



## Lion (*Panthera leo*) movements in a multiuse area of the eastern Panhandle of the Okavango Delta, Botswana

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As global large carnivore populations continue to decline due to human actions, maintaining viable populations beyond protected area (PA) borders is critical. African lions (*Panthera leo*) ranging beyond PA borders regularly prey on domestic livestock causing humans to retaliate or even preemptively kill lions to minimize impacts of lost livestock. To understand how lions navigate high-conflict areas in human-dominated landscapes, lions were observed and monitored in the eastern Panhandle of the Okavango Delta between October 2014 and December 2016, and five lions were fitted with GPS satellite collars from August 2015 to December 2016. Lion prides and coalitions were small, with all prides having four or fewer females and all coalitions having two or fewer males. Home range size varied between the sexes but was not statistically different (males:  $\bar{x} = 584 \text{ km}^2$ ,  $n = 3$ ; females:  $\bar{x} = 319 \text{ km}^2$ ,  $n = 2$ ). There was considerable spatial overlap in home ranges as nonassociating, neighboring collared individuals utilized high levels of shared space (female–female overlap =  $152 \text{ km}^2$ , representing 41–56% of respective home ranges; male–male overlap =  $125\text{--}132 \text{ km}^2$ , representing 16–31% of respective home ranges). However, neighboring lions varied use of shared space temporally as evidenced by low coefficients of association ( $< 0.08$ ), avoiding potentially costly interactions with neighboring individuals. Highest levels of overlap occurred during the wet and early dry seasons when flood waters minimized the amount of available land area. All collared individuals minimized time in close proximity ( $< 3 \text{ km}$ ) to human habitation, but some individuals were able to rely heavily on areas where unmonitored livestock grazed. While most lions exist within PAs, anthropogenic impacts beyond PA boundaries can impact critical populations within PAs. Studying systems beyond park boundaries with high levels of human–lion conflict while also establishing conservation programs that account for both ecological and sociocultural dimensions will better aid lion conservation efforts moving forward.

Key words: African lion, Botswana, home range, human-dominated landscape, livestock, Okavango Delta, overlap, *Panthera leo*, season

Large carnivore populations and geographic ranges are declining around the globe as species in the order Carnivora face pressures such as habitat loss and conflicts with humans (Ripple et al. 2014). Few protected areas (PAs) are large enough to provide ample space for wide-ranging large carnivores (Winterbach et al. 2014), and many species range beyond PA boundaries where they interact with a growing human population (Woodroffe and Ginsberg 1998; Wittemyer et al. 2008). Human-dominated landscapes outside PAs pose many threats to large carnivores—for example, legal (Packer et al. 2011) and

illegal hunting (Liberg et al. 2012), bush meat hunting (Rogan et al. 2017) and prey base depletion (Bauer et al. 2020), and human–wildlife conflicts (Treves and Karanth 2003)—and contribute to population declines both inside and outside reserves (Woodroffe and Ginsberg 1998; Loveridge et al. 2017).

The African lion (*Panthera leo*) is representative of the challenges facing large carnivores living outside reserve boundaries as the species has been extirpated from approximately 87% of its historical range and is now found predominantly inside PAs (Riggio et al. 2013). However, a recent analysis of PAs

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in Africa showed that they are mostly in a state of failure or deterioration and are likely inadequate to protect the declining lion population (Robson et al. 2022), which is down to only ~20,000 individuals (Chardonnet 2002; Bauer and Van der Merwe 2004; Riggio et al. 2013; Bauer et al. 2015, 2016, 2020). Anthropogenic impacts at and beyond reserve boundaries have contributed to these declines—influencing lion population density and structure—by increasing mortality in juveniles, dispersing subadults, and adults (Loveridge et al. 2010, 2017; Elliot et al. 2014; Rosenblatt et al. 2014; Creel et al. 2016; Bauer et al. 2020). Declines in lion populations are often directly related to conflicts over livestock (Loveridge et al. 2010; Bauer et al. 2020). Understanding the movements of large carnivores in human-dominated landscapes beyond reserve boundaries is critical in order to minimize conflicts with humans and maintain healthy populations.

Lions are social felids and the largest of the African carnivores (Estes 1991). They feed on a variety of prey with large ungulates being most common (Hayward and Kerley 2005). Lions have a complex social system and are found in prides and male coalitions. Prides consist of several related adult females and their dependent young (Stander 1992). Females will cooperate to hunt (Stander 1992), rear young (Bertram 1975), and defend both the territory and young (Packer et al. 1990). Females usually remain resident in their natal pride while males are expelled when they reach sexual maturity (Van Orsdol et al. 1985). Males form coalitions that typically consist of related males (Bertram 1976) that dispersed from their natal pride at the same time, but coalitions can also consist of unrelated males (Packer and Pusey 1982). These coalitions are nomadic before they take over a pride of females by challenging and ousting resident male coalitions (Bygott et al. 1979; Van Orsdol et al. 1985). The length of tenure of a coalition can be linked to its size (Van Orsdol et al. 1985), although on average for coalitions of two males, lengths have ranged from 18 months in the Serengeti (Bygott et al. 1979) to 90 months in Queen Elizabeth National Park (Van Orsdol 1981).

Males predominantly hold the responsibility of defending home ranges, but females will also defend against intruding conspecifics (Van Orsdol et al. 1985). Lions will defend their territories through roaring, scent marking, patrolling, and via direct aggressive conflicts with intruders (Schaller 1972; Van Orsdol et al. 1985). Home ranges can vary in size from 20 to 500 km<sup>2</sup> (Van Orsdol et al. 1985; Valeix et al. 2012a; Tuqa et al. 2014), and even larger home ranges have been noted in arid areas (> 2,000 km<sup>2</sup>; Funston 2001; Zehnder et al. 2018). There can be considerable overlap when large home ranges exist but there is typically little overlap with smaller home ranges (Schaller 1972; Van Orsdol 1981; Van Orsdol et al. 1985). Home ranges of resident males and females are not always the same size because a single coalition of males can control an area that incorporates the home ranges of multiple female prides (Van Orsdol et al. 1985).

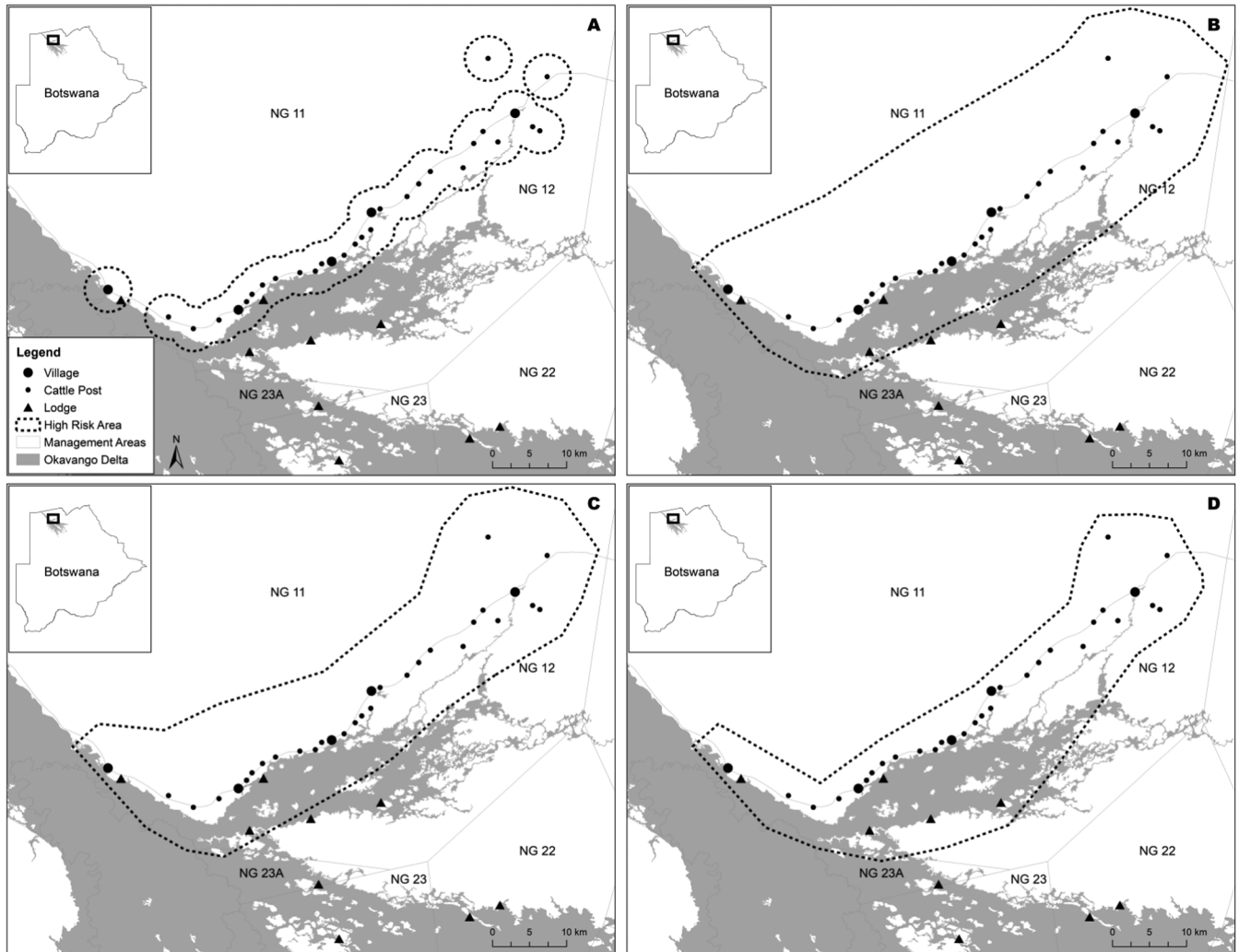
Radiotelemetry and GPS satellite tracking collars have been extensively used to study lion ecology and are well-documented; for example, Scheel and Packer (1991) investigated

hunting behavior, Tambling et al. (2010) used GPS collars to locate feeding sites, and Valeix et al. (2011) focused on movements through patch networks. Our study focused on the lion population of the eastern Panhandle of the Okavango Delta in a human-dominated landscape where villagers reported high levels of livestock losses to lions and other wild carnivores (LeFlore et al. 2019). We monitored the local lion population and investigated their movements within the highly dynamic Delta ecosystem to understand how lions navigate a high-conflict zone outside the borders of PAs. We estimated home range size, space use and overlap, and proximity to areas of risk (human habitation and livestock grazing areas) for collared individuals. We hypothesized that home ranges would be smaller than average home ranges seen in other areas because of high levels of food availability (both wild and domestic; Fynn et al. 2015) present in the area (e.g., Van Orsdol et al. 1985). Furthermore, we anticipated high levels of overlap and space sharing between neighboring prides and coalitions because of the dynamic nature and seasonality of the Delta system and conflict area (Hemson 2003; Kotze et al. 2018).

## MATERIALS AND METHODS

*Study area.*—The eastern Panhandle of the Okavango Delta of northern Botswana lies within the Kavango–Zambezi Transfrontier Conservation Area (KAZA TFCA), an area of critical importance for lion conservation (Funston 2014). The KAZA TFCA is c. 440,000 km<sup>2</sup>, spans five countries, includes 36 PAs, and is home to one of the largest lion populations in Africa (c. 3,500 lions; Funston 2014), classifying it as a lion stronghold (Riggio et al. 2013). The eastern Panhandle connects the Delta to the rest of the KAZA TFCA and supports people, their livestock, and plentiful wildlife (Ramberg et al. 2006; Fynn et al. 2015). Our research encompassed government-defined management areas slated for uses ranging from human habitation and natural resource consumption (Ngamiland [NGs] 11 and 12) to wildlife management and community/internationally run ecotourism (NGs 22, 23, and 23A; Fig. 1). The area lies just north of Moremi Game Reserve and west of Chobe National Park, the southern extremes of the KAZA TFCA in Botswana which has been classified as critical lion habitat (Riggio et al. 2013; Funston 2014). A national hunting ban in Botswana outlawed both safari and subsistence hunting in 2014 (Mbaiwa 2018), though retaliatory lion killings still occur in the study area (Mweze M., personal communication, Dept. of Wildlife and National Parks, Seronga Office, Ngamiland, Botswana, October 2014). The area contains a wide assemblage of wild herbivores (Fynn et al. 2015) and is one of the most sought-after wildlife viewing areas in Africa.

While the Okavango Delta is not a true delta, it is a large inland alluvial fan of the Okavango River and is one of the largest inland “deltas” in the world (McCarthy et al. 2003). The Okavango River is one of southern Africa’s largest rivers and discharges about 10 km<sup>3</sup> of water into the Delta each year (McCarthy et al. 2000; Kgathi et al. 2006). The Delta is composed of a shifting matrix of river channels, swamps, and



**Fig. 1.** Map of the northern Botswana study area showing villages, cattle posts, safari lodges, government-defined management area (NG = Ngamiland) boundaries, and high-risk areas for lions where they may encounter people or livestock. A = high human traffic areas (within 3 km of human habitation); B = cattle grazing area during the wet season; C = cattle grazing area during the early dry season; D = cattle grazing area during the late dry season. Cattle grazing areas estimated based on field observations, expert elicitation, and data presented in [Weise et al. \(2019\)](#).

islands ([McCarthy et al. 2003](#)). The system is fed by seasonal rains that fall in the Okavango River catchment area in Angola and flow into the Okavango River and, to a lesser degree, local rainfall ([Wolski and Savenije 2006](#)). The annual flooding of the Delta is also seasonal, and there is a lag between Angolan rains and peak flooding in the Okavango Delta. The Delta is typically at its lowest across the entire Delta in February and March, when 2,500–4,000 km<sup>2</sup> remain flooded, and at its highest during August, when 6,000–12,000 km<sup>2</sup> are inundated, opposite of the local rainy season ([McCarthy et al. 2003](#)). The eastern Panhandle study area is inundated by the early pulses of flooding, when waters reach the Panhandle starting in February ([McCarthy et al. 2003](#)). Waters remain high into July when they begin slowly receding from our study area and push further southeast to the rest of the Delta. The yearly cycling of the floods is not congruent with the rainy season, which runs from November to March ([Wolski and Savenije 2006](#)), so the Delta becomes an important water source in the Kalahari

environment in the dry season ([McCarthy et al. 2003](#)). Based on temperature, surface water levels, and annual precipitation in 2016, we defined three seasons. The wet season ran from January to March and was characterized by warm days, heavy rainfall, and rising flood waters in the Delta. The early dry season spanned April to July when the flood waters reached their peak and began receding, with little to no rain, and cool winter temperatures. The late dry season spanned August to December and was characterized by the drying of the Delta to its lowest levels where water only remained in permanent channels and hot summer days with temperatures regularly >30°C.

With the cyclical nature of the floods, there are three major hydro-ecological zones in the region: permanent swamp, regularly flooded seasonal floodplains, and occasionally flooded floodplains ([Wolski and Savenije 2006](#)). The floodplains of the Delta are predominantly sandy and the soils accumulate little organic matter. Areas of the Delta with perennial water (permanent swamps) sustain obligate aquatic plant species including

Papyrus (*Cyperus papyrus*) and reed beds of *Phragmites australis* and *Typha bulrushes* (Kgathi et al. 2006; Wolski and Savenije 2006). Emergent sedges dominate areas that seasonally flood, and drier, occasionally flooded areas support various species of grasses (Wolski and Savenije 2006). Islands support riparian forests of semideciduous species comprised of phreatophytic species and salinity-resistant grasses (Wolski and Savenije 2006). Dryland forests that do not flood are fed by rains (Wolski and Savenije 2006) and, in our study area, are composed of Mopane (*Colophospermum mopane*) woodlands (Kgathi et al. 2006).

Local villagers (population c. 5,000; Botswana Population and Housing Census 2011) are agropastoralists, keeping livestock (cattle, *Bos taurus/Bos indicus*; goat, *Capra hircus*; horse, *Equus caballus*; and donkey, *Equus asinus*) and tending crops—for example, sorghum (*Sorghum* spp.), millet (*Pennisetum* spp.), and watermelon (*Citrullus lanatus*) during the growing season (typically December–April). Livestock populations have risen dramatically in the area. Official cattle counts show the population almost doubling over the previous decade (from c. 6,000 in 2006 to c. 11,000 in 2017; Department of Veterinary Services, Seronga office), although actual numbers are likely higher as the Department of Veterinary Services is not always able to census all herds due to logistical constraints. Livestock are occasionally protected overnight (~60% of farmers reported protecting livestock every night in enclosures) in traditional thorn branch or wooden post enclosures, referred to locally as “kraals,” but roam freely during the day (LeFlore et al. 2019, 2020). People live in villages and cattle posts (smaller familial settlements). With extensive human and livestock activity in the area (Fig. 1), the area poses a risk to free-ranging lions. While unguarded livestock represent an easy prey option for lions, people kill lions in response to depredated livestock, the perceived threat of losing livestock, or when missing livestock are believed to have been killed by lions (LeFlore et al. 2019, 2020). Furthermore, lions likely increase their reliance on domestic livestock as a result of seasonal fluctuations in wild prey availability and increased levels of bushmeat hunting (Valeix et al. 2012a). This landscape of risk exists within a critical area for lion conservation and may inhibit lion movements around the southern portion of the KAZA TFCA or even the dispersal of lions throughout the region as communal subsistence farming areas are characterized by high anthropogenic mortality and are often “attractive sinks” (Loveridge et al. 2017).

**Lion tracking.**—We began tracking lion activity in NGs 11, 12, 22, 23, and 23A in October 2014. We used spoor tracking and received tips from local safari guides to locate and identify the various prides and coalitions in the area. Lions were photographed to identify individuals based on their unique whisker spot pattern and identifying marks (e.g., scars, ear notches, etc.; Schaller 1972). Data on demographics, location, pride composition, behavior, and prey species were recorded when lions were observed. Pride composition and demographic information enabled the selective deployment of GPS satellite collars between August 2015 and February 2016 under authority of the Botswanan Department of Wildlife and National Parks (research permit number: EWT 8/36/4 XXVII (61),

darting permit numbers WP/RES 15/2/2 XXVII (22) & WP/RES 15/2/2 XXVII (141) and under UMass IACUC Protocol #2014-0083). Five lions were fitted with Telonics Iridium TGW-4570-3 (Telonics Inc., Mesa, Arizona) GPS satellite/VHF radio collars that recorded a GPS fix five times/day. Based on field observations and local expert elicitation, collars were programmed with two geofences acting as electronic boundaries of GPS points separating the study area into three areas: predominantly wildlife lands, communal grazing lands, and village lands. When a collared lion crossed one of the geofences, our research team was alerted via text message and could then provide villagers with an early warning of potential lion attacks (Weise et al. 2019; LeFlore 2021).

**Data analyses.**—Lion movement data and home range estimation were analyzed using kernel density estimation (KDE) with the *adehabitatHR* package (Calenge 2006) in R statistical software (R Development Core Team 2016). KDE was adapted for use in home range analyses by Worton (1989), is readily used in wildlife ecology studies, and has been shown to be the most reliable contouring method (Powell 2000). KDE has been shown to have advantages over other methods of home range estimation (e.g., minimum convex polygons) because it: (i) can accommodate multiple centers of activity; (ii) does not rely on outlying points to anchor corners; and (iii) is less influenced by distant points (Hemson et al. 2005). Given this, we centered our efforts on KDE home range analyses and estimated home ranges at 95% and 50% isopleths denoting full home ranges and core areas of use, respectively. Lion relocations were analyzed seasonally to capture the effects of the dynamic Delta environment. Male and female home range sizes were compared via two-sided *t*-test, and seasonal comparisons in home range size were made via analysis of variance in R statistical software (R Development Core Team 2016).

We investigated both static and dynamic interactions between collared individuals by season. Static interaction refers to the joint space use between two individuals without consideration of temporal information associated with spatial fixes (Kernohan et al. 2001). Dynamic interaction accounts for both the spatial and temporal movements between two individuals and refers to the relatedness or interdependence of movements of the two individuals (Macdonald et al. 1980; Doncaster 1990). To understand static interactions, we quantified two-dimensional spatial overlap in 95% and 50% KDE home ranges and calculated percent overlap in relation to the home range of each individual. We also calculated the utilization distribution overlap index (UDOVI; Fieberg and Kochanny 2005) to determine the extent of shared space use at the three-dimensional utilization distribution (UD) level. UDOVI is a metric used to examine joint space use between two individuals as a function of the product of their individual UDs, under the assumption that their space use is independent of one another. The metric typically ranges from 0 to 1, with 0 values resulting from two home ranges that do not overlap, and values at 1 for two UDs that are uniformly distributed and have 100% overlap. Values > 1 can result if two UDs are nonuniformly distributed but have a high degree of overlap. UDOVI was calculated with the *adehabitatHR* package (Calenge 2006) in R as:

$$UDOI = A_{ij} \iint UD_i(x, y) \times UD_j(x, y)$$

where  $A_{ij}$  is the area of the intersection between the two home ranges, and  $UD_i$  (resp.  $UD_j$ ) are the value of the utilization distribution of the associated animal  $i$  (resp.  $j$ ) at point  $(x, y)$ ; [Fieberg and Kochanny 2005](#)).

Cole's (1949) coefficient of association (Ca) was used to measure dynamic interaction between collared individuals ([Bauman 1998](#)). Utilizing the *wildlifeDIR* package ([Long et al. 2014](#)), we calculated the Ca as:

$$Ca = (2ST_{\alpha\beta}) / (n_{\alpha} + n_{\beta})$$

where  $ST_{\alpha\beta}$  are the spatially proximal and temporally simultaneous fixes based on user-defined spatial and temporal thresholds (in this case 200 m and 15 min), and  $n_{\alpha}$  (resp.  $\beta$ ) is the total number of all fixes for individual  $\alpha$  (resp.  $\beta$ ; [Long et al. 2014](#)). Ca measures the rate of all fixes within the defined thresholds and is measured on a scale of 0–1.  $Ca > 0.5$  indicates association, while  $Ca < 0.5$  indicates no association ([Kernohan et al. 2001](#)). Ca is a useful metric of attraction or association, as defined by the set thresholds; however, it is subject to the manner in which the spatial and temporal thresholds were determined. We utilized 200 m and 15 min thresholds to define narrow windows for association to minimize the likelihood of artificially inflating levels of association between individuals, and results were consistent when compared across spatial (100–1,000 m) and temporal scales (15–60 min).

## RESULTS

*Demographics and monitoring.*—Between October 2014 and December 2016, we identified and monitored individuals from five prides and five coalitions in our study area ([Table 1](#)). Pride sizes were small with the number of adult females ranging from 1 to 4 and all but one pride having  $\leq 2$  adult females. Adult male coalitions ranged from 1 to 2 individuals and a coalition of young dispersing males contained three individuals. The Airstrip Pride (AP) and Coalition (AC), Cut-tail Pride (CP), Kubu Pride (KP) and Coalition (KC), and Xamaga Coalition (XmC) were present in the study area for the full duration of the study. Other groups—that is, Xakampa Pride (XkP) and Xakampa Coalition (XkC), Hyena Den Pride (HDP), Left-eye Male (LM)—were believed to have immigrated into the area over the course of the study.

The three main prides (AP, CP, and KP) raised young successfully during the study with numbers of young reaching the subadult age group ranging from 2 to 6 per pride ([Table 1](#)). The two AP females birthed six cubs in January 2015, though only two female cubs survived to subadulthood at the end of the study. During the same time frame, the Airstrip Dispersers left their natal pride at  $\sim 2.5$ –3 years of age and were seen periodically in the study area as they began life as a young coalition on their own. The CP also reared two young, though it was not known how many young were first born into the litter. Over

the course of the study, the CP lost the second adult female, though her fate was not known. Two different-aged male cubs were seen with the remaining CP female, and we believed one to be the offspring of the deceased CP female, although only two remained from both litters as the study progressed. These subadult males were  $\sim 2$ –2.5 years old at the end of the study, although the fates of the AP and CP young were not known as the study period concluded. Females from both prides were seen denning toward the end of 2016, but litter sizes could not be determined. The larger KP reared six young males, two of which dispersed from their natal pride toward the end of our study, while the remaining four were seen on their own more frequently but still in close proximity to their natal pride. All six were  $\sim 3$  years old at the end of the study period.

The AP was controlled by a lone male (Airstrip Coalition [AC]) for the majority of the study period ([Table 1](#)). Based on our field observations, the AC formerly was comprised of two males and we are unsure of the fate of the second male. The AC male lost pride tenure in the early dry season of 2016. Another lone male, the XmC, was believed to be in a coalition of three males prior to the start of the study, based on information shared by local guides. Guides believed the two coalition mates were killed by local villagers over the years, but this was not confirmed. The lone AC and XmC males formed a coalition (PiOP Coalition [PC]) of previously nonassociating males during the early dry season 2016. Additionally, we identified a pride of two females (XkP) and a loosely associated coalition (XkC) which consisted of two males who we had not seen previously and likely immigrated during the study period.

Between August 2015 and December 2016, five lions were tracked using GPS satellite collars ([Fig. 2](#), [Table 1](#) in [Supplementary Data SD1](#)). Information about known lion groupings was regularly discussed with local villagers at Kgotlas (community meetings) and collared individuals were assigned local names by community members. The collared AP female (F1) was named Mayenga Nyambi (“Decorated by the Gods”) while the CP female (F2), who was already known to villagers as a cattle killer, was named Maleherehere (“The Sneaky One”). The collared XkC male (M1) was named after one of the area villages (Eretsha), the collared AC male (M2) was named Multwankanda (“The Forager”), and the lone male of the XmC (M3) was named Nduraghumbo (“The Head of the Household”).

*Home range size.*—The 95% KDE home range (henceforth “home range”) sizes from the entire study period varied among the sexes ([Fig. 2](#), [Table 2](#) in [Supplementary Data SD1](#)) and ranged from 421 to 846 km<sup>2</sup> ( $\bar{x} = 584$  km<sup>2</sup>) for males and 270 to 368 km<sup>2</sup> ( $\bar{x} = 319$  km<sup>2</sup>) for females, but were not statistically different ( $t = 1.87$ , d.f. = 2.49,  $P = 0.176$ ). The 50% KDE core home ranges (henceforth “core area/core home range”) spanned 86–180 km<sup>2</sup> for males ( $\bar{x} = 122$  km<sup>2</sup>) and 59–81 km<sup>2</sup> ( $\bar{x} = 70$  km<sup>2</sup>) for females ( $t = 1.66$ , d.f. = 2.51,  $P = 0.213$ ). Lion home ranges were smallest during the wet season (males 179–296 km<sup>2</sup>,  $\bar{x} = 238$  km<sup>2</sup>; females 65–201 km<sup>2</sup>,  $\bar{x} = 133$  km<sup>2</sup>), as were core areas (males 46–54 km<sup>2</sup>,  $\bar{x} = 50$  km<sup>2</sup>; females 15–55 km<sup>2</sup>,  $\bar{x} = 35$  km<sup>2</sup>). All collared individuals utilized larger areas during the early and late dry seasons for both home ranges and

**Table 1.** Lion prides monitored in the northern Botswana study area from October 2014 to December 2016.

Dates	Vernacular ID	Total no. of individuals	Adult males	Adult females	Subadult males	Subadult females	Cubs	Reproduction/notes
October–December 2014	Airstrip Pride	5	0	2	3	0	0	Both females pregnant in December.
	Cut-tail Pride	2	0	2	0	0	?	Unknown litter sizes, both females seen with swollen mammae in November.
	Kubu Pride	10	0	4	0	0	6	Cubs estimated ~6 months in December.
	Airstrip Coalition	2	2	0	0	0	0	Seen with Airstrip Pride females.
	Kubu Coalition	2	2	0	0	0	0	Assumed to father Kubu cubs.
	Total	21	4	8	3	0	6 (?)	
January–December 2015	Airstrip Pride <sup>a</sup>	8	0	2	0	0	6	Cubs estimated born ~January 2015.
	Kubu Pride	13	0	4	6	0	3	Largest stable pride.
	Cut-tail Pride	5	0	2	0	0	3	Three cubs seen by guides end of 2015. Females loosely associate.
	Xakampa Pride	2	0	2	0	0	0	Believed to emigrate from Duba.
	Airstrip Coalition <sup>a</sup>	2	2	0	0	0	0	Fathered Airstrip cubs.
	Airstrip Dispersers	3	3	0	0	0	0	Dispersed from Airstrip Pride ~January 2015.
	Kubu Coalition	2	2	0	0	0	0	Fathered Kubu cubs.
	Xakampa Coalition <sup>a</sup>	2	2	0	0	0	0	Believed to emigrate from Duba.
	Xamaga Coalition <sup>a</sup>	1	1	0	0	0	0	Believed previously in coalition of three.
	Total	38	10	10	6	0	12	
January–December 2016	Airstrip Pride <sup>a</sup>	4	0	2	0	2	?	Both females denning in December.
	Hyena Den Pride	2	0	1	0	1	0	Unknown reproduction.
	Kubu Pride	7	0	3	4	0	0	Four cubs from 2014 remain.
	Cut-tail Pride <sup>b</sup>	5	0	1	2	0	2 + ?	Denning December 2016—two cubs seen, likely more.
	Xakampa Pride	2	0	2	0	0	?	One female seen with swollen mammae in August.
	Kubu Coalition	1	1	0	0	0	0	Unknown.
	Left-Eye Male	1	1	0	0	0	0	Mated with both females of Airstrip Pride.
	PiOP Coalition <sup>a</sup>	2	2	0	0	0	0	Previous Airstrip male and Xamaga male formed PiOP Coalition. Strong association with Maleherehere Pride, including possible mating. Regular revisit to female and den sites after litter was born end of 2016.
	Xakampa Coalition	2	2	0	0	0	0	Unknown. Male slipped collar December 2015, but observed November 2016.
	Total	26	6	9	6	3	2 + ?	

<sup>a</sup>Denotes a lion group with an individual collared in August 2015.

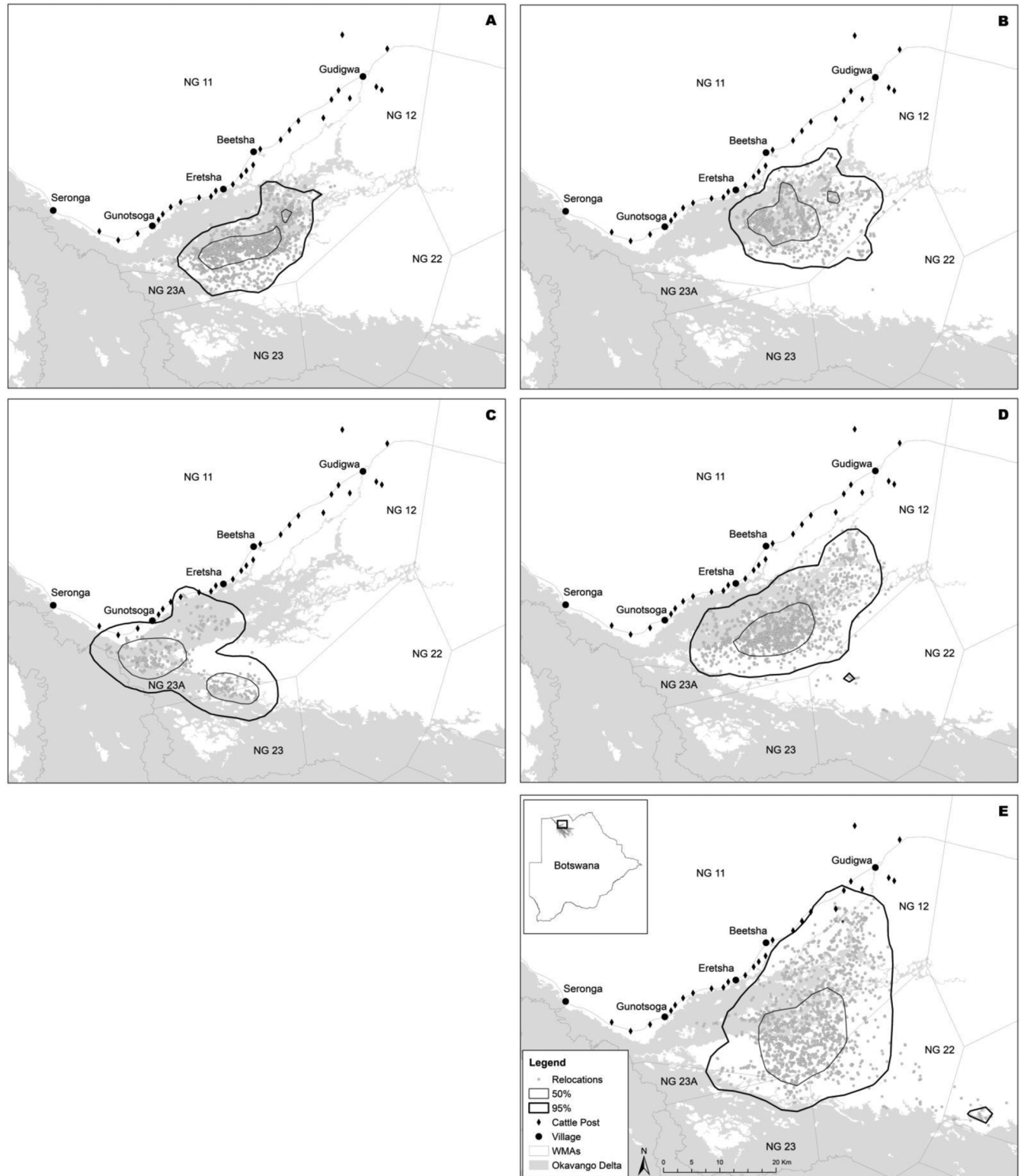
<sup>b</sup>Denotes a lion group with an individual collared in February 2016.

core areas. The home ranges for males ranged from 371 to 717 km<sup>2</sup> ( $\bar{x}$  = 529 km<sup>2</sup>) and females ranged from 160 to 458 km<sup>2</sup> ( $\bar{x}$  = 250 km<sup>2</sup>); core areas ranged from 76 to 214 km<sup>2</sup> ( $\bar{x}$  = 125 km<sup>2</sup>) for males and 29 to 130 km<sup>2</sup> ( $\bar{x}$  = 61 km<sup>2</sup>) for females. Variation in home range size and core area size across the seasons was not significantly different ( $F$  = 2.07, d.f. = 3,  $P$  = 0.157;  $F$  = 1.75, d.f. = 3,  $P$  = 0.211, respectively).

**Static interactions.**—With five lions collared over the course of the study, the number of possible dyads was 10 ( $n \times (n - 1)/2$ ); however, two individuals were never collared at the same time; therefore, the number of possible dyads was nine. All nine dyads had static interactions at the home range contour, meaning they utilized shared space, over the full study duration (Tables 3–7 in [Supplementary Data SD1](#), Figs. 1–8 in [Supplementary Data SD2](#)). Females utilized 152 km<sup>2</sup> of shared space, representing 41–56% of their respective home ranges. Males utilized between 125 and 434 km<sup>2</sup> of shared space, representing 16–90% of their respective home ranges. Male home ranges regularly overlapped with female home ranges and shared space ranged from 117 to 365 km<sup>2</sup>, representing 43–99% of female home ranges and 28–65% of male home ranges. Six of the possible nine dyads had static interaction at core home ranges over the full study duration, two of which were for individuals known to associate with each other, one M–F dyad and

one M–M. Females shared 11 km<sup>2</sup> which represented 14–19% of their core home ranges. One male dyad shared 61 km<sup>2</sup> which represented 34–71% of their core home ranges, and these individuals formed a coalition for part of the study period. Male and female core home ranges regularly overlapped with 24–43 km<sup>2</sup> shared space representing 41–68% of female core home ranges and 13–50% of male core home ranges.

Seasonal static interactions were prevalent in the highly dynamic Delta ecosystem. Seasonal static interactions between the two nonassociating collared females ranged from 22 to 100 km<sup>2</sup> representing 22–75% of individual home ranges. Static interactions were the highest for both individuals during the wet and early dry seasons when the study area is inundated with flood waters. While spatial overlap of home ranges was perpetual for females, their core home ranges only overlapped during the wet season and early dry season (2–24 km<sup>2</sup>, 4–60%). Seasonal static interactions between nonassociating males ranged from 90 to 269 km<sup>2</sup> representing 22–40% of individual home ranges. Two previously nonassociating males (M2 “Multwankanda” and M3 “Nduraghumbo”) began associating in June 2016 during the early dry season and remained as such for the duration of the study. As a result, their static interactions increased substantially during this period. These males utilized 451 km<sup>2</sup> (63–86%) of shared home range space during



**Fig. 2.** All relocations and 50% and 95% contours from kernel density estimation (href) for collared lions in the northern Botswana study area between August 2015 and December 2016. A = Female 1 (Airstrip Pride); B = Female 2 (Cut-tail Pride); C = Male 1 (Xakampa Coalition); D = Male 2 (Airstrip Coalition); E = Male 3 (Xamaga Coalition).

the early dry season 2016 and 457 km<sup>2</sup> (96%) during the late dry season 2016. At the core home range level, this newly formed coalition shared 37 km<sup>2</sup> (17–39%) of space during the early dry season 2016 and 113 km<sup>2</sup> (86–88%) during the late dry season 2016. Seasonal static interactions at the core home range level for nonassociating males were limited, ranging from 0 to 19 km<sup>2</sup> (0–25%) of individual core home ranges. Seasonal static interactions between males and females at the home range level varied widely and ranged from 20 to 410 km<sup>2</sup> (31–100% of female home ranges; 7–92% of males), with the highest amount of overlap reserved for dyads where individuals were known to associate. Males and females shared 0–59 km<sup>2</sup> (0–98% of female; 0–76% of males) of their core home ranges, again with the highest amount of overlap reserved for dyads where individuals associated. In M–F dyads where there was no known association, static interaction was limited at the core home range level (0–10 km<sup>2</sup>; 0–23% for both sexes).

Given the broad range in home range overlap at the two-dimensional level over the course of the study, we calculated three-dimensional space use overlap using UDOI to quantify the extent of shared space use between individuals. While percentages of space use were variable, the 95% contour UDOIs for nonassociating lion dyads were low (<0.30) over the course of the whole study (Supplementary Data SD1, Tables 8 and 9). Seasonally, UDOIs for nonassociating individuals ranged from < 0.01 to 0.40. UDOIs for associating individuals ranged from 0.57 to 0.87 over the course of the whole study and 0.51 to 1.23 seasonally. The highest UDOI registered was for the newly formed PC males (M2 and M3). Other high UDOIs were found between males and females who were known to associate and likely mated with each other (UDOIs 0.51–1.05). At the core area contour, UDOIs were low for all lion dyads throughout the study (0.00–0.13), with the highest of these values resulting from dyads where there was known association. At the seasonal level, nonassociating individuals showed low UDOIs (0.00–0.07), and associating individuals also had little overlap of their UDs (0.06–0.30), though highest levels were found only in individuals known to associate.

*Dynamic interactions.*—While static interactions were present at both home range and core home range levels for nonassociating females, seasonal Ca was 0.00 (Supplementary Data SD1, Tables 10 and 11) as the collared females did not associate at all during the study. Likewise, for nonassociating males, seasonal Ca was extremely low (0.00–0.04). However, over the course of the study, the newly formed PC led to Ca increasing (from 0.01 to 0.47) between males who were believed to be unrelated. Ca among male–female dyads were low (0.00–0.08) between individuals not observed associating, and Ca for male–female dyads known to associate during the study ranged from 0.00 to 0.47. M2 (Multwankanda) was the overlapping individual in known associations described above.

*Proximity to risk.*—All collared individuals spent < 9% of their time within 3 km of human settlements over the course of the whole study (Figs. 1 and 2, Table 12 in Supplementary Data SD1). M1 (Eretsha) had a median distance to the zone of human habitation of 3.7 km and likely had the highest chance of an

encounter with humans. Other individuals had higher median distances to the zone of human habitation (8–10.9 km) and lower risk of encountering humans. M3 (Nduragumbo) did venture closer to humans than usual during the early dry season 2016 (mdn dist. = 4.9 km) and 15% of relocations were within the zone of human habitation. F2 (Maleherehere) was consistently in livestock grazing areas (30–46% of all locations) over the course of the study (Table 13 in Supplementary Data SD1). All other individuals were in livestock grazing areas most often in the late dry season (30–81% of all relocations) when livestock ranged farther south into the delta (Fig. 1), with median distances ranging from 0.0 to 1.8 km for all individuals. Both M1 and F2 were known cattle killers (LeFlore 2021).

## DISCUSSION

These results represent the most thorough assessment to date of lion home ranges, joint space use, and movements in the human-dominated eastern Panhandle of the Okavango Delta, despite our relatively small sample size. Lion home ranges in the eastern Panhandle of the Okavango Delta were relatively large compared to other locations around the continent (Van Orsdol et al. 1985; Loveridge et al. 2009; Tuqa et al. 2014), but were considerably smaller than those found in the more arid Central Kalahari region of Botswana where 95% contour home ranges were >2,000 km<sup>2</sup> (Funston 2001; Zehnder et al. 2018) and 50% core areas were >500 km<sup>2</sup> (Zehnder et al. 2018). In East Africa, lion home range sizes vary dramatically (4–450 km<sup>2</sup>; Schaller 1972; Gittleman and Harvey 1982; Van Orsdol et al. 1985; Tuqa et al. 2014). Variation in home range size is site-specific (Tumenta et al. 2013) but is negatively correlated with population density (Loveridge et al. 2009) and prey abundance (Van Orsdol et al. 1985; Bauer and De Iongh 2005; Loveridge et al. 2009). Average pride sizes were small for collared prides, which could be caused by numerous factors, including the flooding of the region, high levels of intraspecific competition for space due to the flooding regime, low prey densities, and high levels of human–lion conflict in the region (Stander 1992; Hemson 2003; Kotze et al. 2018). Given prevalent bushmeat hunting (Goodheart et al. 2021) and retaliatory killings (LeFlore et al. 2019), lion densities were likely lower than could be sustained by wild prey availability and additional domestic prey, leading to larger home ranges than in other systems with prevalent food sources. Additional research focused on prey densities (wild and domestic) should be conducted in this area to further illuminate this point.

With reasonably large home ranges, nonassociating collared individuals shared extensive amounts of their 95% and 50% core home range. Static overlap was highest during the wet season and early dry season when the area was inundated with flood waters. Our research aligns with published literature showing spatial overlap among nonassociating lion groups (Schaller 1972; Van Orsdol et al. 1985; Spong 2002; Bauer and De Iongh 2005; Davidson et al. 2011; Tumenta et al. 2013; Benhamou et al. 2014; Kotze et al. 2018) and provides additional evidence that previously nonassociating males



occasionally form coalitions later in life (Schaller 1972; Bygott et al. 1979; Packer and Pusey 1982; Benhamou et al. 2014). Overlap at the two-dimensional core home range level was higher in our study than reported elsewhere (Spong 2002), but core home range overlap was low when compared via three-dimensional UDOI. While static interactions were prevalent in our study, dynamic interactions were reserved for associating individuals, suggesting individuals from neighboring nonassociating groups share space but vary use of shared space temporally, avoiding potentially hostile interactions. While Benhamou et al. (2014) found that dynamic avoidance (spatiotemporal movement to minimize interactions) between unrelated lions was rare, avoidance can be facilitated by nonaggressive territorial behaviors, including scent marking (Schaller 1972) and roaring (McComb et al. 1993, 1994). Individuals may operate in an existing dominance hierarchy and move independently when they are navigating shared space (Benhamou et al. 2014). It is also worth noting that lions are known to have a fission–fusion structure to their pride dynamics (Schaller 1972) that are linked to a variety of factors—for example, hunting benefits/prey availability (Schaller 1972; Bertram 1973; Van Orsdol et al. 1985; Packer 1986; Packer and Rutman 1988), cub protection (Pusey and Packer 1994; Mosser and Packer 2009), intraspecific competition (Packer et al. 1990; Grinnell et al. 1995; Mosser and Packer 2009; Miller and Funston 2014), and habitat structure/landscape characteristics (Trinkel et al. 2007; Mosser 2008; Celesia et al. 2009; Mosser and Packer 2009; Kotze et al. 2018). While neighboring individuals and groupings monitored here were believed to be nonassociating, the potential exists for these individuals to be related and thus more tolerant of overlap in shared space use. However, if this were the case, we would expect to see higher dynamic interactions via coefficients of association than observed here.

We suggest that the dynamic Delta landscape and potential interactions with humans likely restrict lion movements in the eastern Panhandle and contribute to spatial overlap in home ranges. Kotze et al. (2018) posited that lion home range overlap was connected to the wetland environment in another region of the Delta. Additional ecological factors (e.g., conspecifics holding neighboring territories, vegetation structure, prey availability, water access) may also restrict lion movements in the region (Dures et al. 2020). While access to water in xeric environments was shown to have fitness advantages and increase territorial exclusivity in lions (Mosser 2008; Valeix et al. 2010, 2012b), in the Delta, flood waters may alter territorial boundaries by washing away scent markings, limiting access to certain areas, and making it more costly to maintain exclusive territories (Davidson et al. 2013; Midlane 2013; Kotze et al. 2018). Pressures from people, conspecifics, and seasonal flooding caused nonassociating individuals to utilize considerable amounts of shared space, limiting the ability of prides and coalitions to maintain exclusive territories. This could lead to potential “crowding,” exacerbating intraspecific competition and causing reduced survival and reproduction (Metcalf et al. 2007; Ordiz et al. 2008; Kotze et al. 2021). If the utilization of shared space leads to territorial disputes, resulting interactions can lead to adult mortality, infanticide, and overall lower

reproductive success (Mosser and Packer 2009; Trinkel et al. 2010). These conditions may be more prevalent when the area is inundated with flood waters during the wet and early dry seasons (Kotze et al. 2018). Anthropogenic mortality in large carnivores is typically additive to natural mortality, not compensatory, causing detrimental demographic impacts (Creel et al. 2016; Loveridge et al. 2017). Subsequently, if anthropogenic mortality causes lower lion densities than would naturally occur, it is likely that higher levels of territorial turnover exist in the area resulting in less overall exclusivity in territories. These continually shifting territorial boundaries likely contribute to increased levels of adult mortality and infanticide, further exacerbating population concerns. While our study was based on a relatively short time frame coinciding with high levels of anthropogenic mortality, we observed more male offspring than females which is often linked to perturbations in the system (Smuts 1976; Whitman and Packer 2007). Long-term studies on lion demographics, genetics, and movements in the region are needed to fully understand these dynamics (Mosser and Packer 2009; Dures et al. 2020).

Both anthropogenic and ecological factors are understood to impact lion movements and intraspecific interactions (Spong 2002; Hemson 2003; Davidson et al. 2011; Kotze et al. 2018; Dures et al. 2020). Most studies involving lion movements and proximity to anthropogenic threats focus on lions who spend most of their time within PA boundaries but may range outside PAs and encounter people (e.g., Loveridge et al. 2010; Tumenta et al. 2013; Zehnder et al. 2018). Findings presented here are one of the few examples where monitored lions ranged entirely beyond PA boundaries in areas of high-conflict potential. While most lions exist within PAs, anthropogenic impacts beyond PA boundaries can impact populations within PAs (Woodroffe and Ginsberg 1998; Loveridge et al. 2010). As has been found in other communal areas, it is possible that the eastern Panhandle qualifies as an “attractive sink” where lions in the region (or dispersing individuals from deeper in the Delta) move toward the villages and are subsequently killed (Loveridge et al. 2010, 2017). While findings presented here were based on a relatively small sample size of collared individuals, they highlight how the movements and space use of this social carnivore can vary based on system-specific ecological and anthropogenic pressures. Studying systems beyond park boundaries with high levels of human–lion conflict and establishing conservation programs accounting for both ecological and sociocultural dimensions will better aid lion conservation efforts moving forward (Decker et al. 2012; Weise et al. 2019; LeFlore et al. 2020; LeFlore 2021).

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### AUTHOR CONTRIBUTIONS

EGL conceived and designed the study and analysis, collected the data, performed the analysis, and drafted the manuscript; TKF and ABS guided study design and conception and contributed to manuscript preparation; all authors revised and approved the manuscript.

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### CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

### DATA AVAILABILITY

Data supporting the conclusions of this article will be made available on request. Inquiries can be directed to the corresponding author.

### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

[Supplementary Data SD1.—Tables.](#)

[Supplementary Data SD2.—Figures.](#)

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