




Cueing on distant conditions before migrating does not prevent false starts: a case study with African elephants

Anne Pandraud¹ · Adrian M. Shrader¹ · Arnold Tshipa^{2,3} · Nobesuthu Ngwenya⁴ · Simon Chamaillé-Jammes^{1,5,6} 

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Abstract

Migratory animals often use environmental cues to time their seasonal migrations. Local conditions may, however, differ from distant ones, and current conditions may poorly predict future conditions. This may be particularly true for early wet season conditions in tropical systems, as storms and associated rainfall events are generally not predictable at the scale of weeks or days and are heterogeneously distributed even at the scale of a few kilometres. How migratory animals cope with such challenges, and the consequences they may have, remain poorly known. We used time-to-event models based on GPS data from 19 African elephant herds from Hwange National Park (Zimbabwe) to study the effect of local and distant rainfall events on the elephants' decision to initiate their wet season migration. Elephants relied more on distant rainfall events occurring along the future migration route than on local events when initiating their migration. Such ability to use distant cues does not, however, ensure an immediate migration success. In over 30% of the cases, the elephants came back to their dry season range, sometimes after having travelled > 80% of the expected migration distance. This happened particularly when there was little additional rain falling during the migration. All elephants successfully migrated later in the season. Our study improves the understanding of the migratory ecology of elephants. More broadly, it raises questions about the reliability of rainfall as a migratory cue in tropical systems, and shed light on one of its potential consequences, the poorly quantified phenomenon of migration *false starts*.

Keywords Climate · Migration · Movement · Sensory ecology · Time-to-event model

Introduction

Migration is a spectacular and well-studied natural phenomenon, key to the conservation of many species (Horns and Şekercioğlu 2018; Kauffman et al. 2021) and with sometimes large ecosystem consequences (Bauer and Hoyer 2014). With migrations, animals most often track food resources in space and time, integrating aspects such as the energetic needs of reproduction, the potential for competition, and the risk of predation into their decision-making process (Cresswell et al. 2011; Avgar et al. 2014; Somveille et al. 2018). Overall, migration should be seen as an adaptive behavioural strategy allowing individuals to best exploit large-scale environmental heterogeneities (Avgar et al. 2014; Cresswell et al. 2011).

Migratory animals use environmental cues to time their seasonal movements (Winkler et al. 2014). Depending on species, factors such as climate and weather events (e.g. temperature, snowfall), photoperiod, wind regimes, or plant phenology can act as cues to trigger migration. For example,

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✉ Simon Chamaillé-Jammes
simon.chamaill@cefe.cnrs.fr

¹ Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Pretoria, South Africa

² Wilderness Safaris, P.O. Box 288, Victoria Falls, Zimbabwe

³ Department of Forest Resources and Wildlife Management, National University of Science and Technology, Ascot, Bulawayo, Zimbabwe

⁴ Zimbabwe Parks and Wildlife Management Authority, Scientific Services, Causeway, P.O. Box CY140, Harare, Zimbabwe

⁵ CEFE, CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France

⁶ LTSER France, Zone Atelier Hwange, Hwange National Park, Bag 62, Dete, Zimbabwe

in northern temperate systems, many ungulates are said to “surf the green wave”, tracking peak forage productivity as it shifts northward (Bischof et al. 2012; Merkle et al. 2016; Aikens et al. 2017). Other species, however, migrate earlier as they track snowmelt (Laforge et al. 2021). In savanna environments, vegetation growth is associated with rainfall and, accordingly, many migrations towards wet season ranges occur at the beginning of the rainy season (Holdo et al. 2009; Bartlam-Brooks et al. 2013; Tshipa et al. 2017).

Species are expected to have evolved to use the most reliable cues allowing them to predict when to migrate. Nevertheless, not all cues are reliable and predictable. The change in day length is a reliable cue of seasonal change as it is invariant from 1 year to another. Temperatures, however, are less reliable, especially under the current conditions of global climate change, but can be used in association with photoperiod to set the timing of migration (Bradshaw and Holzapfel 2008). Rainfall can act as a key migratory cue, for instance in savannas, but rainfall events tend to be stochastic. Specifically, in semi-arid climates, rainfall events are poorly predictable at the scale of weeks or days, and are generally heterogeneous even at the scale of a few kilometres (Whitford and Duval 2019). Hence, local rainfall events may not be a reliable cue of the occurrence and amount of rainfall in distant areas. As such, migratory animals must be flexible to cope with rainfall unpredictability (Winkler et al. 2014). Nevertheless, we have a poor understanding of how animals may use rainfall as a cue for migration timing, and the consequences it can have on migration patterns.

African elephants (*Loxodonta africana*) are a good species with which to understand the challenges associated with rainfall-triggered migrations. As a water-dependent species (Chamaillé-Jammes et al. 2013; Loarie et al. 2009), elephants generally drink every day or two and, therefore, need to settle within 10–20 km of permanent water sources during the dry season (Chamaillé-Jammes et al. 2013). This leads elephants to display a diversity of movement strategies at the annual time scale, with some residing year round near permanent water sources, while others seasonally migrate short to long distances (e.g. Birkett et al. 2012; Garstang et al. 2014; Leggett et al. 2003). Such seasonal migrations are observed in many elephant populations (e.g. Purdon et al. 2018; Tshipa et al. 2017). There has, however, been debate about what cue elephants actually use to initiate these migrations. In particular, suggestions have been made that elephants could be cueing on distant rainfall events, perceived through the hearing of storms or the smell of petrichor (i.e. ‘the smell of rain’, Garstang 2015). Wood et al. (2021) found that elephants could indeed detect some of the key compounds making up this odour (i.e. geosmin, 2-methylisoborneol), but this was investigated only with the compounds in the immediate vicinity of the elephants. A study by Garstang et al. (2014) suggested that elephants could detect rainfall

over large distances, but they did not conduct formal statistical analysis that linked elephant movement decisions to rainfall events. Finally, we do not yet know how elephants might react having started migrating only to find that the rainfall event triggering their migration was an unreliable indicator of the conditions that the elephants met en route.

Here, we studied whether local or distant rainfall events were good predictors of the start of elephant migration in a semi-arid protected area of Zimbabwe. We also focussed on what we call false starts, namely when individuals, after having initiated a migration, reverse direction and return to their dry season range. Such a pattern has been anecdotally reported in several species but seems largely overlooked in the scientific literature on migration. This phenomenon was first mentioned by Pennycuik (1975) who observed that during their migration, some wildebeest (*Connochaetes taurinus*) in Serengeti went back to previously visited areas if the environmental conditions were not optimal (i.e. drought events). In addition, Bartlam-brooks et al. (2013) described the reversal of migration direction in some zebras (*Equus quagga*) when conditions were unusually bad. We hypothesised that the main factor causing false starts are the conditions met during the early stages of migration, and we tested this hypothesis on elephants. In this study, we investigated (1) the role of rainfall in triggering elephant migrations, (2) whether elephants use local or distant cues to initiate migrations, and (3) whether false starts may be caused by local rainfall events not ensuring that the conditions along the route are good during migration.

Methods

Study area

Hwange National Park (hereinafter HNP) covers approximately 15,000 km² of semi-arid dystrophic vegetation near the north-west border of Zimbabwe (19°00' S, 26°30' E. Figure 1). Annual rainfall averages is 600 mm but is highly variable (coefficient of variation ~30%) (Chamaillé-Jammes et al. 2006). As commonly observed in semi-arid systems, the beginning of the wet season is also variable from year to year, usually starting in October or November with erratic thunderstorms. Rainfall events are then commonly observed until May (Fig. 1). More information on rainfall patterns and drivers in southern Africa can be found in Nicholson et al. (2018). In the course of the hot dry season (September–October), most waterholes dry up (Chamaillé-Jammes et al. 2007a) and only artificial waterholes, mostly distributed in the northern and eastern sections of the park, maintain water availability (Chamaillé-Jammes et al. 2007a). Seasonal rivers do exist in the northernmost and southernmost sections of the park, and elephants are known to dig up for

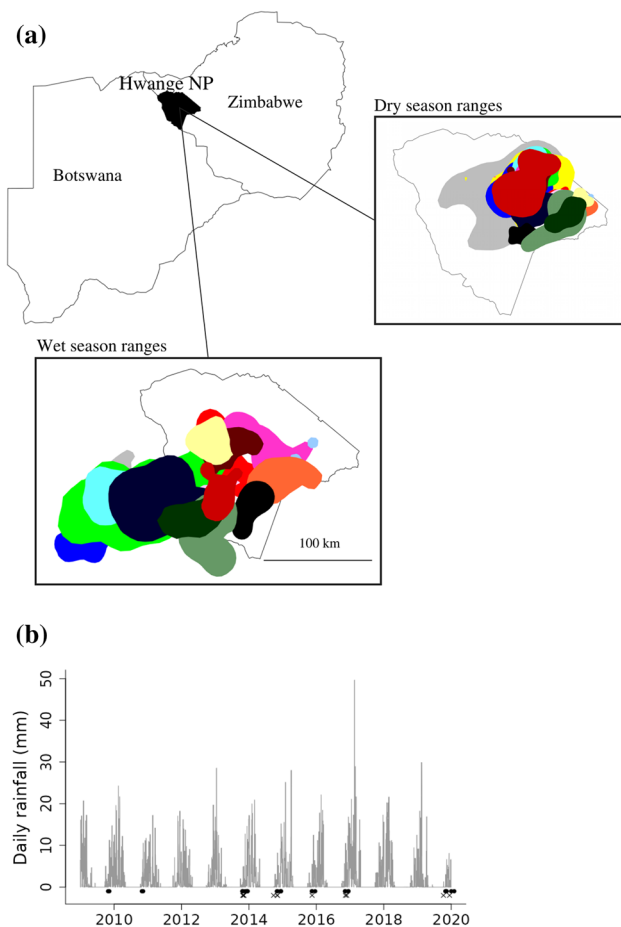


Fig. 1 **a** Map of Hwange National Park. The coloured shapes represent the dry and wet season home ranges of each collared African elephant, **b** dates of elephant departures from their dry season range. The black dots represent the migration date of each elephant, and the crosses represent the date of the false departures. Bars show the average daily precipitations recorded within the larger study area

water in dry riverbeds. The elephants studied here, however, remained in the area of HNP where no rivers are found, and thus had to rely on artificial waterholes for water in the dry season.

The elephant population of HNP is abundant and has been fluctuating between 30,000 and 45,000 elephants for the last 3 decades (Chamaillé-Jammes et al. 2008). During the dry season, these individuals converge in the northeastern section of the park around the available artificial water points (Chamaillé-Jammes et al. 2007c). However, census data have suggested a strong seasonal redistribution of herds during the wet season (Chamaillé-Jammes et al. 2009), and a phenomenon of partial migration (i.e. only some herds migrate) was recently confirmed by GPS tracking (Tshipa et al. 2017). At the beginning of the wet season, some herds undertake large-scale movements that follow an east–west gradient, with around 20% of these herds going as far as

Botswana (Tshipa et al. 2017). Elephants that migrate are generally faithful to their seasonal range, as consecutive dry or consecutive wet seasons range overlap by 70% on average and have centroids often separated by no more than 20 km (Tshipa et al. 2017). The history of this migration is unknown, but the most likely scenario is that elephants had been migrating from the western area of HNP to the Gwaii river 50 km east of HNP before artificial waterholes were created in the twentieth century. Elephants would have then stopped their migration earlier, as the park now provided water and protection from people (Tshipa et al. 2017).

Rainfall data

Only a handful of rain gauges exist in HNP, mostly in the eastern and northern sections, and they often have unreliable data when extrapolated to the whole park. We, therefore, could not obtain reliable ground-based rainfall data across the park. We considered using the Tropical Rainfall Measurement Mission (TRMM) data, but the resolution of 0.25° (~ 25 km) was too coarse for the study. We, therefore, extracted data from the Climate Hazard group Infrared Precipitation with Stations (CHIRPS) database and used the daily estimated rainfall data at a spatial resolution of 0.05° , approximately 5 km (Funk et al. 2015). CHIRPS estimates result from an interpolation of ground data with remote sensed data on cold cloud durations. CHIRPS data are now commonly used in ecology (e.g. Ngoma et al. 2021; Shukla et al. 2014; Workie and Debella 2018). Previous studies have ground-truthed CHIRPS data and found good correlations with data from the local stations (e.g. Dinku et al. 2018). We confirmed that this was the case also in HNP. We assessed the correlation between CHIRPS data and data collected by one weather station located in the north-east of HNP (over the 2010–2016 period) and found a high correlation both at the monthly (Pearson's $r=0.86$) and bi-weekly ($r=0.8$) time scales.

GPS tracking data

Between 2009 and 2019, GPS collars were deployed on 38 adult females each belonging to different herds. Captures were conducted by an experienced veterinarian team, under permits #17/2009, 01/2010, 05/2011, 15/2012, 08/2013, 59/2014, 68/2015, 25/2018, 18/2019 from the Zimbabwe Parks and Wildlife Management Authority. As elephant herds move together, we assumed that the movements of a collared female represented the movements of the whole herd. The collars were deployed in 2009 ($n=10$), in 2012 ($n=13$), in 2014 ($n=9$) and in 2019 ($n=6$), with varying GPS fix rate between years. For the current study, we built a homogeneous dataset by keeping one location per day, which was the lowest fix rate within the original data

and was deemed sufficient to analyse migration timing. As we focussed only on migratory elephants, we arbitrarily restricted our data analysis to the 19 individuals (i.e. herds) whose 90% dry season (September/October) home ranges (estimated using kernel-based approach), did not overlap with their 90% wet season (February/March) home range by more than 5%.

Migration timing and false starts

We determined the timing of migrations using a trajectory segmentation procedure. We used the segmentation-clustering of x , y coordinates approach proposed by Patin et al. (2020) to identify trajectory segments that were in dry and wet season ranges, and intermediate migration routes. A typical output is presented in Online Resource 1. We used the implementation proposed in the *segclust2d* package for R (Patin et al. 2019). We ran the algorithm on the locations collected between the 1st September of 1 year to the 1st April of the following year to cover the end of the dry season and the wet season. We allowed for a maximum of 20 segments, which was well above the actual number of segments retained by the model, and therefore, not constraining. We also enforced a minimum segment length of five locations (i.e. 5 days) to prevent over-segmenting. For each elephant herd, we first identified the dry and wet season ranges. The dry season range comprised locations found in the cluster of locations used at the beginning of the time-series (i.e. in the dry season). The wet season range was usually less well defined. Since the herds had extended wet home ranges, we found that, for most of them, the locations collected during the wet season were divided into different clusters (Online Resource 1). As we limited our study to the wet season East–West movements, we selected the most westerly cluster to represent the wet season home range. This choice is only relevant to one aspect of our study, the percentage of migration distance covered during false starts.

Once seasonal ranges had been identified, we found the date at which an elephant herd left their dry season range for the first time, defined as first day of the segment of locations immediately following the first segment of locations, which by definition is always the dry season range. We recorded whether the elephant came back (i.e. made a false start) or continued (i.e. made a direct migration) before reaching its wet season range. When a false start occurred, we recorded how long it took for the herd to reach the location furthest from the dry season range, the distance between this location and the dry season range, and the overall duration of this false start (out and back from the edge of the dry season range). In only one instance did we observe two false starts by the same herd in the same season, and as we could not analyse this statistically, we only considered the first false start in our analyses.

Statistical analyses

We first investigated whether the timing of the first departure of the elephant herds from their dry season range (either a direct migration or a false start) was triggered by local or distant rainfall events. We did this by fitting time-to-event (TTE) models, which are now commonly used in studies of migration timing (e.g. Fieberg and Delgiudice 2008; Rivrud et al. 2016). These models estimate to what extent predictors of interest affect the rate (the ‘hazard’, in the terminology of survival models to which TTE models relate) at which an event (here, leaving the dry season range) occurs. We fitted competing models that differed by the predictor used in the model. Model 0 was a null model with no predictor, model 1 used the local rainfall of the day as predictor, whereas model 2 used the distant rainfall of the same day. Local rainfall at day t was the average rainfall recorded during day t at the locations that were within the 90% minimum convex polygon (MCP) of all locations used by elephants during the 2 weeks prior day t ($t-15$ to t). We used a MCP approach because the number of locations within a 2-week period was too low to use kernel-based methods. Overall, local rainfall was thus defined as the average rainfall over the area used recently by elephants. By contrast, distant rainfall at day t was the average rainfall recorded during day t at all locations that were within the 90% MCP of all locations outside the dry season ranges and used 2 weeks in the future (t to $t+15$). Distant rainfall was thus defined as the average rainfall over the area used by elephants in the future, and located outside their dry season home ranges. The reasoning here was to test whether, when the herds left their dry season range, it had rained in areas where they would travel through after the departure, and whether the herds would have, therefore, moved towards distant rainfall. We chose a period of 2 weeks, because a previous study (Cushman et al. 2005) demonstrated that there was a time lag of between 15 and 30 days in the response of the herd movement to rainfall. We confirmed that our analyses were not overly sensitive to the choice of the definition of local and distant areas by also fitting all models with data based on 50% MCP. Results did not differ and are, therefore, not presented here.

To test whether the herds would rely more on accumulation of rainfall, which likely better predict vegetation and water conditions than single rainfall events, we fitted two additional models. Model 3 used the accumulated local rainfall over the last 2 weeks as predictor, whereas model 4 used the accumulated distant rainfall over the last 2 weeks. We compared the predictive ability of models 1–4 using the Akaike Information Criterion corrected for small sample size (AICc) and the concordance index (Harrell et al. 1982; Schmid et al. 2016; here, it measures the proportion of time that one departure predicted to occur before another one actually did occur earlier). TTE models require defining a

start date for the analysis, although inference is not sensitive to this choice as long as the event of interest never occurs earlier. We, therefore, selected the 1st of September, as no herd had ever left its dry season range before this date. Following Rivrud et al. (2016), we fitted TTE models as semi-parametric Cox proportional hazard models with time-dependent predictor using the survival package for R (Therneau et al. 2021). We checked that the data respond to the underlying assumption of proportional hazards using the test proposed by Grambsch and Therneau (1994).

We also considered parametric exponential or Weibull models. Weibull models were always better (lower AICc) than exponential models. Results from Cox or Weibull models did not differ qualitatively, and results from more robust Cox models are presented in the main text. Results from Weibull models can be found in Online Resource 3.

We then investigated if the conditions found en route could influence whether the herds made a direct migration or a false start. In particular, we assumed that failure to encounter improved conditions during the trip could lead to the decision to turn back and thus result in a false start. Therefore, we studied whether, during a false start, the herds travelled through places whose conditions improved less than during direct migrations. We estimated the improvement in conditions along the trip using the slope of the regression between 2-week rainfall at visited locations (within a 10 km buffer, to avoid relying on only one CHIRPS pixel), and time. The slope was calculated over the time from the departure of the dry season range to the location furthest away from it for false starts, and over the first 18 days, after dry season range departure for direct migrations, as this was the maximum duration for false starts. We statistically tested our hypothesis using a logistic regression model, with false starts (coded 1) or direct migrations (coded 0) as outcome, and the slope of the 2-week rainfall vs time as a predictor. We initially used mixed-effect logistic regression to account for non-independence of repeated observations across animals, as some were monitored for several years. However, inclusion

of herd identity as random effects led to singular fit, or random effect variance, estimated at zero depending on implementations, and we, therefore, ultimately fitted the model as a fixed-effect-only generalised linear model.

Results

Timing and drivers of first departures from dry season ranges

Overall, the herds initiated their departure at the onset of the rainy season (Fig. 1). As expected, TTE models showed that rainfall was a clear driver of migration timing (Table 1), as models with either local or distant rainfall (i.e. model 1 and 2, respectively), were much better than the null model (model 0). Local and distant rainfall were correlated (Pearson's $r=0.77$), but the comparisons of time-to-event models, however, revealed that distant rainfall was a better predictor of the departure than local rainfall (Table 1). Specifically, model 2 had the lowest AICc and the greatest concordance of all models. The rate at which elephants left their dry season range, estimated using the hazard ratio between a day with a specific distant rainfall amount and a day without distant rainfall, increased as distant rainfall increased (see coefficient in Table 1 and Fig. 2). Although there was some clear uncertainty in the size of the effect of rainfall events, especially large ones (Fig. 2), it should be noted that the effect of these events was clearly large, as shown by the large value of hazard ratio even at the lower limit of the 95% confidence intervals (Fig. 2). Generally, we note that model 1, which used local rainfall, and model 4, which used accumulated distant rainfall, were not competitive against model 2, but were still better than the null model and had some predictive power (Table 1). This was not the case of model 3, which only used accumulated local rainfall as predictor (Table 1). See Online Resource 4 for a visual comparison of all models.

Table 1 Summary statistics of time-to-event models with event being the first departure from the dry season range

Model #	Model predictor	Coefficient	AICc	Concordance
2	Distant rain	0.31 [0.14 to 0.48]	124.87	0.714 [0.60–0.83]
1	Local rain	0.19 [0.05 to 0.33]	131.70	0.587 [0.49–0.69]
4	Acc distant rain	0.04 [0.00 to 0.09]	134.29	0.653 [0.53–0.78]
0	Null		136.38	
3	Acc local rain	0.01 [– 0.01 to 0.04]	137.67	0.544 [0.40–0.69]

Models differ by their predictor (model 0, no predictor; model 1, local rainfall of the day; model 2, distant rainfall of the day; model 3, local rainfall accumulated over the last 2 weeks; model 4, distant rainfall accumulated over the last 2 weeks). For each model, the coefficient associated with the predictor, the Akaike Information Criterion corrected for small sample size (AICc) and the concordance index are shown. Numbers between brackets are 95% confidence intervals. Models are ordered by increasing AICc value, with the best model identified in bold characters

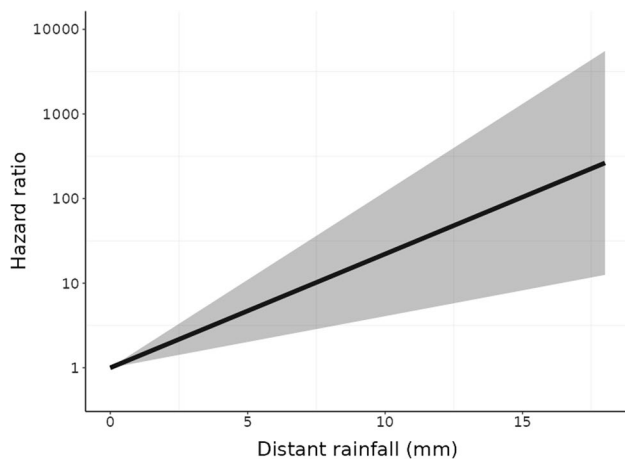


Fig. 2 Influence of distant rainfall events on the rate at which elephants leave the dry season range for the first time within a season, estimated by the hazard ratio (and its 95% confidence interval in grey, and displayed on a log scale) between a day with a specific distant rainfall amount and a day without distant rainfall. Distant rainfall is estimated over the 90% MCP of locations used during the 2 weeks after the elephant left its dry season range. See text for details

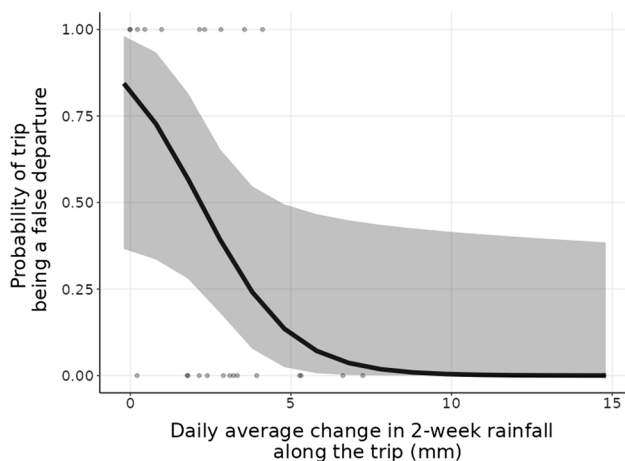


Fig. 3 Probability of the first departure of elephants from dry season range to be a false start, in relation to the daily average change in 2-week rainfall of the places visited during the trip. The estimated curve and its 95% confidence band is shown, as well as data points (false starts for dots at $y=1$, direct migrations for dots at $y=0$)

False start vs direct migration

When the herds left their dry season range for the first time at the start of the wet season, they always travelled towards places where it rained at least as much, and often more, than where they were coming from (Fig. 3). In other words, the daily average change in 2-week rainfall along places visited was always higher than zero. False starts were common, representing 37% ($n=11$) of these first departures from the dry season range. During the false starts,

the herds generally decided to turn around after only a few days (median = 6 days), although it occurred after 2 weeks in a few instances (Table 2). The median total duration of the false starts, including the time to travel back to the dry season range, was 21 days. The herds that made a false start tended to then follow the same route when migrating (Online Resource 2). They travelled between 17 and 63 km before turning around, representing between 22 and 92% of the distance between their dry season ranges and their wet season ranges (Table 2). Half (6 out of 11) of the elephant herds travelled > 50% of their migration distance during the false start, among them four herds walked for more than 80% of their migration distance (Table 2).

We found that the herds were less likely to make a false start when they kept moving towards places where it had rained more in the last 2 weeks than where they were previously (Fig. 3; estimate [95% CI] = -0.71 [-1.55 -0.13], $z = -2.0$, $P = 0.045$). Furthermore, when the daily average change of 2-week rainfall along the route used was above 5 mm per day, elephant herds almost never made a false start (Fig. 3).

Discussion

We have investigated the novel question of how rainfall could trigger migration in tropical ungulates, using the African elephant as a model species. Previous work has made clear that, as for many other species in tropical systems, departures from dry season ranges generally occur at the onset, rather than in the middle or the end, of the wet season (e.g. Bartlam-brooks et al. 2013; Holdo et al. 2009). This is also the case in the population studied here (Tshipa et al. 2017; this study). We, however, reveal some complexity in this apparently simple phenomenon. As suggested in previous work, but not statistically tested and still debated (Garstang et al. 2014; Kelley and Garstang 2013), we found that elephants may use information about distant rainfall to decide whether or not to initiate their migrations. We also show that, despite the use of such information and likely because of the spatial and temporal stochasticity of rainfall, elephants may face unsuitable conditions along their migration routes and revert back temporarily to their dry season ranges. This leads to false starts, a phenomenon that is not widely recognised in the literature, although being anecdotally noted by migration researchers (Pennycuik 1975; Bartlam-brooks et al. 2013). We discuss below how these results enrich our understanding of migration ecology.

It is generally considered that cues used by animals to determine whether it is time to leave are assessed locally, even if they are used as proxies of distant conditions (e.g. Fryxell and Sinclair 1988; Birkett et al. 2012; Bischof et al. 2012; Bartlam-brooks et al. 2013). This explains the practice

Table 2 Information related to false starts

False start ID (HERDID_YEARID)	Duration from the start of false start to the turn-around point (days)	Duration from the turn-around point to the end of the false start (days)	Maximum distance travelled during the false start before the turn-around point (km)	Distance that the elephants would have travelled if they had migrated (km)	Proportion of the migration travelled during false start (%)
H13_2016_first	2	3	23	102	22
H9_2013	4	4	35	38	92
H15_2019	5	1	17	50	34
H5_2014	5	25	44	73	60
H8_2013	6	2	20	38	53
H10_2013	6	16	63	74	85
H3_2014	6	22	27	86	31
H17_2019	14	7	40	86	46
H4_2014	14	18	60	67	89
H13_2015	18	9	47	59	80

The table reports the duration from the start of the false start to the turn-around point, the duration from the turn-around point to the end of the false start of each elephant herd, the distance travelled by each elephant herd during the false start and the proportion of the migration distance they travelled during their false start

of ecologists to extract environmental variables where the animal is when investigating environmental drivers of migration (e.g. Bastille-Rousseau et al. 2019). In their review on cues and strategies of migratory animals, Winkler et al. (2014) reflect this view. This, however, suggests that if animals are able to access direct information about distant conditions, and they should use it and timing should be better explained by distant than by local conditions. This is what we found here with elephants, a species which is believed to have the sensory capacity to hear or smell thunderstorms and rain tens to hundreds of kilometres away (Garstang 2015). Our method did not allow us to define how far elephants may be able to detect distant rainfall events, as we cannot know if they respond to rainfall events located in the closest pixels or the furthest ones.

To the best of our knowledge, experimental demonstrations of such capacity, or of long-range detection, are, however, lacking, which make studies like ours investigating patterns of movement in relation to distant environmental changes valuable. We show that distant conditions better predict migration timing, suggesting that elephants do indeed access, and respond to, information about rainfall distant events. This calls for future studies to both check the generality of our findings, as well as to clarify the sensory mechanisms at play. One possibility is that elephants may use visual cues to detect distant rainstorms (e.g. dark skies, falling rain). African elephants are considered to have reasonable eyesight, but it is best within c.a. 5 m (i.e. the distance they can reach with their trunk; Stone and Halasz 1989; Pettigrew et al. 2010). This makes sense as this is the distance within which they make small-scale foraging decisions. Yet, African elephants have a horizontal streak

of high ganglion cell density within their eyes, which likely allows them to scan the horizon for predators and conspecifics (Stone and Halasz 1989; Pettigrew et al. 2010). However, the extent to which they would be able to visually determine distant rainfall events is unknown. A second possibility is that the elephants were able to detect the distant rainfall events via the infrasound generated by thunder (Garstang 2015). While these infrasounds can travel great distances, they also happen during dry thunderstorms (i.e. thunderstorms that generate lighting but with very little rain reaching the ground; Avery 1993; Rorig et al. 2007). As such, the infrasounds of thunder may not always be a reliable indicator of rainfall. We have very recently demonstrated that elephants have the ability to smell natural water sources but also geosmin and 2-methylisoborneol, key compounds of petrichor, the earthy ‘smell of rain’ that is noticeable by humans during rains occurring after dry spells (Wood et al. 2021). It has been regularly hypothesised that this odour could be used by ungulates like wildebeest, camels, or elephants to decide where to travel (Campbell 1981; Simons 2003; Garstang et al. 2014), but this has not yet been investigated. As olfaction seems to be central to elephants’ lives (Schmitt et al. 2018, 2019; McArthur et al. 2019), we trust that this hypothesis needs to be investigated further. Given their persistence, odours are good candidates of cues allowing to gather information on distant conditions. The use of odours during navigation is well established in some fish and bird species (e.g. Tosi and Sola 1993—who suggest a role for geosmin in eel migrations), but their role in actually triggering migration departure in mammals remains less clear, and is certainly unknown in ungulate migrations.

Nevertheless, it is possible that elephants utilise a range of visual, auditory, and olfactory cues to detect distant rainfall events.

Irrespective of the trigger, migratory elephants left their dry season range at some point during the wet season but not all conducted their migration in one event. We found that what we termed false start occurred ~40% of the time, and that these false starts were more likely to occur when elephants travelled through places where it did not rain more than where they left or travel through. Although we did not have ground-based data describing environmental conditions, we tentatively suggest that our results support a scenario (build from field experience) that elephants that did a false start might have been travelling through places where the initial rains that triggered the departure were not followed by enough rains to replenish or maintain water in the natural ponds that elephants access every day or two (Chamaillé-Jammes et al. 2013). It is important to note that even small amounts of rain (< 10 mm) can dramatically increase the likelihood that elephants leave their dry season range (Fig. 2). Thus, elephants often start migrating when conditions are not yet different from the dry season conditions, with high evaporation rates and high temperatures. The weather of the following days is, therefore, critical to improve conditions along the migration route, which are areas that are avoided by elephants during the dry season because they lack available surface water. Early-season rainfall events are, however, highly unpredictable and heterogeneous, in space and time, and relying on early rainfall expose elephants to uncertainty about conditions that will be met en route. Elephants may bear costs associated with this strategy, at least in terms of time and energy spent travelling during false starts, as shown in our results.

To what extent these costs translate into reduced fitness is unknown, but one could envision that extra-travelling because of false start could particularly affect the survival of young elephants that need to keep up with the herd, and for weaned ones, that need to drink daily and forage by themselves along the way (Shrader et al. 2010). If fitness costs are significant, this would, however, question why elephants adopt this strategy of leaving early, rather than simply waiting until wet season conditions were well established across the whole park. One potential explanation is that elephants need to leave their dry season range, which is likely food-depleted and where competition at waterholes is high. HNP hosts a high abundance of elephants, reaching > 4 km² in the dry season over the sections of the park retaining permanent water (Chamaillé-Jammes et al. 2007a, b, c; Chamaillé-Jammes et al. 2009), and competition for forage in these sections is hypothesised to regulate the elephant population (Chamaillé-Jammes et al. 2008). Therefore, one could expect that some elephants take the chance to leave as soon as they detect that it has rained along their migration route. These

might be sub-dominant herds whose space use and foraging could be constrained by other herds (as observed by Wittemyer et al. 2007), and who would benefit most from reduced competition. This hypothesis is also consistent with the proposed role of dominance in explaining the phenomenon of partial migration (Chapman et al. 2011), a phenomenon that is observed in this population (Tshipa et al. 2017). One could speculate that sub-dominant herds migrate to escape competition, while dominant herds remain resident, benefiting from the local pulse of resource associated with the wet season without experiencing the costs of migration. Further studies are, however, required to test this hypothesis.

Ultimately, our study sheds new light on the migratory ecology of elephants. It also reveals intriguing aspects about the cues used. This leads to a new set of questions about the role of olfaction and the reliability of rainfall as a cue on which to initiate migration. Moreover, our results highlight the potential unavoidable consequences that basing migration on rainfall could have for migratory animals. In particular, we shed light on the concept of migration *false start*, which could help in revealing the reliability of cues that animals used, and be useful for comparative studies. All these are important in the context of a climate that is changing rapidly, leading to a drastic and rapid modification of rainfall dynamics (Nicholson et al. 2018, Douville et al. 2021, for Hwange NP see Chamaillé-Jammes et al. 2007b). We, therefore, call for further research on the flexibility of migratory animal strategies, in particular in rainfall-based tropical systems.

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Author contribution statement SCJ conceived the study. AT and SCJ collected the data. AP and SCJ analysed the data and wrote the initial draft manuscript. The other authors contributed ideas and edited drafts. All the authors agreed upon the publication of the final version.

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Availability of data and material Data are archived and can be visualised on the Movebank (movebank.org) platform [Study name: “African elephant (Migration—GIUM dataset) Chamaillé-Jammes Hwange NP”] and are available on reasonable request.

Code availability Not applicable.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

Ethics approval Ethics approval was not required for this study according to local legislation [Research Act 22/2001]. The study was approved by Zimbabwe Parks and Wildlife Management Authority under permits #17/2009, 01/2010, 05/2011, 15/2012, 08/2013, 59/2014, 68/2015, 25/2018, 18/2019.

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