

A newly discovered wildlife migration in Namibia and Botswana is the longest in Africa

R. NAIDOO, M. J. CHASE, P. BEYTELL, P. DU PREEZ, K. LANDEN
G. STUART-HILL and R. TAYLOR

Abstract Migrations of most animal taxa are declining as a result of anthropogenic pressures and land-use transformation. Here, we document and characterize a previously unknown multi-country migration of Burchell's zebra *Equus quagga* that is the longest of all recorded large mammal migrations in Africa. Our data from eight adult female zebras collared on the border of Namibia and Botswana show that in December 2012 all individuals crossed the Chobe River and moved due south to Nxai Pan National Park in Botswana, where they spent a mean duration of 10 weeks before returning, less directly, to their dry season floodplain habitat. The same southward movements were also observed in December 2013. Nxai Pan appeared to have similar environmental conditions to several possible alternative wet season destinations that were closer to the dry season habitat on the Chobe River, and water availability, but not habitat or vegetation biomass, was associated with higher-use areas along the migratory pathway. These results suggest a genetic and/or cultural basis for the choice of migration destination, rather than an environmental one. Regardless of the cause, the round-trip, straight-line migration distance of 500 km is greater than that covered by wildebeest *Connochaetes taurinus* during their well-known seasonal journey in the Serengeti ecosystem. It merits conservation attention, given the decline of large-scale ecological processes such as animal migrations.

Keywords Animal movement, Botswana, conservation, *Equus quagga*, global positioning system, migration, Namibia, transfrontier, zebra

This paper contains supplementary material that can be found online at <http://journals.cambridge.org>

R. NAIDOO (Corresponding author) WWF-US, 1250 24th Street NW, Washington, DC, USA. E-mail robin.naidoo@wwfus.org

M. J. CHASE* and K. LANDEN Elephants Without Borders, Kasane, Botswana

P. BEYTELL and P. DU PREEZ Directorate of Natural Resource Management, Ministry of Environment & Tourism, Windhoek, Namibia

G. STUART-HILL and R. TAYLOR WWF in Namibia, Windhoek, Namibia

* Also at: Institute for Conservation Research, San Diego Zoo Global, Escondido, USA

Received 18 December 2013. Revision requested 25 February 2014.

Accepted 10 March 2014. First published online 27 May 2014.

Introduction

Seasonal migration, where individuals move to and from geographically separated home ranges to exploit changes in environmental conditions, is common among many taxonomic groups (Dingle & Drake, 2007). The long-distance seasonal migrations of monarch butterflies *Danaus plexippus* in North America, wildebeest *Connochaetes taurinus* in the Serengeti, songbirds across the Americas, and grey *Eschrichtius robustus* and humpback whales *Megaptera novaeangliae* in the Pacific Ocean are among the most spectacular natural phenomena (Wilcove, 2009). However, migrations across many different taxa and in many locations have been extinguished or are under threat from anthropogenic pressures such as habitat destruction, construction of barriers, overexploitation and climate change (Wilcove & Wikelski, 2008; Dobson et al., 2010). In addition, migrations are often poorly understood and many may remain uncharacterized, as evidenced by the rediscovery of a migration of large mammals in Sudan that rivals that of the Serengeti in abundance, which remained largely undocumented until 2007 (Harris et al., 2009; Wilcove, 2009). Yet understanding migrations and the movement ecology of wildlife is an important consideration in the design of functionally connected landscapes, in the management of species of conservation concern and for the protection of threatened natural phenomena (Brower & Malcolm, 1991; Briers, 2002; Crooks & Sanjayan, 2006; Fynn & Bonyongo, 2011; Epps et al., 2011).

Here we document for the first time the existence of a cross-border, long-distance migration of Burchell's zebra *Equus quagga* that ranks as the longest of all known mammal migrations in Africa. This previously undiscovered phenomenon involves several thousand zebras covering a straight-line distance of 500 km over several months, spans parts of Namibia and Botswana and was observed in consecutive years. We explore the influence of the external environment in shaping the migratory route and destination, and hypothesize that this migration may represent a conserved, ancient route rather than a response to current environmental conditions.

Methods

Fieldwork was conducted during the dry season in 2012, in mid September on the Botswana side of the Chobe River and

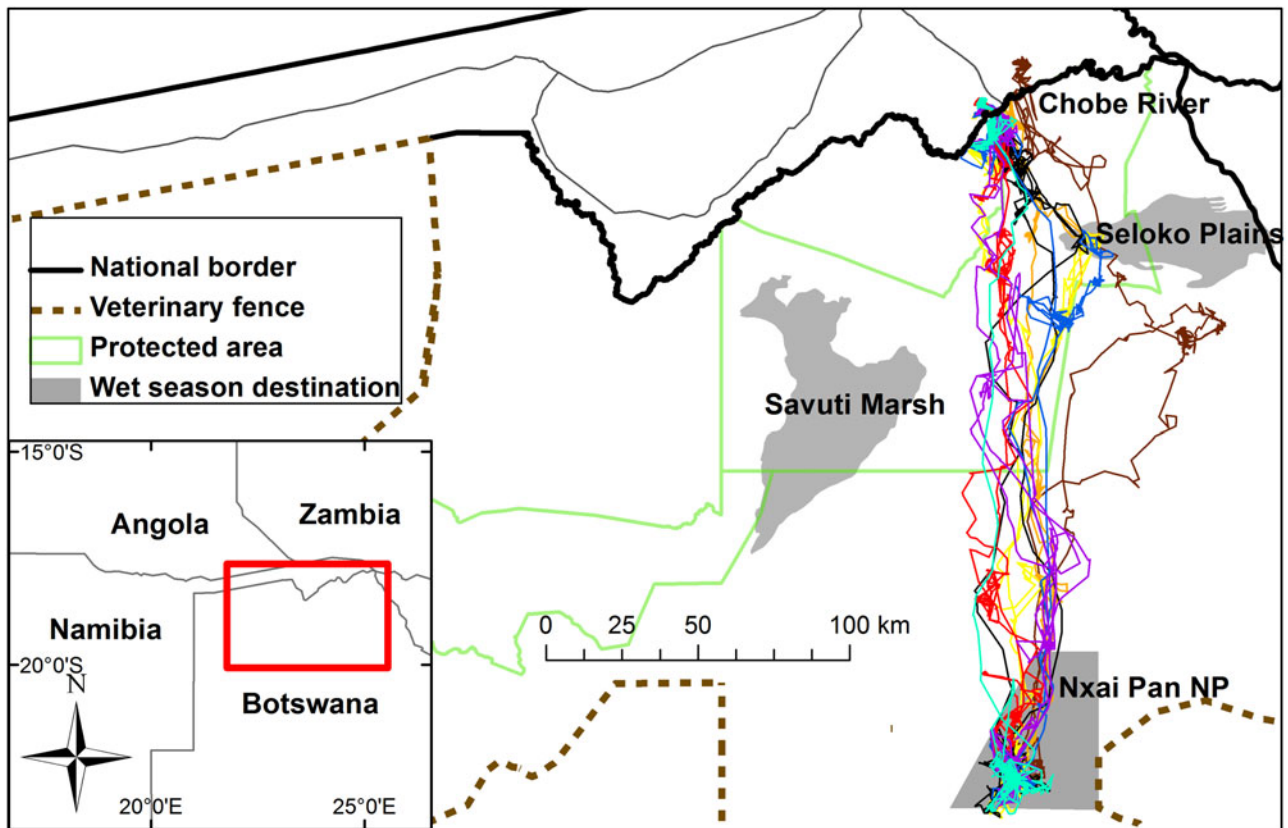


Fig. 1 Movement trajectories of eight female zebra *Equus quagga* collared on the Chobe floodplains in Botswana and Namibia from the late dry season (September–October) 2012 until June 2013. Grey polygons indicate actual (Nxai Pan National Park) and potential alternative (Savuti Marsh and Seloko Plains) migration destinations. The rectangle on the inset indicates the location of the main map in southern Africa.

mid October on the Namibia side (Fig. 1). Adult female zebras ($n = 8$) were darted from the air or ground and immobilized using a mixture of etorphine hydrochloride, azaperone and hyaluronidase. The age and family group size were estimated for each individual, and a satellite-tracking collar attached. Tracking collars (Africa Wildlife Tracking, Pretoria, South Africa) were programmed to record global positioning system (GPS) locations at either 4- or 5-hour intervals. The total number of data points per individual was 562–1,403 (mean $1,008 \pm \text{SD } 215$). Animals were captured and treated according to the protocols approved under research permit 1,537/2010 from the Ministry of Environment and Tourism in Namibia, and EWT 8/36/4 XVII (57) from the Department of Wildlife and National Parks in Botswana.

GPS locations were used to map and animate movement trajectories of all individuals. We calculated net squared displacement distances from the collaring site over time to characterize the scale and timing of migration (Bunnfeld et al., 2011).

We assessed whether migration to Nxai Pan could be driven by unique environmental conditions at the site, first using spatial data layers on soil fertility (a proxy for the nutrition content of forage, and therefore a critical

determinant of grazing potential for herbivores such as zebras; Fynn & Bonyongo, 2011) in Botswana. Nxai Pan is an important wet season habitat for wildlife because of the filling of waterholes and the growth of new grass on the pan (Department of Wildlife and National Parks, 1995). Nxai Pan soils are categorized as fertile to very fertile and are therefore attractive to grazers because of their high nutritional value (Lindsay et al., 1998). There are only two other locations in northern Botswana that have similarly fertile soils; both are closer to the Chobe River and zebras could reach them without having to navigate around fences or other potential anthropogenic barriers (Fig. 1). The Seloko Plains are c. 60 km from zebra dry season ranges along the Chobe River and have fertile to very fertile soils (Lindsay et al., 1998). A small section of the eastern part of these grasslands has been converted to commercial farming but the remainder is unconverted and zebras and other wildlife are present (Chase, 2013). The Savuti Marsh/Matabe Depression (Savuti Marsh hereafter) is c. 100 km from zebra dry season ranges and has moderately fertile to fertile soils. Zebras and other ungulates are known to migrate to Savuti from the Chobe and Linyanti (the Linyanti is the name of the Chobe River further westwards) floodplains (Vandewalle, 2000), and the

grasslands of this marsh support large herds of wildlife (Fynn & Bonyongo, 2011; Sianga et al., 2013). These three sites (Nxai Pan, Seloko Plains and Savuti Marsh) are also broadly classified as tree and grass savannah (Lindsay et al., 1998). Remaining habitats accessible to zebras moving southwards from the Chobe River all occur on moderate- or low-fertility soils that would have limited appeal to migrating grazers.

We characterized environmental conditions at Nxai Pan and at the two potential alternative destinations (Seloko Plains and Savuti Marsh); our hypothesis was that Nxai Pan should appear significantly different to the other two sites if the environment was driving zebra migration there. We used available data on vegetation biomass, tree cover and rainfall, and averaged the values of these variables over all cells in each defined site area (Fig. 1). We assessed whether temporal changes in mean vegetation biomass varied across these three potential wet season migration destinations, using the MODIS 250-m resolution enhanced vegetation index, which is produced at 16-day intervals (Pettorelli et al., 2005). We used remotely sensed data from the Tropical Rainfall Monitoring Mission (half-degree resolution) to characterize daily precipitation levels and cumulative precipitation at Nxai Pan, Seloko Plains and Savuti Marsh during September 2012–March 2013. Finally, we characterized tree cover at each of these three sites by averaging the percentage of each cell covered by woody vegetation, using 250-m MODIS continuous field data from 2010 (Hansen et al., 2003).

We conducted an aerial census of zebras at Nxai Pan, using a fixed-wing aircraft, on 21 February 2013. Strip transects were flown, using standard methodology (Norton-Griffiths, 1978). All zebras within 200 m of either side of a transect were counted, with 27 parallel transects flown during 07.30–10.00. This design ensured 100% coverage of the pan and resulted in a complete census of individuals in the area. High-resolution photographs were taken for more accurate counting post-flight.

To assess the relationship between environmental conditions and zebra movements along the main migratory pathway we calculated the minimum convex polygon across all GPS locations of all individuals moving from the Chobe River to Nxai Pan and back. We then overlaid a 5 × 5 km grid across this polygon and calculated the number of GPS points in each cell separately for two time periods: the southward (4 December 2012–10 January 2013) and the northward (18 February 2013–13 June 2013) migratory phases. We classified grid cells as stopover areas when at least one zebra spent at least 48 consecutive hours in an encamped state in the cell (Morales et al., 2004; Sawyer & Kauffman, 2011).

Using high-resolution imagery from Google Earth we assessed the availability of standing water to zebras in each grid cell as absent (no visual evidence of standing

water), present (1–3 waterholes) or abundant (> 3 waterholes and/or the presence of a stream or river). All cells were categorized by the same observer to maintain consistency. We were unable to assess whether waterholes contained standing water that was accessible to zebras at the time they were encountered, only whether cells contained waterholes or watercourses that had the potential to be filled. Similar to the minimum convex polygon environmental analyses above we also calculated mean cell fractions covered by woody vegetation and mean enhanced vegetation index values for each 5 × 5 km cell, separately for the southward and northward movement phases.

We conducted four separate statistical analyses, using generalized linear models and multi-model inference, to investigate how environmental characteristics of cells along the migratory pathway affected zebra movements.

Southward migration

$$\text{Prob}(Y = y_i) = \frac{e^{-u_i}[u_i]y_i}{y_i!}, y_i = 0, 1, 2, \dots \quad (1)$$

where

$$\begin{aligned} \ln(u_i) = & a + \beta_1 * \text{Water} + \beta_2 * \text{Woody} \\ & + \beta_3 * \text{EVI}_{\text{South}} + \beta_4 * \text{EVI}_{\text{South}^2} \end{aligned}$$

We used a negative binomial regression model to estimate counts of zebra GPS fixes in cells (y_i) as a function of waterholes (Water), the mean cell fraction covered by woody vegetation (Woody), and a second-order polynomial of mean enhanced vegetation index values; a is the regression intercept and β is the regression coefficient of the associated independent variable.

$$\text{Prob.Stopover}_{\text{South}} = \frac{e[a + \beta_1 * \text{Water} + \beta_2 * \text{Woody} + \beta_3 * \text{EVI}_{\text{South}} + \beta_4 * \text{EVI}_{\text{South}^2}]}{1 + e[a + \beta_1 * \text{Water} + \beta_2 * \text{Woody} + \beta_3 * \text{EVI}_{\text{South}} + \beta_4 * \text{EVI}_{\text{South}^2}]} \quad (2)$$

We used a logistic regression model to investigate the probability of a cell being used as a stopover location as a function of waterholes (Water), the mean cell fraction covered by woody vegetation (Woody), and a second-order polynomial of mean enhanced vegetation index values; a is the regression intercept and β is the regression coefficient of the associated independent variable.

Northward migration

$$\text{Prob}(Y = y_i) = \frac{e^{-u_i}[u_i]y_i}{y_i!}, y_i = 0, 1, 2, \dots \quad (3)$$

where

$$\begin{aligned} \ln(u_i) = & a + \beta_1 * \text{Water} + \beta_2 * \text{Woody} \\ & + \beta_3 * \text{EVI}_{\text{North}} + \beta_4 * \text{EVI}_{\text{North}^2} \end{aligned}$$

TABLE 1 Summary statistics for migration movements of eight female zebras *Equus quagga* collared on the Chobe floodplains in Botswana and Namibia (Fig. 1).

ID	Southward journey				Northward journey				
	Departed	Arrived	Days	Distance (km)	Departed	Arrived	Days	Distance (km)	Days at pan
SAT350	15 Dec. 2012	10 Jan. 2013	37	424	18 Mar. 2013	16 May 2013	59	571	67
SAT421	4 Dec. 2012	16 Dec. 2012	12	270	26 Feb. 2013	19 Apr. 2013	52	516	72
SAT500	4 Dec. 2012	19 Dec. 2012	15	290	23 Feb. 2013	25 June 2013	153	570	66
SAT503	8 Dec. 2012	16 Dec. 2012	8	256	20 Mar. 2013	24 Apr. 2013	35	479	94
SAT504	8 Dec. 2012	27 Dec. 2012	19	317	18 Feb. 2013	13 June 2013	115	853	53
SAT505	6 Dec. 2012	13 Dec. 2012	7	266	19 Mar. 2013	6 July 2013	109	808	96
SAT506	5 Dec. 2012	22 Dec. 2012	15	294	23 Feb. 2013	8 May 2013	74	773	63
SAT507*	6 Dec. 2012	15 Dec. 2012	9	281					149*

*Died on 13 May 2013

Variable descriptions are as in (1), with the counts of GPS fixes and the enhanced vegetation index measurements made during the northward migration phase.

$$\text{Prob. Stopover}_{\text{North}} = \frac{e[a + \beta_1 * \text{Water} + \beta_2 * \text{Woody} + \beta_3 * \text{EVI}_{\text{North}} + \beta_4 * \text{EVI}_{\text{North}^2}]}{1 + e[a + \beta_1 * \text{Water} + \beta_2 * \text{Woody} + \beta_3 * \text{EVI}_{\text{North}} + \beta_4 * \text{EVI}_{\text{North}^2}]} \quad (4)$$

Variable descriptions are as in (2), with stopover and enhanced vegetation index measured during the northward migration phase.

Note that we used negative binomial rather than Poisson count data regression because the variance of zebra GPS counts in the cells was substantially greater than the mean of the counts, indicating overdispersed count data (Cameron & Trivedi, 1998). Residuals from each of the preliminary global regression models also showed significant first-order spatial autocorrelation in the residuals, and therefore in addition to the terms noted in equations (1–4) we included a first-order neighbourhood term that contained the sum of the count values of the nine cells in the immediate neighbourhood of the target cell (Dormann et al., 2007). We hypothesized that after correcting for spatial autocorrelation, cells with more waterholes, an optimal enhanced vegetation index value and lower levels of woody vegetation would be used more frequently and would be more likely to be used as stopover points than those with lower levels of each. We tested these hypotheses using a multi-model inference approach, evaluating all 64 possible combinations of independent variables described in equations (1–4). Model-averaged coefficients were calculated based on each model's Akaike weight (Burnham & Anderson, 1998), with means, standard errors, confidence limits, and tests of significance calculated using *MuMin v. 1.9.13* (Barton, 2013), and all other analyses performed in *R v.2.15.1* (R Development Core Team, 2008).

Results

Adult zebras spent several weeks in the vicinity of the Chobe River floodplains, regularly crossing the river to and from Namibia and Botswana. On 26–27 November 2012 all individuals remaining in Namibia crossed the river south into Botswana, with three females moving off the floodplains and adjoining woodlands to an area c. 30 km south in Botswana (Fig. 1). On 3 December 2012 the first significant directional movement due south was observed in one individual, after which seven of the eight zebras moved south to the Nxai Pan, arriving during 14–27 December (Table 1). The remaining female zebra spent several weeks south of Seloko Plains, eventually arriving at Nxai Pan on 9 January 2013. By December 2013 the surviving GPS-collared zebras (n = 6) were again making their way south from the Chobe floodplains towards Nxai Pan.

The straight-line distance between the outer extent of the Chobe dry season range and the pan at Nxai Pan National Park is almost exactly 250 km. Most of this ground was covered during a 2-week period in December 2012 (median 14 days, range 7–37) during which movement was highly linear and unidirectional, with some individuals travelling > 50 km per day. Total distances travelled by individuals on their southward journey to Nxai Pan ranged from 256 km for an individual with highly directional movement to 424 km for an individual that deviated to Seloko Plains before eventually moving to Nxai Pan (mean $300 \pm \text{SD } 54$ km; Table 1).

The timing of the movement away from the Chobe floodplains appears to be related to the amount and timing of rainfall at the destination in Nxai Pan rather than at the Chobe origin. A major rainfall event (37 mm, nearly 10% of the region's annual precipitation) occurred in the Nxai Pan area on 4 December 2012, several days before the zebras began their rapid, unidirectional movement south (Fig. 2). There was no rainfall event of comparable magnitude in the Chobe region before the long-distance migration southward.

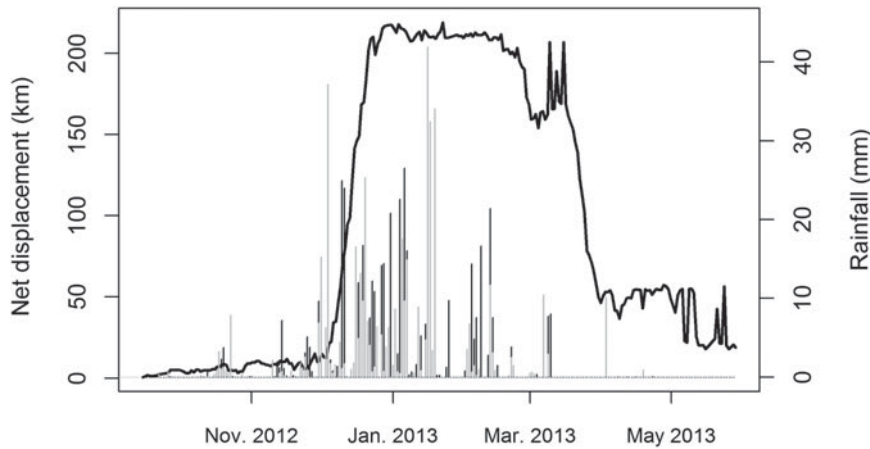


FIG. 2 Timing of daily rainfall and zebra migration during September 2012–May 2013. The thick black line represents the mean net displacement away from dry season home ranges for nine zebras. Vertical lines represent daily rainfall over dry season ranges (black) and the Nxai Pan wet season range (grey).

Zebras spent a mean of 73 days in the Nxai Pan area (range 53–96), mostly on the pan itself. We counted 1,534 zebras in the area during our aerial survey on 21 February 2013, although correspondence with safari guides in the park indicated that in the 2 weeks prior to our survey there had been more zebras in the vicinity of the pan.

Return trajectories of zebras moving from the Nxai Pan north to the Chobe River were less direct and took significantly longer. The mean return time was 85 days (vs 15 days for the southward journey; $t = 4.33$, $P = 0.004$) and mean distance travelled was $653 \pm \text{SE } 153$ km (vs 302 km; $t = 5.79$, $P = 0.0006$). The mean distance of actual movement trajectories of the seven zebras that survived to complete the entire return journey from the Chobe floodplains to Nxai Pan was 955 km (range 735–1,170 km).

Environmental characteristics of Nxai Pan overlapped with the two possible alternative wet season destinations for Chobe River zebras. Woody vegetation cover, a measure of broad habitat type, was similar at all three potential destinations (Nxai Pan, $18.0 \pm \text{SE } 3.7\%$; Seloko Plains, $17.1 \pm \text{SE } 2.6\%$; Savuti Marsh, $20.0 \pm \text{SE } 5.3\%$), as was total rainfall during September 2012–March 2013 (Nxai Pan, 444 mm; Seloko Plains, 477 mm; Savuti Marsh, 470 mm). The area of Nxai Pan used by zebras had a consistently lower mean vegetation biomass than Savuti Marsh. However, biomass levels at Nxai Pan and Seloko Plains were similar from mid December to early February, which encompasses most of the wet season period that zebras were present at Nxai Pan (Fig. 3). Biomass levels at Nxai Pan dropped below those of Seloko Plains in mid February; at the same time the zebras began to move back north towards the Chobe River floodplains (Table 1).

As suggested by initial analyses, averaged coefficients across all model combinations showed that spatial autocorrelation in zebra location data was strong, with coefficients on the first-order neighbourhood variable significantly greater than zero in all four analyses (Table 2). Controlling for this autocorrelation the probability of a 5×5 km cell being used as a stopover point (i.e. where zebras stopped for

at least 48 hours during the migratory phases) appeared unrelated to waterhole abundance, enhanced vegetation index or woody vegetation cover (Table 2). The number of GPS relocations in cells along the southward migratory pathway also appeared unrelated to waterhole abundance, enhanced vegetation index or woody vegetation cover. However, cells with higher numbers of GPS fixes during the northward migratory phase contained higher densities (and presence) of waterholes than those used less frequently (Table 2). The top 10 models for each of our four analyses accounted for 68–100% of the cumulative Akaike model weight, indicating that a relatively small fraction of models (15%) had high explanatory power (Supplementary Table S1).

Discussion

Prior to the discovery of this migration it was unclear where Chobe River zebras moved to in the wet season, with local residents and wildlife professionals only aware that animals left at the beginning of the wet season and returned the following dry season (Chase, 2011). Similarly, the appearance of zebras on the Nxai Pan in the wet season is an annual occurrence but there was no evidence that animals originated as far away as the Chobe River. The timing of the migration from the Chobe River appeared to coincide with heavy, episodic rainfall events early in the wet season at Nxai Pan. Other migratory ungulate species (Sinclair & Norton-Griffiths, 1979), as well as zebras in the recently re-established migration from the Okavango Delta to the Makgadikgadi Pans (Bartlam-Brooks et al., 2011), also appear to time migration to rainfall events, and zebras are able to orient long-range movements to environmental conditions outside their perceptory range (Brooks & Harris, 2008). However, as we have only observed two southward migration onsets we are unable to assess statistically the nature of the relationship between timing of rainfall and migration without a substantially longer time series.

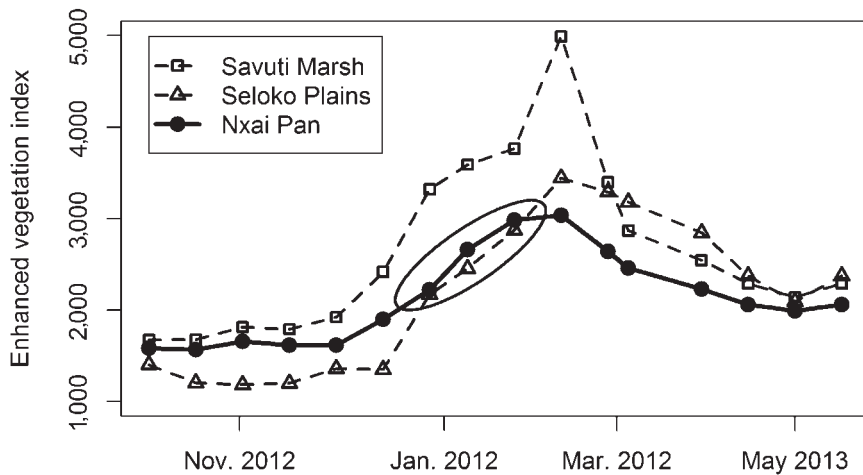


FIG. 3 Temporal pattern of mean enhanced vegetation index (September 2012–May 2013) at the Nxai Pan wet season migration destination and two alternative destinations (Seloko Plains and Savuti Marsh). The ellipse indicates the near-identical values at Nxai Pan and Seloko Plains during the core wet season time when zebras were at Nxai Pan.

Our aerial census showed that there were at least 1,500 zebras on Nxai Pan in the wet season of 2012–2013, with anecdotal information indicating this number may have been substantially higher a few weeks before our census. This figure is similar to dry season estimates of zebra numbers (1,558–3,593) on the Chobe floodplains during 2007–2012, which were also estimated from strip-transect surveys (MC, unpubl. data). Combined with the facts that all eight of the female zebras we collared in 2012 moved from the Chobe River to Nxai Pan, the six surviving zebras repeated this southward movement to Nxai Pan in December 2013, and zebra numbers on the Chobe floodplains during the wet season (255) are an order of magnitude lower than during the dry season (Chase, 2013), this suggests that most of the zebras on the Chobe floodplains may be moving to Nxai Pan in the wet season. Further censuses and satellite tracking of more individuals over time could confirm the annual periodicity of the migration, as well as the fraction of Chobe animals that move to Nxai Pan vs those that remain or migrate elsewhere. Additional studies are also needed to determine whether other ungulates such as the wildebeest, long-distance migrants that move in tandem with zebras in other ecosystems (e.g. Serengeti, Liuwa Plains—Mussuma Transfrontier Conservation area; Harris et al., 2009), perform the same Chobe–Nxai Pan migration.

The reasons for such a long-distance migration, with closer and apparently suitable alternative destinations bypassed, remain unknown. Our analyses of potential environmental drivers of the migration are preliminary and our hypothesis that the migration is a fixed behaviour rather than a variable response to environmental conditions needs further testing. Seloko Plains and Savuti Marsh have similar levels of woody vegetation, soil fertility and rainfall to Nxai Pan, and wet season vegetation biomass was similar for Seloko Plains and Nxai Pan. Vegetation biomass was higher at Savuti Marsh than Nxai Pan, which, if anything, suggests greater grazing availability and therefore higher suitability for zebras migrating from the Chobe floodplains. We were

unable to quantify access to drinking water at any of the three locations but at the time of migration Savuti Marsh held water for the first time in 28 years and was therefore much wetter than either Seloko Plains or Nxai Pan. Access to water would therefore not have been a problem at that site, although it is possible that having been dry for so long the marsh is still an unfavoured destination that will need to be rediscovered by migratory ungulates. Also, we could not quantify predation risk, which is an important driver of migration in ungulates (Fryxell & Sinclair, 1988), although lions *Panthera leo*, the main predators of zebras in this region, are present in sufficient numbers to draw tourists in both Savuti Marsh and Nxai Pan (Power & Compion, 2009; Johnson, 2010).

With no obvious environmental differences between Nxai Pan and the other two possible destinations for zebras from Chobe River, this migration may represent an ancient, conserved phenomenon that has a genetic basis and/or is an outcome of learned behaviour and cultural transmission between individuals and social groups (Alerstam, 2006; Bolger et al., 2008). Research has shown that the Okavango–Makgadikgadi zebra migration in Botswana, itself a long-distance event involving c. 15,000 zebras, reoccurred during 2008–2009 for the first time following the removal of a veterinary fence that had blocked the route during 1968–2004. This completely separate migration suggests a conserved memory of an ancient route that may be genetically encoded (Bartlam-Brooks et al., 2011), and raises the question of why zebras from Chobe River move to Nxai Pan rather than the nearby Makgadikgadi Pans (and vice versa). This fixed-route phenomenon has also been observed in pronghorn *Antilocapra americana* in the USA, where individuals in the Grand Teton National Park area have used the same seasonal migration pathway, as narrow as tens of metres in some places, since the Holocene era (Berger et al., 2006).

Our analyses imply that zebra movement and stopovers along the migratory pathway between dry and wet season

TABLE 2 Coefficients for regression models relating environmental characteristics to the count of zebra locations in 5×5 km cells along the migratory pathway (negative binomial regression model) and to the probability of a cell being a stopover point on the migration route (logistic regression model) during both northward and southward movement phases.

	South			North				
	Estimate \pm SE	Confidence limits	z	P	Estimate \pm SE	Confidence limits	z	P
Cell counts during migration								
Intercept	0.723 \pm SE 1.294	-1.824–3.270	0.56	0.58	1.497 \pm SE 2.944	-4.300–7.294	0.51	0.61
Sum of first-order neighbours ¹	0.231 \pm SE 0.035	0.163–0.300	6.63	< 0.001	0.867 \pm SE 0.013	0.035–0.087	4.64	< 0.001
Waterholes abundant ²	0.408 \pm SE 0.305	-0.192–1.008	1.33	0.18	1.149 \pm SE 0.345	1.149–2.506	5.28	< 0.001
Waterholes present ²	0.305 \pm SE 0.329	-0.342–0.953	0.92	0.36	0.948 \pm SE 0.339	0.280–1.617	2.78	0.01
Mean enhanced vegetation index	-0.0005 \pm SE 0.001	-0.003–0.002	0.43	0.67	-0.0001 \pm SE 0.003	-0.006–0.006	0.03	0.98
Square of mean enhanced vegetation index	-8.69E-08 \pm SE 1.83E-07	-4.50E-07–2.7E-07	0.47	0.64	-1.30E-07 \pm SE 5.16E-07	-1.10E-06–8.9E-07	0.25	0.80
Mean % woody vegetation	0.028 \pm SE 0.037	-0.046–0.103	0.74	0.46	-0.050 \pm SE 0.035	-0.120–0.019	1.42	0.16
Probability of a cell being a stopover point								
Intercept	-5.94 \pm SE 802	-1587–1575	0.01	0.99	-10.52 \pm SE 981	-1943–1922	0.01	0.99
Sum of first-order neighbours ¹	10.08 \pm SE 2.21	5.7–14.4	4.54	< 0.001	6.82 \pm SE 1.41	4.05–9.6	4.82	< 0.001
Waterholes abundant	5.39 \pm SE 1486	-2920–2931	0.00	1.00	8.85 \pm SE 1003	-1966–1983	0.01	0.99
Waterholes present	5.29 \pm SE 1514	-2977–2987	0.00	1.00	14.51 \pm SE 1441	-2824–2853	0.01	0.99
Mean enhanced vegetation index	-0.0006 \pm SE 0.005	-0.010–0.009	0.13	0.89	0.0015 \pm SE 0.0015	-0.021–0.024	0.13	0.90
Square of mean enhanced vegetation index	-3.92E-08 \pm SE 8.23E-07	-1.66E-06–1.58E-06	0.05	0.96	-6.01E-07 \pm SE 1.91E-06	-4.36E-06–3.16E-06	0.31	0.75
Mean % woody vegetation	0.004 \pm SE 0.183	-0.357–0.364	0.02	0.98	-0.07 \pm SE 0.10	-0.28–0.13	0.71	0.48

¹Coefficients significantly different from 0 ($P < 0.05$) are shown in bold.

²Coefficients on Waterholes present and Waterholes abundant are relative to reference level of factor variable (Waterholes absent).

endpoints are unrelated to either spatial or temporal variation in vegetation, and cells with waterholes are not used preferentially as stopover points, although cells with waterholes had higher numbers of zebra GPS counts than those without for the northward (but not southward) migration. As with the actual and alternative wet season destinations there does not appear to be a strong response to fluctuating environmental conditions along the migratory pathway.

Comparing our data with those compiled in a review (Harris et al., 2009) shows that the newly discovered zebra migration ranks as the longest large-mammal migration in Africa. The round-trip length of this migration is longer than long-distance movements of zebras and wildebeest in the Serengeti ecosystem (A.R.E. Sinclair, pers. comm.; Harris et al., 2009). It is also longer than migrations of topi *Damaliscus lunatus*, Mongalla gazelle *Gazella thomsonii albonotata*, and white-eared kob *Kobus kob* in southern Sudan (Harris et al., 2009) and of wildebeest in Angola and Zambia (Harris et al., 2009), although data for these species and locations are incomplete. Although migrations of greater distances occurred in the past (Harris et al., 2009) there are no extant large-mammal migrations in Africa that are longer than the one we document here.

This discovery is important in light of the effects of anthropogenic activities on large-mammal migrations in and around the study area during the last half-century. The erection of veterinary control fences during 1950–1980 disrupted many large-scale migrations, severing connectivity between the dry season grassland habitats of the Makgadikgadi Pans, Savuti Marsh and the Kalahari Desert and wet season strongholds in the Okavango Delta and the Chobe/Linyanti Rivers (Williamson & Williamson, 1984; Mbaiwa & Mbaiwa, 2006; Ferguson & Hanks, 2010). As a consequence, populations of migratory ungulate species such as the zebra, wildebeest and buffalo *Syncerus caffer* declined and, decades later, continue to show little sign of recovery (Perkins, 2010). Nor are these disruptions consigned to the distant past; in 2005 a fence erected along the Boteti River excluded most of the river from the Makgadikgadi Pans National Park, rendering adjacent dry season habitat inaccessible and resulting in the deaths of > 300 migrating zebras that were confronted with an unknown barrier (Gibson, 2010).

As with the Serengeti migration, the Namibia–Botswana zebra migration involves the crossing of an international border, and therefore cross-country cooperation will be required to ensure its persistence. Given the documented disappearance of numerous wildlife migrations, the speed at which migratory populations can be lost as a result of anthropogenic perturbations (Bolger et al., 2008; Wilcove, 2009) and the growing recognition of wildlife-based economies as engines for rural development in sub-Saharan Africa (Lindsey et al., 2007; Jones et al., 2012) we suggest that ensuring the persistence of one of Africa's longest wildlife

migrations should be a high conservation priority. The proposed Kavango–Zambezi Transfrontier Conservation Area (KAZA TFCA, 2013), spanning parts of Namibia, Botswana, Angola, Zambia and Zimbabwe, covers the entire migration route and therefore would provide an ideal platform from which to pursue targeted international conservation activities. These should include continued tracking of individuals to assess year-to-year variation in movements, an assessment of potential threats and impediments to migration (e.g. the construction of new fences or roads, the expansion of agriculture or human settlements), co-ordinated monitoring of population vital rates and the development of innovative mechanisms (such as payments for environmental services) that provide incentives for the conservation of the migration corridor.

In a human-dominated world in which wildlife migrations are disappearing, the discovery of a previously undocumented migration of zebras across hundreds of kilometres and over international borders provides hope that the conservation of large-scale ecological phenomena, among other biodiversity conservation goals, continues to be a worthwhile pursuit in the Anthropocene era (Caro et al., 2012).

Acknowledgements

We thank Hans Swartbooi, Lise Hanssen, Carl-Heinz Moeller, Michelle Kastern, Werner Kilian and Johannes Kapner for help in the field, Alicia Ellis, Colby Loucks, Sylvia Thompson, David Wilcove, Tony Sinclair, Dave Ward, Raymond Peters and two anonymous reviewers for their constructive comments, and the Namibia Ministry of Environment and Tourism, the Botswana Department of Wildlife and National Parks, the Eppley Foundation, the Paul G. Allen Family Foundation, and the San Diego Zoo Global Wildlife Conservancy for funding and logistical support.

References

- ALERSTAM, T. (2006) Conflicting evidence about long-distance animal navigation. *Science*, 313, 791–794.
- BARTLAM-BROOKS, H.L.A., BONYONGO, M.C. & HARRIS, S. (2011) Will reconnecting ecosystems allow long-distance mammal migrations to resume? A case study of a zebra *Equus burchelli* migration in Botswana. *Oryx*, 45, 210–216.
- BARTON, K. (2013) MuMIn: Multi-model inference. *R v. 1.9.13*. <http://CRAN.R-project.org/package=MuMIn> [accessed 14 April 2014].
- BERGER, J., CAIN, S.L. & BERGER, K.M. (2006) Connecting the dots: an invariant migration corridor links the Holocene to the present. *Biology Letters*, 2, 528–531.
- BOLGER, D.T., NEWMARK, W.D., MORRISON, T.A. & DOAK, D.F. (2008) The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, 11, 63–77.
- BRIERS, R.A. (2002) Incorporating connectivity into reserve selection procedures. *Biological Conservation*, 103, 77–83.
- BROOKS, C.J. & HARRIS, S. (2008) Directed movement and orientation across a large natural landscape by zebras, *Equus burchelli antiquorum*. *Animal Behaviour*, 76, 277–285.
- BROWER, L.P. & MALCOLM, S.B. (1991) Animal migrations: endangered phenomena. *American Zoologist*, 31, 265–276.
- BUNNEFELD, N., BÖRGER, L., VAN MOORTER, B., ROLANDSEN, C.M., DETTKI, H., SOLBERG, E.J. & ERICSSON, G. (2011) A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology*, 80, 466–476.
- BURNHAM, K.P. & ANDERSON, D. (1998) *Model Selection and Multimodel Inference: a Practical Information-theoretic Approach*. Springer, New York, USA.
- CAMERON, A.C. & TRIVEDI, P.K. (1998) *Regression Analysis of Count Data*. Cambridge University Press, New York, USA.
- CARO, T., DARWIN, J., FORRESTER, T., LEDOUX-BLOOM, C. & WELLS, C. (2012) Conservation in the anthropocene. *Conservation Biology*, 26, 185–188.
- CHASE, M.J. (2011) *Status of Wildlife Populations and Land Degradation in Botswana's Forest Reserves and Chobe District*. Elephants Without Borders, Kasane, Botswana.
- CHASE, M. (2013) *Status of Wildlife Populations and Land Degradation in Botswana's Forest Reserves and Chobe District*. Elephants Without Borders, Kasana, Botswana.
- CROOKS, K.R. & SANJAYAN, M. (eds) (2006) *Connectivity Conservation*. Cambridge University Press, Cambridge, UK.
- DEPARTMENT OF WILDLIFE AND NATIONAL PARKS (1995) *Makgadikgadi/Nxai Pan Management Plan*. Ministry of Commerce and Industry, Gabarone, Botswana.
- DINGLE, H. & DRAKE, V.A. (2007) What is migration? *BioScience*, 57, 113–121.
- DOBSON, A.P., BORNER, M., SINCLAIR, A.R.E., HUDSON, P.J., ANDERSON, T.M., BIGURUBE, G. et al. (2010) Road will ruin Serengeti. *Nature*, 467, 272–273.
- DORMANN, C.F., MCPHERSON, J.M., ARAUJO, M.B., BIVAND, R., BOLLIGER, J., CARL, G. et al. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, 30, 609–628.
- EPPS, C.W., MUTAYOBA, B.M., GWIN, L. & BRASHARES, J.S. (2011) An empirical evaluation of the African elephant as a focal species for connectivity planning in East Africa. *Diversity and Distributions*, 17, 603–612.
- FERGUSON, K. & HANKS, J. (eds) (2010) *Fencing Impacts: A Review of the Environmental, Social and Economic Impacts of Game and Veterinary Fencing in Africa with Particular Reference to the Great Limpopo and Kavango–Zambezi Transfrontier Conservation Areas*. Mammal Research Institute, Pretoria, South Africa.
- FRYXELL, J.M. & SINCLAIR, A.R.E. (1988) Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution*, 3, 237–241.
- FYNN, R.W.S. & BONYONGO, M.C. (2011) Functional conservation areas and the future of Africa's wildlife. *African Journal of Ecology*, 49, 175–188.
- GIBSON, D. (2010) Environmental assessment of Botswana's fences. In *Fencing Impacts: A Review of the Environmental, Social and Economic Impacts of Game and Veterinary Fencing in Africa with Particular Reference to the Great Limpopo and Kavango–Zambezi Transfrontier Conservation Areas* (eds K. Ferguson & J. Hanks), pp. 121–127. Mammal Research Institute, Pretoria, South Africa.
- HANSEN, M.C., DEFRIES, R.S., TOWNSEND, J.R.G., CARROLL, M., DIMICELI, C. & SOHLBERG, R.A. (2003) Global percent tree cover at a spatial resolution of 500 meters: first results of the MODIS vegetation continuous fields algorithm. *Earth Interactions*, 7, 1–15.

- HARRIS, G., THIRGOOD, S., HOPCRAFT, G., CROMSIGT, J.P.G.M. & BERGER, J. (2009) Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research*, 7, 55–76.
- JOHNSON, S. (2010) Chapter 3: Tourism and heritage development. In *Makgadikgadi Framework Management Plan*. Centre for Applied Research and Department of Environmental Affairs, Government of Botswana, Gaborone, Botswana.
- JONES, B.T.B., DAVIS, A., DIEZ, L. & DIGGLE, R.W. (2012) Community-based natural resource management (CBNRM) and reducing poverty in Namibia. In *Biodiversity Conservation and Poverty Alleviation: Exploring the Evidence for a Link* (eds D. Roe, J. Elliott, C. Sandbrook & M. Walpole), pp. 191–205. John Wiley & Sons, Ltd., London, UK.
- KAZA TFCA (2013) Kavango–Zambezi Transfrontier Conservation Area. <http://www.kavangozambezi.org> [accessed 5 April 2014].
- LINDSAY, K., MUIR, A. & ROBSON, K. (1998) *Pilot Botswana Range Inventory and Management Project*. Ministry of Agriculture, Gaborone, Botswana.
- LINDSEY, P.A., ROULET, P.A. & ROMANACH, S.S. (2007) Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation*, 134, 455–469.
- MBAIWA, J.E. & MBAIWA, O.I. (2006) The effects of veterinary fences on wildlife populations in the Okavango Delta, Botswana. *International Journal of Wilderness*, 12, 17–41.
- MORALES, J.M., HAYDON, D.T., FRAIR, J., HOLSINER, K.E. & FRYXELL, J.M. (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, 85, 2436–2445.
- NORTON-GRIFFITHS, M. (1978) *Counting Animals*. African Wildlife Leadership Foundation, Nairobi, Kenya.
- PERKINS, J. (2010) Fences and landscape scale degradation. In *Fencing Impacts: A Review of the Environmental, Social and Economic Impacts of Game and Veterinary Fencing in Africa with Particular Reference to the Great Limpopo and Kavango-Zambezi Transfrontier Conservation Areas* (eds K. Ferguson & J. Hanks), pp. 108–120. Mammal Research Institute, Pretoria, South Africa.
- PETTORELLI, N., VIK, J.O., MYSTERUD, A., GAILLARD, J.-M., TUCKER, C.J. & STENSETH, N.C. (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, 20, 503–510.
- POWER, R.J. & COMPION, R.X.S. (2009) Lion predation on elephants in the Savuti, Chobe National Park, Botswana. *African Zoology*, 44, 36–44.
- R DEVELOPMENT CORE TEAM (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- SAWYER, H. & KAUFFMAN, M.J. (2011) Stopover ecology of a migratory ungulate. *Journal of Animal Ecology*, 80, 1078–1087.
- SIANGA, K., BONYONGO, M.C. & FYNN, R. (2013) *Seasonal Movements of Plains Zebra Equus burchelli in Savuti-Mababe-Linyanti (SLE) Ecosystem in Northern Botswana*. University of Botswana, Gaborone, Botswana.
- SINCLAIR, A.R.E. & NORTON-GRIFFITHS, M. (eds) (1979) *Serengeti: Dynamics of an Ecosystem*. University of Chicago Press, Chicago, USA.
- VANDEWALLE, M.E. (2000) *Movement of Zebra and Wildebeest in Relation to Environmental Factors in Northern Botswana*. University of the Witwatersrand, Johannesburg, South Africa.
- WILCOVE, D.S. (2009) *No Way Home: The Decline of the World's Great Animal Migrations*. Island Press, Washington, DC, USA.
- WILCOVE, D.S. & WIKELSKI, M. (2008) Going, going, gone: is animal migration disappearing? *PLoS Biology*, 6(7), e188.
- WILLIAMSON, D. & WILLIAMSON, J. (1984) Botswana's fences and the depletion of Kalahari wildlife. *Oryx*, 18, 218–222.

Biographical sketches

ROBIN NAIDOO is a conservation scientist who has worked in Africa on various issues for over a decade. MIKE CHASE is an expert on elephant ecology and conservation. PIET BEYTELL is a conservation biologist with the Namibian government. PIERRE DU PREEZ is Namibia's chief conservation biologist and runs the country's rhino recovery programme. KELLY LANDEN is based in Botswana and helps run Elephants Without Borders. GREG STUART-HILL has decades of experience in community-based conservation and rangeland management in southern Africa. RUSSELL TAYLOR is a regional expert in the conservation of large wildlife and natural resources management.