Corridors of tolerance through human-dominated landscapes facilitate dispersal and connectivity between populations of African lions *Panthera leo*

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Abstract Globally, little is known about the dispersal abilities of carnivores, their survival in non-protected areas, and the connectivity between protected and non-protected populations. More than a decade of sighting data for 496 known African lions *Panthera leo*, with 189 individuals engaging in dispersing activities plus an exchange of cross-site information, has provided unique insight into connectivity and survival in unprotected and protected areas in Kenya. In particular, three individuals, across two generations residing solely in unprotected landscapes, demonstrated connectivity between three protected areas that, to our knowledge, have not previously been recognized as harbouring connected populations. These observations suggest that unprotected areas and the human communities that reside in them may successfully create corridors of tolerance that facilitate connectivity and the long-term persistence of lion populations, both within and outside protected areas.

Keywords Carnivore, community conservation, corridor, dispersal, Kenya, lion, *Panthera leo*, tolerance

The growth of human populations and associated development are causing carnivore populations to become increasingly fragmented (Crooks et al., 2011), and dispersal between populations has become ever more important to maintain population viability (Clobert et al., 2012). Dispersal is broadly defined as the permanent movement of an individual out of its natal range, either alone or with cohorts (Bekoff, 1989; VanderWaal et al., 2009). Migrating individuals can recolonize and protect dwindling local populations from extinction (Brown & Kodric-Brown, 1977; Hanski, 1999).

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Although wildlife dispersal is one of the most important ecological processes, it remains one of the least understood, particularly for large carnivores, given their longevity, large ranges, and the lack of empirical data across broad areas (Vandermeer & Carvajal, 2001; Bowler & Benton, 2005; Hellgren et al., 2005). Reliable empirical data on dispersal patterns, particularly long-distance and multi-generational movements, are required. The scarcity of such data could inhibit effective conservation (Verner, 1992; Fagan & Calabrese, 2006; Hilty et al., 2012).

Connectivity has primarily been framed through a focus on habitats that can promote and enhance linkages of populations, also known as corridors (Bennett, 1999). In addition to sufficient habitat, the tolerance of human communities is a primary factor for large carnivore population connectivity and long-term viability (Decker & Purdy, 1988; Carpenter et al., 2000). Conserving large carnivore populations depends on local communities to maintain or, at least, not reduce carnivore numbers occurring within human-populated areas. This means people, in particular those rearing livestock, need to take effective measures to protect livestock from predators and tolerate carnivore-related losses (Riley et al., 2002; Gehrt et al., 2010).

Numerous studies have demonstrated that large carnivores exhibit population declines in landscapes where livestock production is the primary source of income. These declines are largely a result of retaliatory killing in response to livestock depredation (Weber & Rabinowitz, 1996; Linnell et al., 1999; Woodroffe, 2000; Frank & Woodroffe, 2001; Polisar et al., 2003). Other studies have, however, indicated that predators can survive in heavily human-impacted areas if there is human tolerance for such species (Hilty et al., 2012).

We present observational dispersal data on multiple generations of African lions *Panthera leo* that resided in and dispersed through unprotected human- and livestock-dense areas. Our observations of lion dispersal arose from data on 496 known lions of the Amboseli–Tsavo ecosystem in Kenya over a 14-year period (2004–2018). This 6,000 km^2 ecosystem comprises unprotected and protected areas, including Amboseli and Chyulu Hills National Parks and neighbouring Tsavo West and Kilimanjaro National Parks. Data were primarily collected within three of the communally-owned Maasai group ranches (Mbirikani, Eselenkei, Olgulului). We expanded the study area from 1,320 km^2 in 2004–2008, to 3,109 km^2 in 2009 and 3,684 km^2 during 2010–2018 (Fig. 1). Observations on individual lions

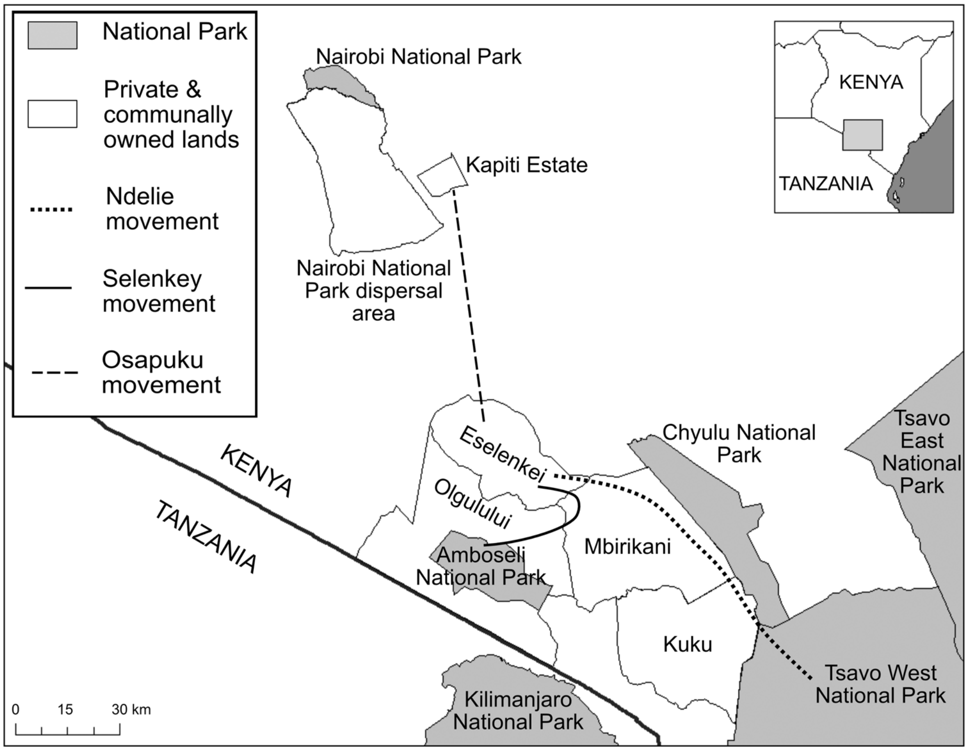

FIG. 1 The study area (the communally-owned Group Ranches: Mbirikani, Eselenkei, Olgulului and Kuku) and neighbouring National Parks, showing three of the main dispersal events between the protected areas: Ndelie, lion no. 29 dispersed from Tsavo West National Park to Eselenkei Group Rranch during 2007–2010; Selenkay, lion no. 61, dispersed from Amboseli National Park to Eselenkei Group Ranch during 2009–2010, and Osapuku, lion no. 164, dispersed from Eselenkei Game Ranch to Kapiti plains in 2014.

facilitated the compilation of a reference database of all lions of known age and subsequent analyses of long-distance and multi-generational dispersal patterns (Dolrenry, 2013; Dolrenry et al., 2016). We documented 189 individuals engaging in dispersal activities (i.e. permanently moving out of their natal range). The longest observed Euclidean dispersal distances were c. 200 km travelled by three dispersing males. Nearly 30% (n = 56) of dispersing individuals originated from a nearby protected area. Specifically, three dispersal events associated with protected areas, occurring over 7 years, provide an understanding of the linkages between protected and unprotected areas, and how human tolerance may have contributed to these connections.

The first of these dispersal events occurred in 2007: male lion no. 29, Ndelie, first observed as a subadult with a female companion of the same age (estimated to be 3 years old, and a sibling), dispersed from Tsavo West National Park into the neighbouring community lands. In 2010 he established himself as pride male on Eselenkei Group Ranch, a Euclidian distance of 110 km from the initial observation location (Dolrenry, 2013).

The second event occurred in 2009: female lion no. 61, Selenkay, with two female cohorts of the same age (c. 2 years and 1 month old), dispersed an observed Euclidian distance of 52 km from Amboseli National Park to Eselenkei Group Ranch. Selenkay and Ndelie resided together and bred successfully for 3 years.

The third event provided evidence of linkages between three protected areas. Male lion no. 164, Osapuku, was born to Selenkay and Ndelie in July 2011, one of a litter of four cubs (three males and one female). There was a female cub from Selenkay's sister, lion no. 59, also sired by Ndelie, who associated with them to form a cohort of five individuals. In 2012, at the age of 1.3 years, Osapuku dispersed together with his cohorts. They stayed within the broader study area for another 1.5 years although they split into two smaller groups (one male and one female together and two males and one female in another group). Before dispersing from the study area during the first months of 2014, Osapuku was observed on his own several times on the northern boundaries of Eselenkei Group Ranch. In October 2014 a male lion was photographed in the Kapiti plains, an area of privately owned ranches that are not under any formal protection but that have varying levels of wildlife conservation activities that support coexistence (M. Mbithi, pers. comm.). The Kapiti plains area is known to be used extensively by lions that are residents of Nairobi National Park (Rudnai, 1979). The lone male lion was not one of the identified individuals of the Park (M. Mbithi, pers. comm.). Photographs of the male were compared to the database of lions for the Amboseli–Tsavo ecosystem (Dolrenry, 2013) and, based upon vibrissa spot patterns, he was independently identified by two trained biologists as Osapuku. To reach the Kapiti plains from his natal area, he traversed a developing area of high human density (a settlement of 5,000–10,000 people), and travelled c. 200 km (Fig. 1). This was the first time in 20 years that a new individual was observed intermingling with the lions of Nairobi National Park (M. Mbithi, pers. comm.).

Following dispersal out of protected areas, these individual lions resided on unprotected community lands amongst high densities of humans and livestock. The lions Ndelie, Selenkay and their offspring were responsible for a minimum of 146 depredation events, totalling losses of at least 216 head of livestock. We documented these individuals being hunted by Maasai warriors a minimum of 53 times. Although a total of 267 hunts were recorded within the study area during 2010–2018, $< 4\%$ resulted in a lion being killed. More than 95% of these hunts were halted, primarily by non-governmental conservation organizations and the Kenya Wildlife Service (Hazzah et al., 2014). Inside the study area, before conservation interventions (2001–2002), there were approximately 20–30 lions killed each year on the Group Ranches (Hazzah et al., 2014). Once conservation initiatives facilitated tolerance towards lions, the number reduced to 0–2 lions per year (Hazzah et al., 2014). Outside the study area, a minimum of 38 (20%) of known dispersers were killed (poisoned, snared or speared) whilst dispersing.

Osapuku has spent his entire life outside protected areas. We postulate that because of living in a landscape where humans, not lions, are the apex predator, Osapuku and the other lions learned how to move and subsist near people, allowing him to traverse a densely populated area before arriving at an area of refuge within the Kapiti region (Mogensen et al., 2011; Valeix et al., 2012; Ordiz et al., 2013).

Although Maasai pastoralists of the Amboseli region had decimated the lion population by the early years of the 21st century (Chardonnet, 2002), current tolerance of lions by the human communities, presumably because of conservation initiatives (Hazzah et al., 2014), has seemingly allowed these lions to survive to adulthood, breed and successfully disperse (Packer et al., 1991; Björklund, 2003; Trinkel et al., 2008; Dolrenry et al., 2016). As shown in previous studies within the ecosystem (Okello, 2009; Hazzah et al., 2014; Dolrenry et al., 2016), with high levels of local participation in conservation and a greater sense of ownership of their environment, tolerance for lions increases.

To our knowledge, this is the first time that links have been observed between the lion populations of Tsavo West, Amboseli and Nairobi National Parks. We believe the increased and sustained human tolerance over several lion generations, in addition to continued availability of habitat and prey, have contributed to the survival of dispersers into and out of the study population, which, as shown by other studies (Andrewartha, 1954; den Boer, 1968, 1981, 1990; Hansson, 1991; Fahrig & Merriam, 1994; Sweanor et al., 2000), contributes to increased viability of the lion metapopulation. In addition to habitat preservation, promoting connectivity by increasing the tolerance of human communities for, and acceptance of, large carnivores and concurrently allowing the carnivores to learn how to coexist in human- and livestock-dominated landscapes, facilitates a more connected metapopulation (Carpenter et al., 2000; Crooks & Sanjayan, 2006; Groom & Harris, 2008; Maclennan et al., 2009; Hazzah et al., 2013, 2014; Dolrenry et al., 2014; Blackburn et al., 2016).

The future of African lions lies in the hands of the human communities (Adams & McShane, 1996; Western & Wright, 2013) and the stories of the successful dispersal of these lions provide an example of how human tolerance can engender connectivity. In conclusion, we suggest a broadening of the definition of corridors, particularly for the large carnivore species that are a challenge to human–wildlife coexistence. Additionally, we urge conservationists to establish comprehensive databases that promote consistent data structure for shared and verifiable research. Such databases should capture the necessary individual information and facilitate engagement in broad-scale collaborations that create opportunities for the exchange of knowledge and best practices, particularly in identifying dispersing animals so as to improve the understanding of connections between sites (Dolrenry et al., 2014). Nevertheless, without forbearing communities exemplifying the necessary tolerance to allow lions to move through their space, the functional metapopulation model of lions in East Africa could be lost.

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Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards, and was conducted under Permit No. MOEST 13/C689, Animal Use Protocols R191 University of California, Berkeley, and L400 University of Wisconsin, Madison, USA.

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