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

David S. Jachowski [a,b,*], Rob Slotow [b], Joshua J. Millspaugh [a]

[a] Department of Fisheries and Wildlife Sciences, University of Missouri, 302 Natural Resources Bldg., Columbia, MO 65211, USA
[b] Amarula Elephant Research Programme, School of Life Sciences, University of KwaZulu-Natal, Westville Campus, Pvt. Bag 54001, Durban 4000, South Africa

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.

© 2013 Elsevier Ltd. All rights reserved.

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,

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 ⩾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 ⩾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 ⩾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
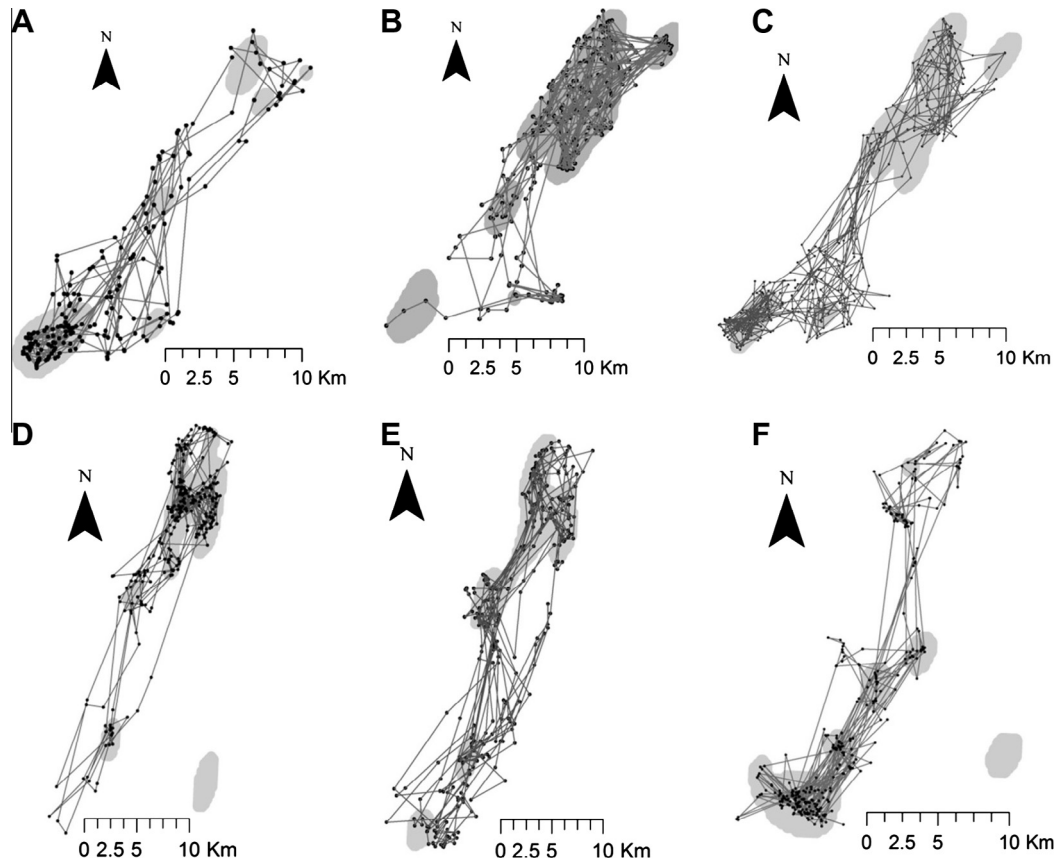
Fig. 1. Examples of seasonal elephant family group movements in Phinda Private Game Reserve (A–C) and iSimangaliso Wetland Park (D and F). Points represent the locations of elephant family groups collected using global position collars, lines connect sequential points, and gray polygons represent core areas of use for the particular family group. Movement corridors of ⩾5 km in length link core areas in the northern and southern portions of each reserve.

by elephants was defined by Douglas-Hamilton et al. (2005, p. 162) as when "elephants cross unprotected areas swiftly down travel corridors" in order to "minimize the time spent in dangerous areas." To evaluate if elephants were moving more "swiftly" along corridors in our study areas, we used the Hawth's Tools (Beyer, 2004) in ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, California, USA) to estimate the speed (km/hr) and direction of movement (path tortuosity) by elephant family groups (Dai et al., 2007; Vanak et al., 2010). We quantified movement metrics for elephant family groups when they were moving between core areas separated by ⩾5 km (i.e. movement corridors), and other times during our study. We used a mixed model ANOVA to evaluate if tortuosity and log-transformed speed of movement differed between periods of time when the elephants used corridors and core areas. Within our model, the type of location (either corridor or non-corridor) was our fixed effect, elephant family group was the random effect, and year was the repeated effect. We also compared movement speed and tortuosity between reserves for periods of time when elephants were not utilizing corridors. We used mixed model ANOVA to evaluate if either speed or bearing of elephant movement during each period differed, based on the reserve sampled. Similar to above, within the model, reserve was the fixed effect and our random effect was individual elephant family group and year was the repeated effect.

2.3. Within-reserve movement analyses

In addition to observing long-term differences in elephant population physiological states between reserves, we also identified brief periods of time when individual family groups in

iSimangaliso consistently exhibited elevated or basal physiological states that allowed for finer-scale analyses of corridor use. We previously identified discrete time periods of inference for individual family groups when (1) we collected ⩾2 fecal samples from a single known family group so that not more than 168 h passed between consecutive samples and (2) FGM values from those samples were consistently above or below the average value expected for that group over the duration of our study, allowing us to generalize that the family group was in an elevated or basal physiological state (see Jachowski et al., 2013a). We then tested our predictions by comparing the number of corridor movements, as well as movement speed and tortuosity, during periods of elevated verses basal physiological state. We used a mixed-model ANOVA to assess the effect of the average stress hormone concentration for each period of inference on corridor movement speed (km/hr) and tortuosity (calculated similar to above), and we treated the family group sampled as a random effect.

3. Results

All three of the family groups present in iSimangaliso had core areas separated by at least 5 km (Table 1). On average, the distance between proximate core areas was 5.5 km (range = 0.7–10.8, SE = 1.3). In contrast, only 3 of 5 family groups present in Phinda had core areas separated by at least 5 km (Table 1). Average distance between core areas at Phinda was 3.3 km (range = 0.5–9.6, SE = 0.6). When focusing only on core areas separated by ⩾5 km that were used in this study (our minimum criterion for identifying a movement corridor), average shortest distance between core

Table 1
Attributes of corridor movements between core areas by African elephant family groups in iSimangaliso Wetland Park and Phinda Private Game Reserve, South Africa between 2004 and 2008.

Reserve	Elephant family group	Period of GPS collar monitoring	Number of core areas of use		Average (SE) number of corridor movements[*]		Corridor movements per year (SE)	Average (SE) speed (km/h)	
			Total	Total ⩾ 5 km apart[*]	Wet season	Dry season		Core area	Corridor
iSimangaliso	AM51	11/2005–9/2008	4	2	4.3 (1.7)	3.0 (1.0)	6.3 (0.89)	0.18 (0.01)	0.47 (0.05)
	AM53	11/2005–9/2007	3	1	11.0 (5)	9.0 (2.0)	20.0 (7.00)	0.46 (0.05)	0.56 (0.11)
	AM54	11/2005–4/2008	6	2	14.0 (8.2)	7.0 (2.0)	28.0 (10.17)	0.21 (0.01)	0.32 (0.02)
Phinda	Aniella	11/2004–4/2006	6	2	19.5 (0.5)	36.0 (0.0)	37.0 (10.11)	0.22 (0.01)	0.32 (0.03)
	Enigma	6/2005–10/2006	5	2	16.0 (−)	7.5 (4.5)	15.5 (3.50)	0.29 (0.01)	0.28 (0.03)
	OT	7/2004–10/2006	4	1	12.0 (3.0)	6.7 (4.3)	14.7 (6.98)	0.28 (0.01)	0.33 (0.02)

[*] Corridors were included in the analysis only if they linked core areas that were at least 5 km from each other. Seasons are divided equally into six month intervals based on rainfall patterns (Jachowski et al., 2012).

areas was slightly smaller in Phinda ($\bar{x} = 7.3$ km, SE = 1.0) than iSimangaliso ($\bar{x} = 9.8$ km, SE = 1.0).

3.1. Reserve-level movement analysis

We found no support for our first prediction that elephants in an elevated physiological state were less likely to use corridors between core areas of use. Even though movements of elephant family groups had been tracked for a longer period of time at iSimangaliso, our analyses showed that elephant family groups in Phinda more often moved along corridors between core areas separated by ⩾5 km (Table 1). However, when accounting for the effect of year and family group, we did not find a significant difference in the use of corridors based on reserve alone ($F_{1,19} = 2.27$, $P = 0.1485$). This result is likely due in part to the high amount of variability in movement between core areas by individual elephant family groups (Table 1), where the number of times per year that family groups used corridors in iSimangaliso (6.3–28) was similar to the range of values in Phinda (14.7–37). There was no significant difference in the number of movements between core areas between the wet and dry season ($F_{1,19} = 0.38$, $P = 0.5444$).

In support of our second prediction, we found that elephants in an elevated physiological state were more likely to exhibit streaking behavior. Elephant family groups in both reserves were significantly more likely to exhibit faster movement speeds (Table 1 and Fig. 1) when they occupied movement corridors in comparison to core use areas (iSimangaliso, $F_{1,2568} = 68.10$, $P < 0.0001$; Phinda, $F_{1,2319} = 8.04$, $P = 0.0046$). However, the degree to which speeds differed between corridors and core areas was inconsistent between reserves. Elephant family groups in iSimangaliso moved 77% faster when in corridors as opposed to core use areas (Table 1), whereas family groups in Phinda moved 20% faster (Table 1) when in corridors as opposed to core use areas (Fig. 2). We found that in iSimangaliso, elephant movements were significantly more unidirectional (Fig. 2) and showed less tortuosity in corridors than in core use areas ($F_{1,2568} = 27.04$, $P < 0.0001$). In Phinda, elephant movement tortuosity did not differ significantly between corridor and core area movements ($F_{1,2306} = 0.08$, $P = 0.7782$).

When comparing elephant corridor movement behavior between reserves, we observed no significant difference in speed ($F_{1,699} = 2.87$, $P = 0.0909$) or movement tortuosity ($F_{1,699} = 0.51$, $P = 0.4763$). While the speed of movement by elephant family

groups in corridors was on average 0.10 km/h faster in iSimangaliso ($\bar{x} = 0.41$ km/h, SE = 0.02) than in Phinda ($\bar{x} = 0.31$ km/h, SE = 0.04), the high amount of variability in movement characteristics exhibited by family groups using corridors in iSimangaliso (Table 1) likely made such reserve-level comparisons difficult to detect. Evidence from elephant movements in core areas further suggests that elephant family groups in iSimangaliso in general exhibited more rapid movements compared to elephants in Phinda ($F_{1,4169} = 7.05$, $P = 0.008$). However, elephant movement tortuosity in core areas did not differ between reserves ($F_{1,4169} = 0.43$, $P = 0.5131$).

3.2. Within-reserve movement analyses

In iSimangaliso, where we intensively monitored the physiological state of specific family groups for seven discrete periods of time, we observed similar results for the within-reserve-level analyses. Elephant family groups only made use of corridors during two of the five periods (40%) when we categorized a family group as elevated, compared to family groups in basal physiological states that used corridors during both periods (100%) (Table 2). However, when corridor use rates were corrected for unequal time that family groups were in discrete physiological states (ranging from 17.8 to 313.0 h), elephant family groups exhibited similar rates (0.01–0.04 corridor movements per week) of corridor use (Table 2), suggesting no relationship between physiological state and the frequency of corridor movements.

In support of our second prediction, we observed a significant positive effect of increased FGM concentration on elephant family group corridor movement speed ($F_{3,180} = 46.10$, $P < 0.0001$) and decreased tortuosity ($F_{3,180} = 18.24$, $P < 0.0001$). However, our confidence in this relationship is limited by the small number of periods we were able to monitor corridor behavior ($n = 4$), particularly for certain family groups. Only three family groups existed within iSimangaliso, and we determined periods of inference for two of those family groups. For one of the two family groups we only identified a single extended period when the group was in a basal physiological state, and in support of both of our predictions, during that period the family groups exhibited a considerably higher frequency of corridor use in addition to slower corridor movement speeds and higher tortuosity (Table 2). For the one family group that we monitored in both basal and elevated
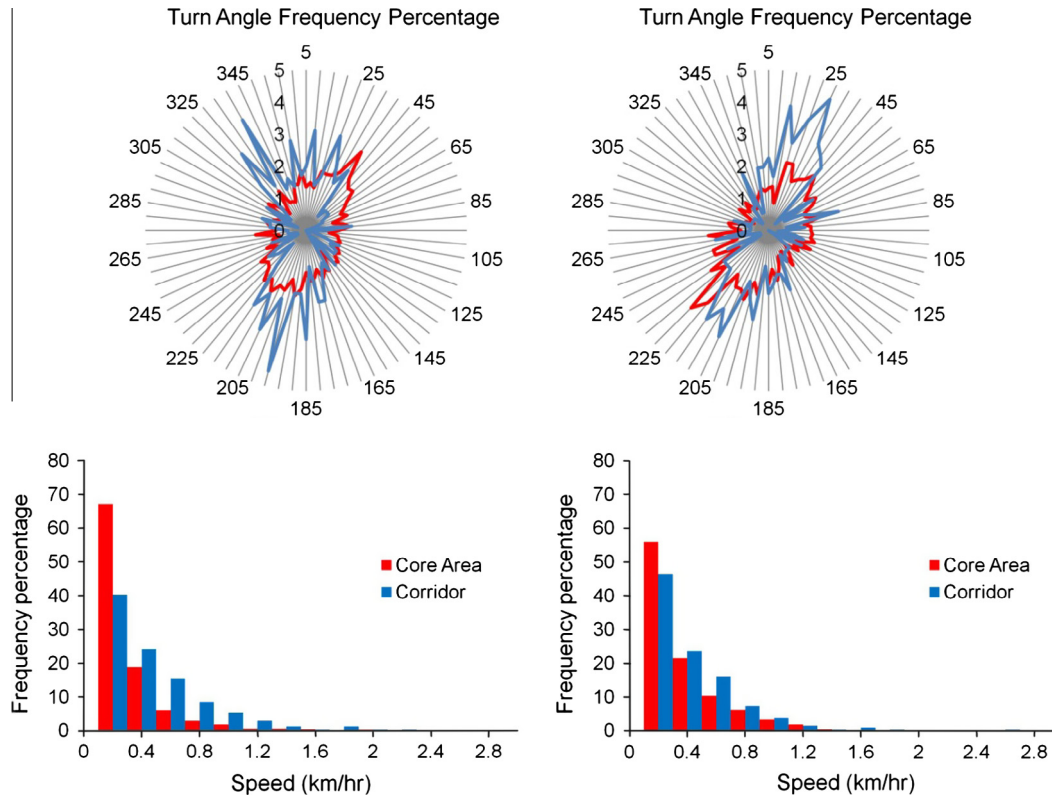
Fig. 2. Variation in frequency distributions (represented in percentage of total observations) of turn angles and movement speed for elephant family groups in iSimangaliso Wetland Park (left) and Phinda Wildlife Reserve (right). Elephant movement in core areas (red) was more varied in direction and generally at slower speeds than was movement in corridors (blue), where elephant movement was more consistently unidirectional and at faster speeds. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Corridor movement attributes for short-term analyses of elephant family groups in iSimangaliso Wetland Park when distinct elevated or basal physiological states were identified for periods during our study.

Average FGM[a] concentration	Family group	Length of monitoring period [b] (min)	Total number of corridor movements	Average number of corridor movements per week	Average (SE) corridor movement speed (km/h)	Average (SE) corridor movement tortuosity
61.09	AM53	4650	1	0.04	2.42 (0.12)	10.57 (2.76)
59.61	AM54	2820	0	–	–	–
57.32	AM51	1770	0	–	–	–
51.25	AM53	10,350	1	0.02	1.60 (0.11)	27.37 (8.37)
49.52	AM53	1080	0	–	–	–
27.79	AM53	14,910	1	0.01	1.87 (0.23)	29.59 (6.81)
26.80	AM54	18,776	4	0.04	0.63 (0.42)	103.04 (4.71)

[a] Fecal glucocorticoid metabolite concentration averaged across individuals of a family group during a period of inference.
[b] Periods of inference were identified based on (1) all fecal samples being collected consistently from a known family group with no gaps over 1 week in time between consecutive samples and (2) all samples consistently exhibiting an elevated or basal physiological state compared to the average of the total population over the duration of our study (see Jachowski et al., 2013b).

physiological states, we did not observe a difference in speed ($F_2 = 2.23$, $P = 0.1211$) or tortuosity ($F_2 = 1.40$, $P = 0.2593$).

4. Discussion

The continued use of corridors regardless of the physiological state of the elephant population suggests that corridor use is an essential aspect of elephant behavior. We have previously shown that elephants in iSimangaliso, that are in an elevated physiological state, restrict their space use patterns within a smaller proportion of the reserve (Jachowski et al., 2012). Despite this type of refuge behavior, we found that elephants in an elevated physiological state still made movements between core areas at a similar rate to when the elephant population was in a basal physiological state.

Collectively, this suggests that, in response to elevated physiological states, the complete abandonment of corridors by elephants is less likely to be observed than generally altered habitat selection and space use patterns (Jachowski et al., 2012), and supports previous findings that suggest the availability of corridors is of critical importance in the spatial ecology and conservation of elephants (Douglas-Hamilton et al., 2005; Kioko and Selo, 2011; Jones et al., 2012; Pittiglio et al., 2012).

Rather than limiting the use of corridors, elephants in an elevated physiological state are more likely to exhibit streaking behavior among core areas. A flight response has commonly been observed in a variety of vertebrates experiencing an elevated physiological state (Wingfield and Romenofsky, 1997; Wingfield et al., 1998), including elephants that were experiencing relatively short-term

or acute elevations in stress hormone concentrations (Viljoen et al., 2008). We observed that elephants in an elevated physiological state over a relatively long time period (>2 yrs), are similarly more likely to exhibit streaking behavior than are elephants in a basal physiological state. Taken together, streaking behavior may therefore be a facultative behavioral response to either acute or chronic elevations in stress hormone levels when elephants are outside of core areas of use.

The relationship we observed between streaking behavior by elephants and their elevated physiological state potentially has broad implications to the conservation and management of elephants and other vertebrate species. More rapid movement along corridors by chronically stressed elephants is likely an adaptive response to avoid further exposure to stressors (Boonstra, 2013). However, there are likely physiological costs to long-term streaking behavior that could result in a decline in fitness and even mortality. For example, prolonged rapid movements by elephant family groups in iSimangaliso immediately following release was implicated in the death of at least one elephant calf (C. Dickson, University of KwaZulu-Natal, unpublished report). Future research on corridor use behavior needs to determine (including over larger spatial scales) if elephants can account for the potential energetic cost of making a corridor movement, similar to their known cognitive ability to evaluate social interaction and predation risk based on past experience (McComb et al., 2011). If there is a threshold at which elephants abandon corridors when the perceived costs of making corridor movements outweigh the benefits, such information could be used to improve existing attempts to model population connectivity and the use of corridors under different management scenarios (e.g. McRae et al., 2008; Cushman et al., 2010). Furthermore, individual family groups often vary in behavioral responses to threats based on matriarch age and experience (McComb et al., 2011), and we observed that family groups within populations similarly vary in frequency of corridor use, as well as speed and tortuosity while in corridors. Thus, there is also a need to consider the role of matriarchs and elephant social structure in understanding how individual family groups are likely to utilize corridors when in a heightened physiological state.

When observing or predicting disturbances that elevate stress hormone concentrations (Burke et al., 2008; Gobush et al., 2008; Woolley et al., 2008), managers should plan for an increased probability of streaking behavior, and limit human disturbance within corridors between core use areas. Stress-driven behavior is particularly a concern for areas where humans are likely to encounter elephants while in corridors, either between reserves (sensu Douglas-Hamilton et al., 2005), or between core areas within the same reserve (this study). Given that elephants in an elevated physiological state are prone to aggressive encounters with humans (Jachowski et al., 2012), predicting when and where corridor movements are likely to occur is key to minimizing human–elephant conflict. Operationally, this could most easily be carried out by mapping core areas and corridors used by elephants within reserves, and limiting human use and disturbance of those areas. Alternatively, if complete exclusion of human disturbance is not feasible, managers could track elephant family groups by monitoring real-time data via GPS collars to determine when corridors are being used. Such an alert system could be automated using mapping software similar to the system currently in use to alert managers when elephants enter camps or forest plantations (Slotow, 2012), thereby providing real-time information to managers regarding when and where elephants enter corridors so that human access to these areas might be restricted at that time.

Corridors are referred to as pathways of connectivity between reserves or protected areas at large spatial scales (Hilty et al., 2006), but are ideally defined by an understanding of the appropriate spatial and temporal scale (Noss, 1991). This study presents the first example to our knowledge of corridor behavior by a large mammal existing between core areas within a single, small reserve. These findings are particularly important in the context of growing human disturbance within many protected areas that result in fragmentation of habitat, where managers increasingly need to consider and conserve habitat connectivity at multiple spatial scales (Murphy et al., 2010). Corridor behavior occurring at such relatively fine spatial and temporal scales presents a number of analytical and interpretive issues regarding current attempts to model space use. While a variety of quantitative approaches exist, the most common approach involves the use of utilization distributions to analyze the clustering of animal locations, and smoothing over the extent of the locations to create a probabilistic surface of use (Kernohan et al., 2001). Using these types of surface maps, biologists and managers frequently focus conservation and management attention on areas that receive the highest frequency of use (Marzluff et al., 2004; Millspaugh et al., 2006). Here we show definable movement corridors within two protected areas that are used infrequently, but when used, are likely important to animals whether in elevated and basal physiological states. Thus, for elephants and likely other species, there is a need to identify, define, and understand these seldom-used, high value spaces that are frequently ignored in typical space use analyses.

5. Conclusion

We found that even at relatively fine, within-reserve, spatial scales, corridors are of importance to elephants. Corridors were consistently utilized by elephants, despite potential additive physiological costs to movement over long distances between core areas of use. Therefore, our findings support the general working concept that efforts to ensure habitat connectivity facilitate corridor movements and are likely of critical importance to animal conservation (Noss, 1996; Hilty et al., 2006). However, even where habitat within reserves might appear intact or connected via corridors, we have demonstrated that disturbance within protected areas can result in streaking behavior that, over the long-term, could have detrimental physiological and behavioral consequences to the individual, as well as influencing human conflict and broader ecosystem function. We recommend that conservation planners and managers consider corridors at multiple spatial and temporal scales, as well as how potential physiological stressors are likely to influence movement along these important movement corridors.

References

Beier, P., Noss, R.F., 1998. Do habitat corridors provide connectivity? Conserv. Biol. 12, 1241–1252.

Berger, J., 2004. The last mile: how to sustain long-distance migration in mammals. Conserv. Biol. 18, 320–331.

Beyer, H.L., 2004. Hawth's Analysis Tools for ArcGIS. <http://www.spatialecology.com/htools> (Downloaded June 2007).

Blank, M.D., 2010. Safe passages for fish and other aquatic species. In: Bechmann, J.P., Clevenger, A.P., Huijser, M., Hilty, J.A. (Eds.), Safe Passages. Island Press, Washington DC, pp. 75–96.

Boonstra, R., 2013. Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. Funct. Ecol. 27, 11–23.

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

Burke, T., Page, B., van Dyk, G., Millspaugh, J., Slotow, R., 2008. Risk and ethical concerns of hunting male elephant: behavioural and physiological assays of the remaining elephants. PLoS ONE 3, e2417.

Caro, T., Jones, T., Davenport, T.R.B., 2009. Realities of documenting wildlife corridors in tropical countries. Biol. Conserv. 142, 2807–2811.

Chester, C.C., 2006. Conservation Across Borders. Island Press, Washington DC.

Chetkiewicz, C.B., St. Clair, C.C., Boyce, M.S., 2006. Corridors for conservation: integrating pattern and process. Annu. Rev. Ecol. Evol. Sys. 37, 317–342.

Clevenger, A.P., Ford, A.T., 2010. Wildlife crossing structures, fencing, and other highway design considerations. In: Bechmann, J.P., Clevenger, A.P., Huijser, M., Hilty, J.A. (Eds.), Safe Passages. Island Press, Washington DC, pp. 17–50.

Croze, H., Moss, C.J., 2011. Patterns of occupancy in time and space. In: Moss, C.J., Croze, H., Lee, P.C. (Eds.), The Amboseli Elephants. University of Chicago Press, Chicago, pp. 89–108.

Cushman, S.A., Chase, M., Griffin, C., 2010. Mapping landscape resistance to identify corridors and barriers for elephant movement in Southern Africa. In: Cushman, S.A., Huettmann, F. (Eds.), Spatial Complexity, Informatics, and Wildlife Conservation. Springer-Verlag, Tokyo, pp. 349–367.

Dai, X., Shannon, G., Slotow, R., Page, B., Duffy, K.J., 2007. Short duration daytime movements of a cow herd of African elephants. J. Mammal. 88, 151–157.

Douglas-Hamilton, I., Krink, T., Vollrath, F., 2005. Movements and corridors of African elephants in relation to protected areas. Naturwissenschaften 92, 158–163.

Druce, H.C., Pretorius, K., Slotow, R., 2008. The response of an elephant population to conservation area expansion: Phinda Private Game Reserve, South Africa. Biol. Conserv. 141, 3127–3138.

Eads, D.A., Jachowski, D.S., Biggins, D.E., Livieri, T.M., Matchett, M.R., Millspaugh, J.J., 2012. Resource selection models are useful in predicting distributions of black-footed ferrets in prairie dog colonies. West N. Am. Nat. 72, 206–215.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Syst. 34, 487–515.

Gitzen, R.A., Millspaugh, J.J., Kernohan, B.J., 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. J. Wildl. Manage. 70, 1334–1344.

Gobush, K.S., Mutayoba, B.M., Wasser, S.K., 2008. Long-term impacts of poaching on relatedness, stress physiology, and reproductive output of female African elephants. Conserv. Biol. 22, 1590–1599.

Hanski, I., 1998. Metapopulation dynamics. Nature 396, 41–49.

Hilty, J.A., Lidicker, W.Z., Merenlender, A.M., 2006. Corridor Ecology. Island Press, Washington, D.C..

Hobbs, R.J., 1992. The role of corridors in conservation: solution or bandwagon. Trends Ecol. Evol. 7, 389–392.

Jachowski, D.S., Slotow, R., Millspaugh, J.J., 2012. Physiological stress and refuge behavior by African elephants. PLoS ONE 7, e31818.

Jachowski, D.S., Slotow, R., Millspaugh, J.J., 2013a. Unravelling complex associations between physiological state and movement in African elephants. Funct. Ecol.. http://dx.doi.org/10 1111/1365-2435.12118.

Jachowski, D.S., Slotow, R., Millspaugh, J.J., 2013b. Delayed physiological acclimatization by African elephants following reintroduction. Anim. Conserv.. http://dx.doi.org/10.1111/acv.12031.

Jones, T., Bamford, A.J., Ferrol-Sculte, D., Hieronimo, P., McWilliam, N., Rovero, F., 2012. Vanishing wildlife corridors and options for restoration: as case study from Tanzania. Trop. Conserv. Sci. 5, 463–474.

Joshi, R., Singh, R., 2009. Wildlife corridors and Asian elephants (*Elaphas maximus*): lessons from Rajaji National Park, North-West India. J. Am. Sci. 5, 31–40.

Kernohan, B.J., Gitzen, R.A., Millspaugh, J.J., 2001. Analysis of animal space use and movements. In: Millspaugh, J.J., Marzluff, J.M. (Eds.), Radio tracking and Animal Populations. Academic Press, San Diego, California, pp. 126–166.

Keyghobadi, N., Roland, J., Matter, S.F., Strobeck, C., 2005. Among and within patch components of genetic diversity respond at different rates to habitat fragmentation: an empirical demonstration. Proc. R. Soc. London B 272, 553–560.

Kioko, J.M., Selo, S.O., 2011. Elephant corridor use and threats in the eastern range of Amboseli elephants, Kenya. Pachyderm 49, 70–78.

Lagendijk, D.D.G., Mackey, R.L., Page, B.R., Slotow, R., 2011. The effects of herbivory by a mega- and mesoherbivore on tree recruitment in sand forest, South Africa. PLoS ONE 6, e17983.

Marzluff, J.M., Millspaugh, J.J., Hurvitz, P., Hancock, M.S., 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. Ecology 85, 1411–1427.

McComb, K., Shannon, G., Durant, S.M., Sayialel, K., Slotow, R., Poole, J., Moss, C., 2011. Leadership in elephants: the adaptive value of age. Proc. R. Soc. London B 278, 3270–3276.

McRae, B.H., Dickson, B.G., Keitt, T.H., Shah, V.B., 2008. Using circuit theory to model connectivity in ecology, evolution and conservation. Ecology 89, 2712–2724.

Millspaugh, J.J., Nielson, R.M., McDonald, L.M., Marzluff, J.M., Gitzen, R.A., Rittenhouse, C.D., Hubbard, M.W., Sheriff, S.L., 2006. Analysis of resource selection using utilization distributions. J. Wildl. Manage. 70, 384–395.

Mpanduji, D.G., East, M., Hofer, H., 2009. Analysis of habitat use by and preference of elephants in the Selous-Niassa wildlife corridor, southern Tanzania. Afr. J. Ecol. 47, 257–260.

Murphy, M.A., Evans, J.S., Storfer, A., 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. Ecology 91, 252261.

Noss, R.F., 1987. Corridors in real landscapes: a reply to Simberloff and Cox. Conserv. Biol. 1, 159–164.

Noss, R.F., 1991. Landscape connectivity: different functions at different scales. In: Hudson, W.E. (Ed.), Landscape Linkages and Biodiversity. Island Press, Washington, D.C., pp. 27–39.

Noss, R.F., 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conserv. Biol. 10, 949–963.

Pan, W., Lin, L., Luo, A., Zhang, L., 2009. Corridor use by Asian elephants. Integrat. Zool. 4, 220–231.

Pittiglio, C., Skidmore, A.K., van Gils, H.A.M.J., Prins, H.H.T., 2012. Identifying transit corridors for elephant using a long time-series. Int. J. Appl. Earth Obs. Geoinform. 14, 61–72.

Powell, R.A., Zimmerman, J.W., Seaman, D.E., 1997. Ecology and Behaviour of North American Black Bears: Home Ranges, Habitat and Social Organization. Chapman and Hall, London, UK.

Roever, C.L., van Aarde, R.J., Leggett, K., 2013. Functional connectivity within conservation networks: Delineating corridors for African elephants. Biol. Conserv. 157, 128–135.

Sawyer, S.C., Epps, C.W., Brashares, J.S., 2011. Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? J. Appl. Ecol. 48, 666–678.

Seaman, D.E., Powell, R.A., 1990. Identifying patterns and intensity of home range use. Int. Conf. Bear Res. Manage. 8, 243–249.

Shannon, G., Page, B., Slotow, R., Duffy, K., 2006. African elephant home range and habitat selection in Pongola game reserve, South Africa. Afr. Zool. 41, 37–44.

Slotow, R., 2012. Fencing for purpose: a case study of elephants in South Africa. In: Somers, M.J., Hayward, M.W. (Eds.), Fencing for Conservation: Restriction of Evolutionary Potential or a Riposte to Threatening Processes? Springer-Verlag, New York, New York, pp. 91–104.

Soulé, M.E., Estes, J.A., Berger, J., Del Rio, C.M., 2003. Ecological effectiveness: conservation goals for interactive species. Conserv. Biol. 17, 1238–1250.

van Aarde, R., Ferreira, S., Jackson, T., Page, B., 2008. Elephant population biology and ecology. In: Scholes, R.J., Mennell, K.G. (Eds.), Elephant Management: A Scientific Assessment for South Africa. Wits University Press, Johannesburg, pp. 84–145.

van Winkle, W., 1975. Comparison of several probabilistic home-range models. J. Wildl. Manage. 54, 322–330.

Vanak, A.T., Thaker, M., Slotow, R., 2010. Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? Biol. Conserv. 143, 2631–2637.

Viljoen, J.J., Ganswindt, A., du Toit, J.T., Langbauer, W.R., 2008. Translocation stress and faecal glucocorticoid metabolite levels in free-ranging African savanna elephants. S. Afr. J. Wildl. Res. 38, 146–152.

Wingfield, J.C., Romenofsky, M., 1997. Corticosterone and facultative dispersal in response to unpredictable events. Ardea 85, 155–166.

Wingfield, J.C., Maney, D.L., Breuner, C.W., Jacobs, J.D., Lynn, S., Ramenofsky, M., Richardson, R.D., 1998. Ecological bases of hormone-behavior interactions: the "emergency life history stage". Am. Zool. 38, 191–206.

Woolley, L., Millspaugh, J.J., Woods, R.J., van Rensburg, S.J., Mackey, R.L., Page, B., Slotow, R., 2008. Population and individual elephant response to a catastrophic fire in Pilanesburg National Park. PLoS ONE 3, e3233.