were identified from pictures using unique stripe patterns and facial markings (McDougal, 1977).

## 2.2 | Data analysis

We inferred social networks among tigers in the study area using the R package CMRnet, which was designed to construct networks from spatially explicit capture-mark-recapture (CMR) data (Silk et al., 2021). We used detections of uniquely identified tigers by camera traps as captures and thinned detections so only a single detection per location could occur in a 24-h period. We defined an interaction between tigers as two individuals occurring at the same camera station within a 72-h window. We chose this window as it gives time for tigers to detect and respond to scent marks by conspecifics in their territory (Mohorović & Krofel, 2020; Smith et al., 1989). It also allows for multiple associations between tigers within a camera trapping session, while avoiding spurious associations from using too expansive of a window. We included all known resident tigers, and all unknown individuals (potential transients or dispersers) who were detected at a minimum of two camera stations and more than 7 days apart. We inferred weighted nondirectional social networks for each study year using a network window of 364 days, and additionally constructed a global network by using a network window encompassing all 9 years of the study.

We estimated node-level metrics of degree, betweenness, and eigencentrality for each individual during each study year, and used permutation tests and mixed effects models to look for differences in each of the node-level metrics by sex and residency status. These network metrics were selected to represent different aspects of social

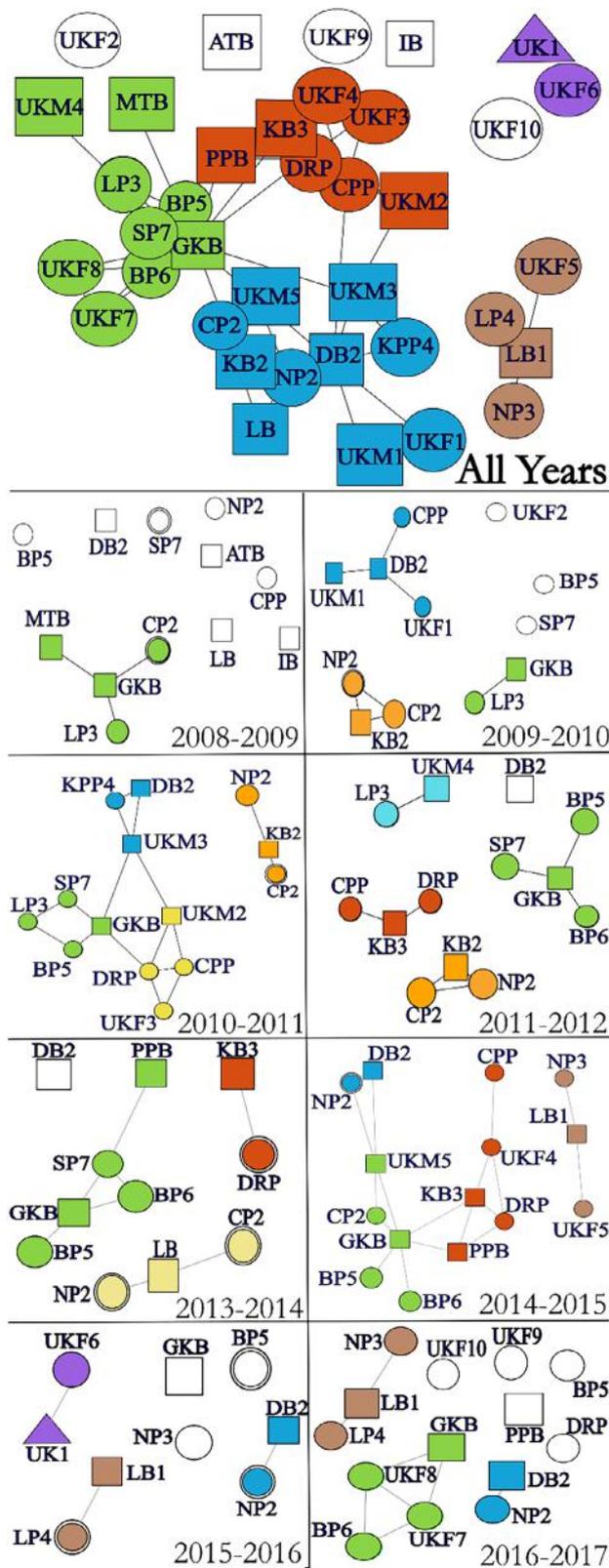
importance within networks. Degree is defined as the number of links of a node (Sosa et al., 2021). Degree thus represents the frequency of an individual's interactions with others, reflecting that individual's social activity (Sosa et al., 2021). Betweenness is defined as the number of times a node is included in the shortest path when considering all combinations of two nodes (Sosa et al., 2021). Betweenness thus indicates how much a node connects within network clusters and may convey information about an individual's role in social transmission (Newman, 2005; Sosa et al., 2021). Although betweenness is a useful metric in social network analysis, it is known to be sensitive to sampling effort (Krause et al., 2015; Sosa et al., 2021). Eigencentrality is defined as the first nonnegative eigenvector value obtained by transforming the adjacency matrix linearly. Eigencentrality thus represents an individual's social capital or importance within a network (Brent et al., 2011; Sosa et al., 2021). We performed a jackknife analysis following Wey et al. (2008) to assess robustness of network metrics by simulating deletion of 5%, 10%, 20%, 30%, 40%, and 50% of all detection data. Jackknife resampling was performed 100 times at each removal level and the range of results were compared to mean observed estimates obtained from the global all-years analysis to ensure robustness of metrics to sampling variation.

We also constructed a female only model to test for the effects of reproductive status, defined as a binomial indicating whether a female was observed with cubs or juveniles. We used the R package ANTs (Sosa et al., 2020) to create a null model set containing 10,000 permuted networks with node label swaps of the appropriate fixed effects and to run mixed-effects models. The model for all tigers contained fixed effects of sex and residency status, while the female only model contained fixed effects for residency status and reproductive status, with both models containing study year as a random effect. Residency status was defined as a binomial indicating an individual who had been detected on cameras in the same location during two consecutive seasons, or in the case of females were observed with cubs or juveniles. Significance of fixed effects was determined by comparing the coefficient values for each fixed effect to the distribution of fixed-effects coefficients from permuted networks.

Additionally, we examined networks for patterns of node interactions by sex, residency, and reproductive status using three different methods. First, we performed a node-level swap by sex and residency on our pooled network by sex and residency to generate 10,000 permuted networks and generated values of Newman's assortativity index (Newman, 2002) for both the true network and our permuted networks. Newman's assortativity index is

defined as the Pearson correlation coefficient between pairs of linked nodes and is valued between  $-1$  (indicating association exclusively with individuals with opposite

characteristics) and  $1$  (indicating association with individuals of same characteristic), with zero indicating random assortment. Next, we performed an identical permutation process on each annual network, with node-level swaps by sex, residency, and reproductive status. For both the pooled and annual networks we determined significance of each effect by comparing observed estimates to the distribution of estimates from permuted networks (Silk et al., 2021). Finally, we tested whether the degree of interaction between two nodes was predicted by nodes having identical attributes for sex or residency status, and whether the edge involved a female with cubs or juveniles. Degree of interaction was defined as the number of interactions between individuals taken from the adjacency matrix of each annual social network. We defined sex and residency as whether both individuals sharing an edge in a network were of the same sex or had the same residency status, respectively. The dataset was composed of all edges in annual networks (i.e., dyads of connected nodes), and we ran a mixed effects model containing all potential fixed-effects and study year as a random effect. We assessed significance of fixed effects by examining confidence intervals of beta coefficients.

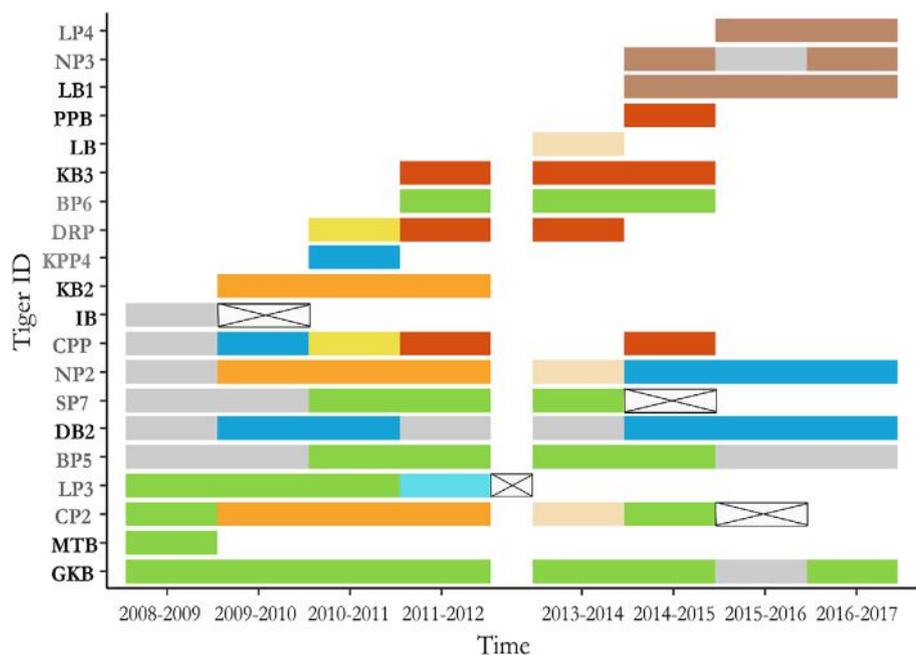


### 3 | RESULTS

We observed considerable variation in social networks between years (Figure 2). While some annual networks showed considerable connectivity in networks (e.g., 2014 and 2010), others were composed solely of disconnected components—disjunct dyads and triads of individuals (e.g., 2009). Resident individuals were present in the study system an average of 4.5 years (SE = 0.64; Figure 3), with males ( $\bar{x} = 5.5$ , SE = 0.81) residing slightly longer than females ( $\bar{x} = 3.4$ , 0.92).

We observed high variability in individual node metrics from the global model (Figure 2) with degree ranging from 0 to 13, betweenness ranging from 0 to 223, and eigencentrality ranging from 0 to 0.99. Both betweenness and degree were robust to deletions of detection data, but

FIGURE 2 Visualizations of social networks for tigers in Chitwan National Park, Nepal, between 2008–2017. A global network showing relationships across all study years and annual networks are shown for each study year (excluding 2012–2013). Shape of nodes indicates sex of individual (square = male, circle = female, triangle = unknown). Double circles indicate females observed with cubs during each study period. Colors indicate groups indicated by cluster analysis. Length of edges indicates strength of relationship.



**FIGURE 3** Timeline of when individual tigers were detected during camera surveys in Chitwan National Park, Nepal, between 2008–2017. Females and males are indicated with gray and black names respectively. Bar colors indicate the clustered subgroups which tigers belonged to from annual social network analyses (see Figure 2), while gray bars indicate that tigers were not linked to any other individuals. Hollow boxes with an “X” indicate the year in which an individual died. Camera traps were not deployed in 2012–2013.

**TABLE 1** Beta coefficients and 90% confidence intervals of null models, estimated using permutation tests, for fixed effects from generalized linear mixed models of network metrics (degree, betweenness, eigencentrality, and assortativity) from social network analysis of tigers in Chitwan National Park, Nepal, between 2008–2017.

Network metric	Fixed effect	$\beta$	90% CI (null model)	
Degree	Sex	0.35	(−0.33, 0.32)	***
	Residency	0.45	(−0.38, 0.44)	***
	Reproductive status (female only)	0.027	(−0.45, 0.44)	
Betweenness	Sex	3.27	(−1.8, 2.0)	***
	Residency	−1.7	(−3.3, 2.3)	
	Reproductive status (female only)	−0.88	(−0.89, 1.1)	
Eigencentrality	Sex	0.048	(−0.12, 0.14)	
	Residency	0.21	(−0.15, 0.17)	***
	Reproductive status (female only)	0.16	(−0.081, 0.21)	

Note: Statistically significant fixed effects are indicated with asterisks. Reproductive status refers to when females were observed with cubs.

eigencentrality values were consistently lower than observed mean metric values (Figure S1). From these individual metrics we were able to identify influential individuals within the networks, in particular the male “GKB” had the highest values for degree and betweenness and the female “NP2” who had the highest eigencentrality value. Both of these individuals were present across multiple years of the study and were associated with different individuals from year-to-year (Figure 3).

Males had a higher number of annual interactions between individuals, as indicated by degree, than females [Table 1;  $\bar{x}_{\text{males}} = 5.1$  (SE = 0.85),  $\bar{x}_{\text{females}} = 3.6$  (SE = 0.47)], and residents had higher numbers of

interactions than nonresidents [Table 1;  $\bar{x}_{\text{res}} = 4.4$  (SE = 0.65),  $\bar{x}_{\text{nonres}} = 3.1$  (SE = 0.50)]. There was no difference in betweenness by residency status [Table 1;  $\bar{x}_{\text{res}} = 1.6$  (SE = 0.62),  $\bar{x}_{\text{nonres}} = 3.2$  (SE = 1.6)]. Males had higher values for betweenness than random [Table 1;  $\bar{x}_{\text{males}} = 3.8$  (SE = 1.4),  $\bar{x}_{\text{females}} = 0.61$  (SE = 0.29)], but the differences varied considerably between years (Figure 4). Contrastingly, we observed no differences in eigencentrality by sex [Table 1;  $\bar{x}_{\text{males}} = 0.19$  (SE = 0.044),  $\bar{x}_{\text{females}} = 0.24$  (SE = 0.065)], but residents had higher eigencentrality than random [Table 1;  $\bar{x}_{\text{res}} = 0.24$  (SE = 0.042),  $\bar{x}_{\text{nonres}} = 0.032$  (SE = 0.027); Figure 5]. Our female-only models showed no evidence of differences by

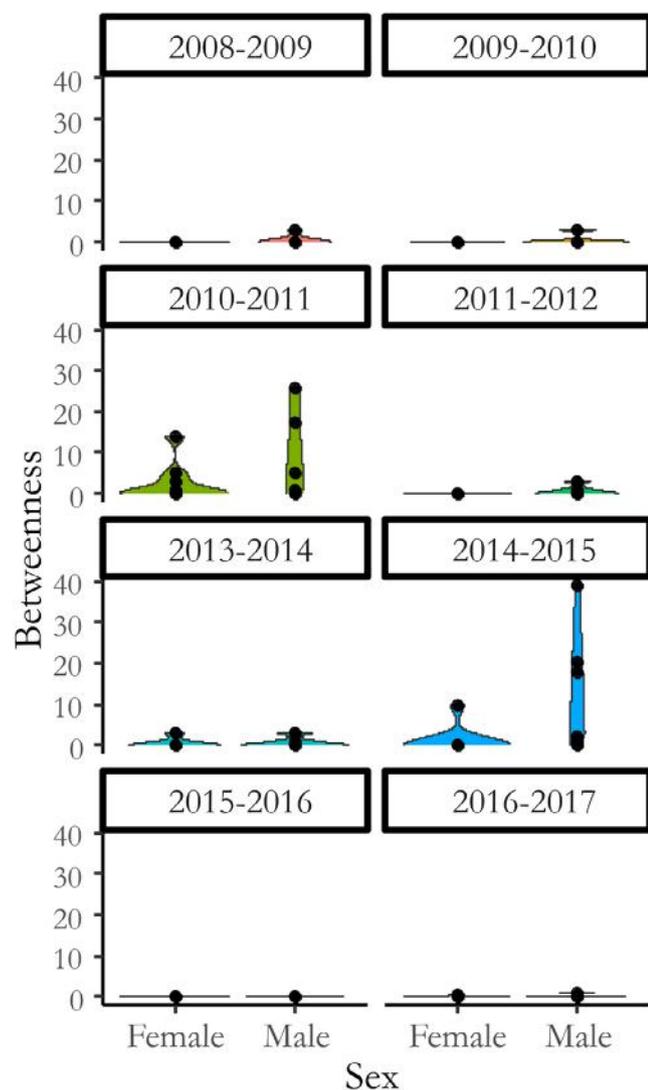


FIGURE 4 Annual comparisons of betweenness by sex for tigers in Chitwan National Park, Nepal, between 2008–2017.

reproductive status by degree [Table 1;  $\bar{x}_{\text{repro}} = 4.1$  (SE = 0.83),  $\bar{x}_{\text{nonrepro}} = 3.4$  (SE = 0.57)], betweenness [Table 1;  $\bar{x}_{\text{repro}} = 0.0$  (SE = 0.0),  $\bar{x}_{\text{nonrepro}} = 0.95$  (SE = 0.45)], or eigencentrality [Table 1;  $\bar{x}_{\text{repro}} = 0.31$  (SE = 0.081),  $\bar{x}_{\text{nonrepro}} = 0.12$  (SE = 0.049)].

Individuals were more likely to associate with individuals of the opposite sex (i.e., heterophily) in our pooled all-years network (Assortativity =  $-0.57$ , 90%  $\text{CI}_{\text{NULL}} = -0.36, 0.26$ ), but there was no evidence of assortativity by residency status (Assortativity =  $0.098$ , 90%  $\text{CI}_{\text{NULL}} = -0.38, 0.27$ ). Assortativity in our annual networks was highly variable, though all networks had negative assortativity indices not all networks were different than random (Figure S2). The pooled dataset of network edges contained 72 total edges. Edges composed of individuals of opposite sexes ( $\beta = -0.35$ , SE = 0.18) or individuals of the same residency status ( $\beta = 0.48$ ,

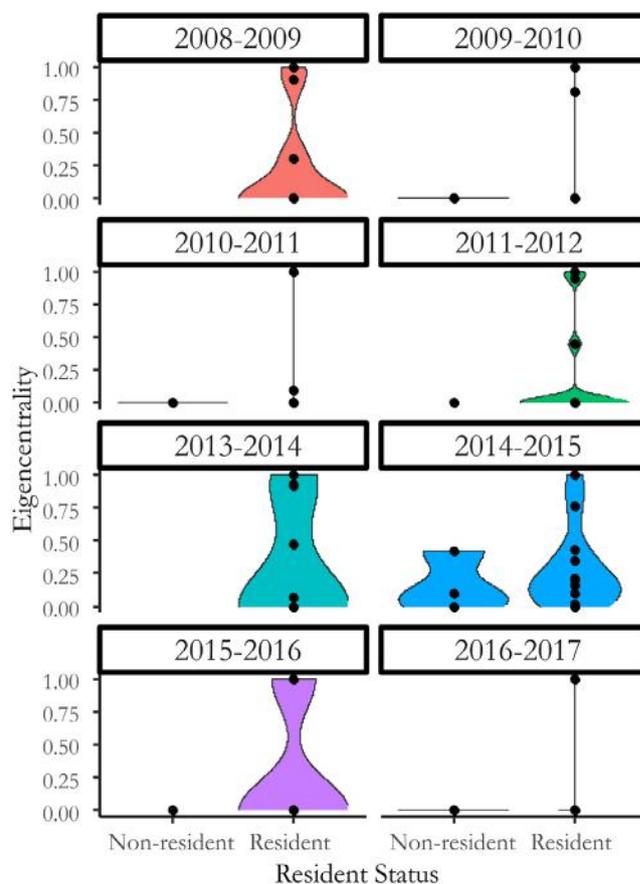


FIGURE 5 Annual comparisons of eigencentrality by residency status for tigers in Chitwan National Park, Nepal, between 2008–2017.

SE = 0.19) had higher edge degrees, though there was no effect from having a reproductive female on an edge ( $\beta = 0.17$ , SE = 0.16).

## 4 | DISCUSSION

Methods for integrating camera trap data into social network analysis have recently emerged, promising to yield insights on behavioral ecology and population dynamics across many systems and species. As camera trap data is widely used for monitoring endangered and elusive species, these new techniques also provide a way to noninvasively investigate social behaviors that would otherwise be overlooked in species of conservation concern or that may be sensitive to changing environments. For the first time, we leveraged existing camera trap data on endangered tigers in Nepal to examine the social networks of these animals over 8 years. Our analysis generated four key insights. First, tiger social networks are fickle, with new clusters forming and others dissolving frequently

through the years. Second, males are more likely than females to form bridges between other tigers. Third, residents are more likely than nonresidents to connect to the wider network. Fourth, interactions between two animals are more frequent if they are of the opposite sex or are both residents.

Tiger networks were highly variable through time. Most associations were temporary, lasting one season. Tiger clusters in the overall network tended to include about three to four animals. However, the identity of these animals changed often through time indicating high turnover of individuals in the clusters. For example, although male “GKB” consistently associated with three females, the identity of those females changed through time (eight different females). Those male–female clusters that appeared stable tended to last about 3 years before dissolving with new clusters forming around a single male. The exact causes of major changes to network configurations are unknown. Changes in animal residence are likely one driving factor. For example, competition between adult males can sometimes end in injury or death for the defeated animal (Carter et al., 2015; Kenney et al., 2014). In our case, it is possible that male KB2 defeated and ousted male MTB, evidenced by one of the females (“CP2”) associated with MTB becoming associated with KB2 after his arrival. Likewise, the disappearance of male KB3 in 2014–2015 (who had been a resident in the two preceding years) may have precipitated a breakdown of the network, leading to disjunct individuals in the following year. Indeed, the removal of certain individuals can have disproportionate effects on network structure, depending on the network position of those individuals (Franz et al., 2015). Alternatively, environmental changes, such as flooding or fluctuations in prey distributions, may shift tiger activity and associations, thereby restructuring the network through time. Interestingly, two major floods of the Narayani river that runs across our study system occurred in 2008 and 2011 (Kafle, 2020), possibly reshaping the tiger networks.

Although the networks were highly variable across years, some small clusters maintain their integrity across several years. Males were usually the nodes maintaining cluster integrity, as they more often connected nodes together than females. For example, males were the bridges between multiple clusters during the 2 years (2010–2011 and 2014–2015) with the greatest interconnectivity between clusters. High betweenness scores for males likely reflects the tiger breeding system. Males move large distances to find and mate with multiple females, while simultaneously excluding other males from mating with the females within their territory (Smith, 1993; Sunquist, 1981). Thus, through their

large territorial movements, males maintain associations with multiple females, which is evidenced by their connections with other tigers through time. Territorial male pumas (*Puma concolor*) also structured interactions among pumas in the Greater Yellowstone Ecosystem, USA (Elbroch et al., 2017). In addition to the transmission of genes, animals with high betweenness may play outsized roles in the exchange of disease and information (Balasubramaniam et al., 2016; Pasquareta et al., 2016), for example, via scent marking. Tigers regularly leave and check for scent marks to obtain information on their conspecifics, such as identity, sex, health status, and hormonal and reproductive state (Smith et al., 1989). This likely helps them discriminate conspecifics as neighbors or strangers or as potential mates or competitors, thereby determining their level of aggression or tolerance toward conspecifics (Müller & Manser, 2007). By linking clusters together, scent marking by males could also indirectly facilitate disease spread through a population. In Nepal, tigers have been found positive for several pathogens common in large felids, including leptospirosis, canine parvovirus-2, feline herpesvirus, and feline coronavirus (McCauley et al., 2021). Canine distemper has been detected in tiger populations in Russia and India, with the deposit of urine and feces considered a possible mechanism for transmission (Gilbert et al., 2015). Disease transmission in tiger populations—which are small—could significantly increase their extinction risk (Gilbert et al., 2014). Linking disease ecology to tiger social networks can help us understand the transmission pathways and consequences to tigers, both at individual and population levels.

Resident tigers were more central in the networks than nonresidents. This suggests that residents were more interconnected with other individuals in the network. This may reflect greater dominance positions of residents than nonresidents. Resident tigers can establish dominance by successfully defending their territory from neighboring tigers and nonresidents looking to establish a territory of their own. In rhesus macaques (*Macaca mulatta*), dominants across all age categories were more central in the networks, playing key roles in social contact, social grooming, and social play (Wooddell et al., 2020). Likewise, dominant red foxes (*Vulpes vulpes*) held central positions in their networks (Dorning & Harris, 2019). Alternatively, residents are more central because of tiger spatial organization (Smith, 1993; Smith et al., 1987). That is, adjacent residents frequently interact with each other when maintaining territorial boundaries (e.g., via scent marking) helping form interconnected networks. Whereas, nonresidents may only opportunistically

interact with conspecifics while searching for vacant territories, mates, or food but otherwise avoid agonistic interactions with residents. Importantly, individuals in more central positions often experience increased fitness and may have disproportionately large influence on group dynamics and function (Modlmeier et al., 2014; Pinter-Wollman et al., 2013). In the case of tigers, for example, females can inherit part or all of the territory of their mothers (Singh & Qureshi, 2020; Smith et al., 1987; Goodrich et al., 2010), indicating that resident females confer an advantage to their offspring. Given their high centrality, we might expect that the death or removal of resident tigers would influence tiger networks more so than nonresidents. Thus, tracking residency status of tigers may be a useful proxy for animal fitness and an important way to monitor population dynamics, especially when combined with the regional or national-scale population surveys that are regularly conducted.

Going beyond network position, our analysis of dyad interactions indicated that individuals of opposite sex associated more strongly than individuals of the same sex and that residents associated more strongly together than with nonresidents. These stronger associations again reflect both the breeding strategy and spatial organization of tigers. As interactions between individuals of the same sex can lead to the lost access to resources or mates, these interactions may be more aggressive and territorial than between individuals of different sexes. Thus, such interactions would be rare given the costs. Likewise, as residents have longer land tenure in an area than nonresidents they are more likely to associate with other nearby residents through time. Importantly, these patterns of associations can have fitness consequences. For example, at prey carcasses, pumas preferentially tolerated those individuals that had previously shared food with them (Elbroch et al., 2017). This result suggests that these animals can recall past experiences and exhibit strategic thinking. As a corollary, resident tigers may be more willing to share food resources with known associates, such as individuals of the opposite sex or other nearby residents, than unknown individuals. Crucially, the kinship between tigers (i.e., the genetic relatedness of two individuals) may influence their interactions with conspecifics. For example, in slender mongooses (*Galerella sanguinea*), a solitary carnivore species, associations of related males gained reproductive benefits via increased territorial and female defense (Graw et al., 2019). Furthermore, information on relatedness between tiger individuals could help ascertain whether there is heritability of network position (e.g., daughter inheriting mother's territory) or assortative associations (e.g., sisters or brothers more likely to associate) (Ilany & Akçay, 2016).

Our social network analysis can easily be applied to other species and systems. Indeed, use of camera traps may be a cost-efficient method to monitor the social networks of multiple species from a single array, and thus provide insight into the differences in network structure and function while controlling for extrinsic factors such as human development, climate, and topography. Additionally, social network analyses can allow inference into sexual relationships between individuals and provide information on parentage and mate choice that would otherwise be difficult to obtain barring genetic analyses or extensive focal sampling. Finally, these methods may be particularly well suited for studying the social networks of secretive, wide ranging species whose interactions are frequently difficult to observe by researchers except under the most fortunate circumstances.

We recommend that future research explicitly collect data that inform social network analysis of tigers. Key data include residency status, scent-marking locations, relatedness between individuals, prey abundances, and tolerance to sharing prey carcasses with neighbors (Barlow et al., 2009; Barocas et al., 2020; Elbroch et al., 2017; Melzheimer et al., 2020). Combined with population counts via systematic camera trap monitoring campaigns, these additional data can help us better understand individual behavior and population dynamics that would improve tiger conservation planning. For example, tigers that kill livestock or threaten human safety may exhibit certain social network positions, such as being less central to the network. In Namibia, researchers found that cheetah (*Acinonyx jubatus*) predation of young calves was more strongly related to the locations where cheetahs exchanged social information with each other via scent marking than with specific cheetahs (Melzheimer et al., 2020). A better understanding of the factors that predict interactions between tigers in turn can help predict the propensity for tigers to come into conflict with human settlements. Social network data can also inform us on how tigers may respond to both environmental and anthropogenic disturbances. For example, we might find that infrastructure development—occurring across tiger range (Carter et al., 2020)—disrupts tiger social networks in ways that increase mortality (e.g., via tigers fighting or infanticide) or decrease fitness (e.g., by altering residency patterns). Insights on conspecific interactions of tigers might also help predict the effects on translocating a tiger to a new population or the outcomes of reintroducing tigers to a new location entirely. Merging the growing suite of tools for analyzing social networks with camera trapping field surveys holds tremendous promise for advancing our knowledge of behavioral and population ecology of solitary, endangered species, like tigers.

## AUTHOR CONTRIBUTIONS

Neil H. Carter conceived the idea and wrote the paper. Evan Wilson performed the analysis. Bhim Gurung assisted with data collection and analysis. All authors contributed to the drafts of the paper.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are available upon reasonable request from the corresponding author.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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