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Corridor use and streaking behavior by African elephants in relation to physiological state

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ABSTRACT

Wildlife populations occur in increasingly fragmented landscapes, making corridor ecology important to conservation managers. Human disturbance has been identified as a proximate cause of limiting corridor use or increasing streaking behavior by wild elephants, but there are likely to be physiological triggers that directly initiate these risk averse behaviors. We simultaneously monitored elephant stress hormone concentrations and movement in two reserves to test whether elephants in an elevated physiological state restricted use of corridors, or, if they still used corridors, exhibited relatively rapid unidirectional movements indicative of streaking behavior. Contrary to predictions, the elephant population in an elevated physiological state did not reduce use of corridors between core areas. However, as predicted, when the population was in an elevated physiological state, elephant family groups exhibited less tortuosity, and moved 77% faster when in corridors as opposed to core areas, compared to only a 20% difference between corridor and core area speed when not in an elevated physiological state. Rapid movement along corridors by elephants in elevated physiological states is likely an adaptive behavioral response to avoid further exposure to stressors. Furthermore, because chronically stressed elephants can be more aggressive towards humans, understanding when and where elephants exhibit streaking behavior can guide human–elephant conflict mitigation. We demonstrate that corridor use can exist at relatively fine spatial scales within fenced reserves, and the persistent use of corridors regardless of physiological state suggests that they are likely an important, but neglected, component of animal spatial ecology within reserves.

1. Introduction

The provision of corridors is essential in species conservation and protected area planning (Hobbs, 1992; Noss, 1996; Beier and Noss, 1998; Fahrig, 2003). With increasing human disturbance and habitat fragmentation, connectivity of wildlife populations enhances gene flow (Keyghobadi et al., 2005), population viability (Brown and Kodric-Brown, 1977; Hanski, 1998), conservation of critical processes such as migration (Berger, 2004) and key species interactions (Soulé et al., 2003). The conservation of corridors is particularly important for wide-ranging species, because they have evolved to rely on long-distance movements to fulfill basic life history strategies (Berger, 2004).

In response to these challenges, multiple conservation initiatives have been developed that can be both large and small in spatial extent; ranging from international, landscape-scale such as the Yellowstone to Yukon initiative (Chester, 2006), to designing movement corridors over individual roads, fences or dams (Clevenger and Ford, 2010; Blank, 2010). In practice, current attempts to identify, plan and prioritize corridors for species conservation largely focuses on an individual species' movement characteristics in response to habitat conservation and management within corridors (e.g. Chetkiewicz et al., 2006; Sawyer et al., 2011). However, little attention is given to the underlying behavioral and physiological processes that could restrict or modify use of corridors.

For elephants, corridor conservation has been a topic of increased importance in both Asia (Joshi and Singh, 2009; Pan et al., 2009) and Africa (Douglas-Hamilton et al., 2005; Mpanduji et al., 2009; Cushman et al., 2010; Kioko and Selo, 2011; Pittiglio et al., 2012; Roever et al., 2013). In Africa, threats to corridors are growing (Caro et al., 2009), and movements by elephants are increasingly restricted to core protected areas (Croze and Moss, 2011). In response to broken or narrow corridors between protected areas, elephants restrict movements between protected areas, or exhibit rapid movements (i.e., "streaking behavior") between protected areas (Douglas-Hamilton et al., 2005). In addition to large, landscape-level movements between protected areas,

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restricted and directed space use patterns also can occur at finer scales within fenced reserves (Druce et al., 2008; Woolley et al., 2008; Vanak et al., 2010). In fenced reserves, elephants establish core use areas where they spend a majority of time despite a wider area being available to them (Druce et al., 2008; Jachowski et al., 2012). Furthermore, elephants may make relatively quick and unidirectional movements between these core use areas, demonstrating corridor use at fine spatial scales (Jachowski et al., 2013a).

Human disturbance has been identified as a proximate cause of limiting corridor use (Jones et al., 2012) or increasing streaking behavior by wild African elephants (*Loxodonta africana*) (Douglas-Hamilton et al., 2005), but there are likely to be physiological triggers that directly initiate the behavioral response. For example, elephants translocated within Kruger National Park made quick unidirectional movement back towards the original capture site and exhibited heightened stress hormone concentrations (Viljoen et al., 2008). When elephants within fenced reserves are in an elevated physiological state, they are more likely to exhibit restricted space use patterns indicative of refuge behavior (Jachowski et al., 2012), and typically venture outside of refugia only when they temporarily exhibit basal physiological conditions (Jachowski et al., 2013a). Therefore, we predicted that elevated stress hormone concentrations would likely be associated with one of two behaviors in corridors. First, we tested the prediction that elephants are less likely to make corridor movements when their physiological state is elevated than when it is basal. Second, when elephants in an elevated physiological state use corridors between core areas, we predicted that movement between refugia is likely to be more rapid and unidirectional, similar to "streaking behavior" observed in free-ranging elephant populations (Douglas-Hamilton et al., 2005).

2. Methods

2.1. Study sites

We selected two elephant populations in South Africa, each of which was confined by electrified boundary fences: iSimangaliso Wetland Park (28°49′–27°55′S, 32°68′–32°22′E) and Phinda Private Game Reserve (27°92′–27°68′S, 32°44′–32°20′E). These reserves are located in the KwaZulu–Natal Province and have similar rainfall and climatic conditions, with a wet season from November to April and a dry season from May to October (Shannon et al., 2006; Jachowski et al., 2012). During this study, approximately 45 elephants were present in iSimangaliso Wetland Park (hereafter referred to as iSimangaliso), with females forming three primary family groups (van Aarde et al., 2008). Elephants in iSimangaliso generally restricted their movements to the Western Shores section of the reserve (329 km^2) that was bordered by the St. Lucia Estuary to the east, and by electrified fence along its other boundaries (Jachowski et al., 2012). Phinda Private Game Reserve (hereafter referred to as Phinda) is 180 km^2 in size and contained an estimated population of 98 elephants, with females forming at least five family groups (Druce et al., 2008; Lagendijk et al., 2011) that ranged over almost the entire reserve (Jachowskiz et al., 2012).

We previously found that elephants in iSimangaliso were consistently in an elevated physiological state compared to Phinda (Jachowski et al., 2012, 2013b). Between 2001 and 2006 we collected 195 and 406 fecal samples from elephants in Phinda and iSimangaliso respectively (for details, see Jachowski et al., 2012). In the laboratory, we assayed fecal samples for the presence of fecal glucocorticoid metabolite (FGM) concentrations, a proxy of physiological stress, using corticosterone I^{125} radioimmunoassay kits (MP Biomedicals, Solon, OH). We found that over the course of our study, elephants sampled in Phinda consistently maintained lower FGM concentrations compared to iSimanagliso (Jachowski et al., 2012, 2013b). Both reserves were elongated in shape and each of them likely contained corridors through its center that elephants followed to reach primary use areas generally located at opposite ends of their respective reserves (Jachowski et al., 2012). The difference in physiological status between reintroduced elephant populations in the two reserves, and the similarity in the configuration of the reserves allowed for direct comparisons of elephant populations in differing physiological states.

2.2. Reserve-level movement analyses

We used multiyear movement data sets from elephant family groups in iSimangaliso ($n = 3$) and Phinda ($n = 5$) between 2004 and 2008. Details on Global Positioning System (GPS) tracking of elephants in these reserves have been described elsewhere (see Jachowski et al., 2012, 2013a). The length of time GPS collars remained on an adult female in each family group varied by family group, with elephant family groups in Phinda on average being monitored for 20 months (range = 16–27, SE = 3.51) and family groups in iSimangaliso on average being monitored for 28 months (range = 22–34, SE = 3.48). GPS collars were programmed to record locations of elephants at 6–12 h intervals. We filtered data so that all analyses were conducted using locational fixes separated by 12 ± 2 h in each of our two study sites, resulting in an annual average of 595.5 (SE = 9.6) and 541.8 (SE = 10.0) point locations for subsequent movement analysis for each elephant family group in Phinda and iSimangaliso respectively.

Corridors are ideally defined by identifying the appropriate spatial and temporal scale for a specific species or population (Noss, 1987, 1991). During a study of the Laikipia–Samburu elephant population that occurs across a wide swath of Kenya primarily outside of protected areas, Douglas-Hamilton et al. (2005) identified corridors of elephant movement among "home sectors", where elephant corridor movements were defined as continuous movements $\geqslant 10$ km. For our study, where populations of elephants were fenced into relatively small reserves, we selected a smaller distance as a basis for identifying corridors of movement between core areas of use (Fig. 1). We selected $\geqslant 5$ km as the criterion based on >30 yrs of elephant monitoring data from Amboseli National Park, where Croze and Moss (2011, p. 99) report that movements by elephant family groups of distances greater than 5 km to new areas of "core occupancy" were rare events.

We estimated core use areas for each elephant family group in both reserves from 2004 to 2008. We represented space use by each elephant family group by creating 95% fixed kernel utilization distributions (UDs) (van Winkle, 1975) using the plug-in method of bandwidth selection (Gitzen et al., 2006). We then estimated core areas of use for each elephant family group using the Area Independent Method for defining core areas (Seaman and Powell, 1990; Powell et al., 1997; Eads et al., 2012).

To evaluate our first prediction, that elephants in an elevated physiological state are less likely to make corridor movements, for each season of monitoring we counted the number of times each elephant family group moved between adjacent core use areas that were $\geqslant 5$ km apart (i.e. made a corridor movement) (Fig. 1). We then conducted a mixed model analysis of variance (ANOVA) to assess if the number of movements between core areas differed between reserves and by season, where reserve and season were fixed effects within our model, individual elephant family group was a random effect, and year was the repeated effect.

To test our second prediction, that movement through corridors between core areas is likely to be more rapid and unidirectional when elephants are in an elevated physiological state, we compared corridor movement speed and tortuosity between elephant family groups in iSimangaliso and Phinda. "Streaking" behavior