# 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).

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

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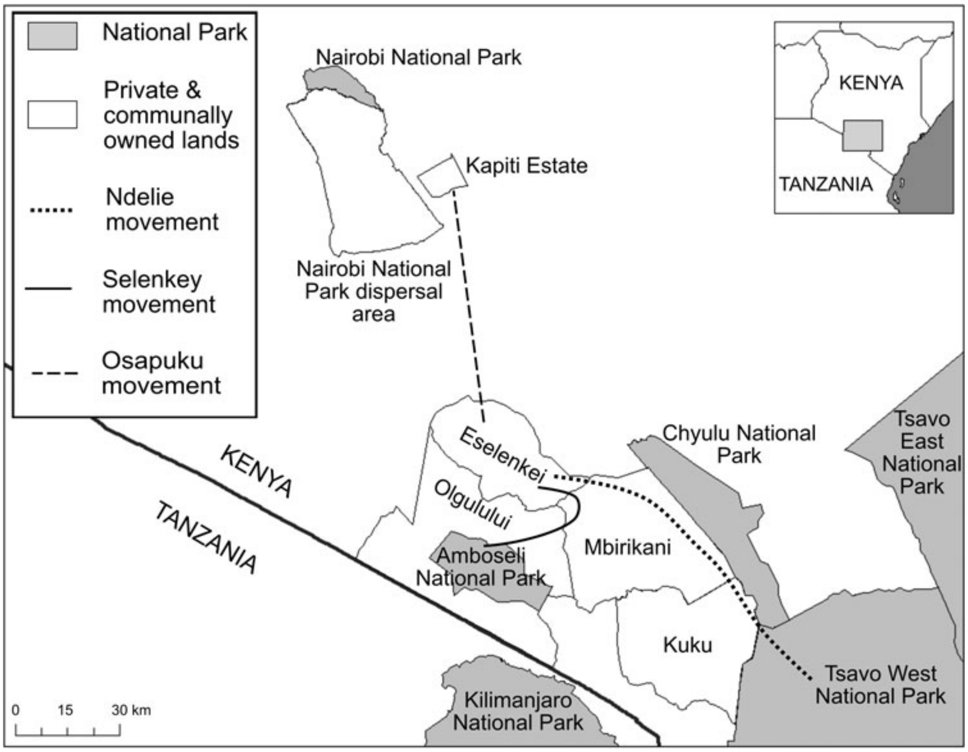


FIG. 1 The study area (the communally-owned Group Ranches: Mbirikani, Eselenkei, Olgulului and Kuku) and neighbouring National Parks, showing three of the main dispersal events between the protected areas: Ndelie, lion no. 29 dispersed from Tsavo West National Park to Eselenkei Group Rranch during 2007–2010;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

## References

Adams, J.S. & McShane, T.O. (1996) *The Myth of Wild Africa: Conservation Without Illusion*. University of California Press, Berkeley, USA.

Andrewartha, H.G. & Birch, L.C. (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago, USA.

Bekoff, M. (1989) Behavioral development of terrestrial carnivores. In *Carnivore Behavior, Ecology, and Evolution* (ed. J.L. Gittleman), pp. 89–124. Cornell University Press, Ithaca, USA.

Bennett, A.F. (1999) *Linkages in the Landscape: the Role of Corridors and Connectivity in Wildlife Conservation*. IUCN, Gland, Switzerland, and Cambridge, UK.

Björklund, M. (2003) The risk of inbreeding due to habitat loss in the lion (*Panthera leo*). *Conservation Genetics*, 4, 515–523.

Blackburn, S., Hopcraft, J.G.C., Ogutu, J.O., Matthiopoulos, J. & Frank, L. (2016) Human–wildlife conflict, benefit sharing and the survival of lions in pastoralist community-based conservancies. *Journal of Applied Ecology*, 53, 1195–1205.

Bowler, D.E. & Benton, T.G. (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, 80, 205–225.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, 58, 445–449.

Carpenter, L.H., Decker, D.J. & Lipscomb, J.F. (2000) Stakeholder acceptance capacity in wildlife management. *Human Dimensions of Wildlife*, 5, 5–19.

Chardonnet, P. (2002) *Conservation of the African Lion: Contribution to a Status Survey*. International Foundation for the Conservation of Wildlife, Paris, France.

Clobert, J., Baguette, M., Benton, T.G., Bullock, J.M. & Ducatez, S. (2012) *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK.

Crooks, K.R., Burdett, C.L., Theobald, D.M., Rondinini, C. & Boitani, L. (2011) Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 2642–2651.

Crooks, K.R. & Sanjayan, M. (eds) (2006) *Connectivity Conservation*. Cambridge University Press, Cambridge, UK.

Decker, D.J. & Purdy, K.G. (1988) Toward a concept of wildlife acceptance capacity in wildlife management. *Wildlife Society Bulletin*, 16, 53–57.

den Boer, P.J. (1968) Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica*, 18, 165–194.

den Boer, P.J. (1981) On the survival of populations in a heterogeneous and variable environment. *Oecologia*, 50, 39–53.

den Boer, P.J. (1990) The survival value of dispersal in terrestrial arthropods. *Biological Conservation*, 54, 175–192.

Dolrenry, S. (2013) *African lion (*Panthera leo*) behavior, monitoring, and survival in human-dominated landscapes*. PhD thesis. University of Wisconsin, Madison, USA.

Dolrenry, S., Hazzah, L. & Frank, L.G. (2016) Conservation and monitoring of a persecuted African lion population by Maasai warriors. *Conservation Biology*, 30, 467–475.

Dolrenry, S., Stenglein, J., Hazzah, L., Lutz, R.S. & Frank, L. (2014) A metapopulation approach to African lion (*Panthera leo*) conservation. *PLOS ONE*, 9, e88081.

Fagan, W.F. & Calabrese, J.M. (2006) Quantifying connectivity: balancing metric performance with data requirements. In *Connectivity Conservation* (eds K.R. Crooks & M. Sanjayan), pp. 297–317. Cambridge University Press, Cambridge, UK.

Fahrig, L. & Merriam, G. (1994) Conservation of fragmented populations. *Conservation Biology*, 50–59.

Frank, L.G. & Woodroffe, R. (2001) Behavior of carnivores in exploited and controlled populations. In *Carnivore Conservation* (eds J.L. Gittleman, S.M. Funk, D. Mcdonald & R.K. Wayne), pp. 419–442. Cambridge University Press, Cambridge, UK.

Gehrt, S.D., Riley, S.P. & Cypher, B.L. (2010) *Urban Carnivores: Ecology, Conflict, and Conservation*. John Hopkins University Press, Baltimore, USA.

Groom, R. & Harris, S. (2008) Conservation on community lands: the importance of equitable revenue sharing. *Environmental Conservation*, 35, 242–251.

Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, New York, USA.

Hansson, L. (1991) Dispersal and connectivity in metapopulations. *Biological Journal of the Linnean Society*, 42, 89–103.

Hazzah, L., Dolrenry, S., Kaplan, D. & Frank, L. (2013) The influence of park access during drought on attitudes toward wildlife and lion killing behaviour in Maasailand, Kenya. *Environmental Conservation*, 40, 266–276.

Hazzah, L., Dolrenry, S., Naughton-Treves, L., Edwards, C.T., Mwebi, O., Kearney, F. & Frank, L. (2014) Efficacy of two lion conservation programs in Maasailand, Kenya. *Conservation Biology*, 28, 851–860.

Hellgren, E.C., Onorato, D.P. & Skiles, J.R. (2005) Dynamics of a black bear population within a desert metapopulation. *Biological Conservation*, 122, 131–140.

Hilty, J.A., Lidicker, Jr, W.Z. & Merenlender, A. (2012) *Corridor Ecology: the Science and Practice of Linking Landscapes for Biodiversity Conservation*. Island Press, Covelo, USA.

Linnell, J.D.C., Odden, J., Smith, M.E., Aanes, R. & Swenson, J.E. (1999) Large carnivores that kill livestock: do 'problem individuals' really exist? *Wildlife Society Bulletin*, 27, 698–705.

Maclennan, S.D., Groom, R.J., Macdonald, D.W. & Frank, L.G. (2009) Evaluation of a compensation scheme to bring about pastoralist tolerance of lions. *Biological Conservation*, 142, 2419–2427.

Mogensen, N.L., Ogutu, J.O. & Dabelsteen, T. (2011) The effects of pastoralism and protection on lion behaviour, demography and space use in the Mara Region of Kenya. *African Zoology*, 46, 78–87.

Okello, M. (2009) Reconciling people's livelihoods and environmental conservation in the rural landscapes in Kenya: opportunities and challenges in the Amboseli landscape. *Natural Resource Forum*, 33, 123–133.

Ordiz, A., Bischof, R. & Swenson, J.E. (2013) Saving large carnivores, but losing the apex predator? *Biological Conservation*, 168, 128–133.

Packer, C., Pusey, A.E., Rowley, H., Gilbert, D.A., Martenson, J. & O'brien, S.J. (1991) Case study of a population bottleneck: lions of the Ngorongoro Crater. *Conservation Biology*, 5, 219–230.

Polisar, J., Maxit, I., Scognamillo, D., Farrell, L., Sunquist, M.E. & Eisenberg, J.F. (2003) Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. *Biological Conservation*, 109, 297–310.

Riley, S.J., Decker, D.J., Carpenter, L.H., Organ, J.F., Siemer, W.F., Mattfeld, G.F. & Parsons, G. (2002) The essence of wildlife management. *Wildlife Society Bulletin*, 585–593.

Rudnai, J. (1979) Ecology of lions in Nairobi National Park and the adjoining Kitengela Conservation Unit in Kenya. *African Journal of Ecology*, 17, 85–95.

Sweanor, L.L., Logan, K.A. & Hornocker, M.G. (2000) Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology*, 14, 798–808.

Trinkel, M., Ferguson, N., Reid, A., Reid, C., Somers, M., Turelli, L. et al. (2008) Translocating lions into an inbred lion population in the Hluhluwe-iMfolozi Park, South Africa. *Animal Conservation*, 11, 138–143.

Valeix, M., Hemson, G., Loveridge, A.J., Mills, G. & Macdonald, D.W. (2012) Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology*, 49, 73–81.

Vandermeer, J. & Carvajal, R. (2001) Metapopulation dynamics and the quality of the matrix. *The American Naturalist*, 158, 211–220.

VanderWaal, K.L., Mosser, A. & Packer, C. (2009) Optimal group size, dispersal decisions and postdispersal relationships in female African lions. *Animal Behaviour*, 77, 949–954.

Verner, J. (1992) Data needs for avian conservation biology: have we avoided critical research? *Condor*, 301–303.

Weber, W. & Rabinowitz, A. (1996) A global perspective on large carnivore conservation. *Conservation Biology*, 10, 1046–1054.

Western, D. & Wright, M. (2013) *Natural Connections: Perspectives in Community-Based Conservation*. Island Press, Washington, DC, USA.

Woodroffe, R. (2000) Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation*, 3, 165–173.