


RESEARCH ARTICLE

Fruit bat migration matches green wave in seasonal landscapes

Edward Hurme^{1,2,3}  | Jakob Fahr^{1,3}  | Eidolon Monitoring Network⁴ |
 Bakwo Fils Eric-Moise⁵  | C. Tom Hash⁶  | M. Teague O'Mara^{1,7}  | Heidi Richter⁸ |
 Iroro Tanshi^{9,10}  | Paul W. Webala¹¹ | Natalie Weber^{1,2}  | Martin Wikelski^{1,2,3}  |
 Dina K. N. Dechmann^{1,2,3} 

¹Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, Germany; ²Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany; ³Department of Biology, University of Konstanz, Konstanz, Germany; ⁴Eidolon Monitoring Network, www.eidolonmonitoring.com; ⁵Department of Biological Sciences, Faculty of Sciences, University of Maroua, Maroua, Cameroon; ⁶ICRISAT Sahelian Center, Niamey, Niger; ⁷Southeastern Louisiana University, Hammond, LA, USA; ⁸Department of Biology, Bellevue College, Bellevue, WA, USA; ⁹Department of Biological Sciences, Texas Tech University, Lubbock, TX, USA; ¹⁰Department of Animal and Environmental Biology, University of Benin, Benin City, Nigeria and ¹¹Department of Forestry and Wildlife Management, Maasai Mara University, Narok, Kenya

Correspondence

Edward Hurme

Email: ehurme@ab.mpg.de

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Abstract

1. Migrating grazers and carnivores respond to seasonal changes in the environment and often match peaks in resource abundance. However, it is unclear whether and how frugivorous animals use phenological events to time migration, especially in the tropics.
2. The straw-coloured fruit bat *Eidolon helvum*, Africa's most gregarious fruit bat, forms large seasonal colonies throughout much of sub-Saharan Africa. We hypothesized that aggregations of *E. helvum* match the timing of their migration with phenologies of plant growth or precipitation.
3. Using monthly colony counts from across much of the species' range, we matched peak colony size to landscape phenologies and explored the variation among colonies matching the overall closest phenological event.
4. Peak colony size was closest to the peak instantaneous rate of green-up, and sites with closer temporal matching were associated with higher maximum greenness, short growing season and larger peak colony size. *Eidolon helvum* seem to time their migrations to move into highly seasonal landscapes to exploit short-lived explosions of food and may benefit from collective sensing to time migrations.
5. The link between rapid changes in colony size and phenological match may also imply potential collective sensing of the environment. Overall decreasing bat numbers along with various threats might cause this property of large colonies to be lost.
6. Remote sensing data, although, indirectly linked to fruiting events, can potentially be used to globally describe and predict the migration of frugivorous species in a changing world.

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KEYWORDS

Africa, colony counts, enhanced vegetation index, green-up, phenology, resource tracking, start of season

1 | INTRODUCTION

Migration is an adaptation to resource fluctuations, often in seasonal environments, in which animals travel to track nutritional benefits, find conditions beneficial for reproduction, or escape predators, diseases or competition (Alerstam et al., 2003; Dingle & Drake, 2007; Fleming & Eby, 2003; Jachowski & Singh, 2015). Many long-distance migrants are valuable ecosystem service providers (Convention on the Conservation of Migratory Species of Wild Animals, 2011) but are increasingly threatened due to human encroachment on critical habitat (Wilcove & Wikelski, 2008). Understanding the environmental drivers of migration and its timing across taxa is crucial to avoid Allee effects leading to the collapse of populations and the loss of the economically and ecologically valuable services they provide (Berdahl et al., 2016; Costanza et al., 1997).

Many species track resources during migration, such as elephants following precipitation-driven vegetation dynamics in the savanna landscape (Bohrer et al., 2014), ungulates wandering to optimize nutritional content of the grasses they eat (Bischof et al., 2012; Merkle et al., 2016) and migrating birds tracking vegetation dynamics or snowmelt across continents (Curk et al., 2020; Thorup et al., 2017). Flying animals like birds and bats can easily travel long distances and have the potential to match seasonal peaks in resources during migration particularly well. However, directly tracking long-distance migrants, especially small animals, is often difficult or impossible due to technological limitations. Light loggers and stable isotope analysis can infer migratory routes at coarse scales, but require either recapturing the animals or detailed isotopic maps (Lisovski et al., 2012; Ossa et al., 2012). Alternatively, records of species occurrence can be associated with environmental data to aid our understanding of the drivers of migration (Kelly et al., 2016; Laughlin et al., 2016).

Remote sensing measurements can reflect seasonal changes in landscape phenology that correlate with migration (Feng et al., 2013; Schwartz, 1998). For example, vegetation in many environments is strongly seasonal, which is detected from satellite imagery as the annual change of greenness. A season typically starts with a 'green-up' period in which plants begin to grow, followed by a peak in greenness. It is then terminated by the 'brown-down' in which plants defoliate or die (Huete et al., 2006; Saleska et al., 2007). The time period when the rate of plant growth is highest is often defined as the beginning of the season and is measured as the peak in the 'instantaneous rate of green-up' (IRG), the first derivative of greenness. On the ground, this is usually associated with the appearance of immature leaves and can provide nutritious forage for some herbivorous species (Bischof et al., 2012; Fryxell, 1991; Middleton et al., 2018). Peaks in IRG can move across a landscape over time, resulting in a 'green wave', typically moving

towards higher altitudes or higher latitudes in temperate areas (Schwartz, 1998).

Animals adapted to foraging at a specific stage in the green-up process would then follow this food availability, a phenomenon known as 'surfing the green wave' (forage-maturation hypothesis; Fryxell, 1991; Hebblewhite et al., 2008). Green wave surfing has been predominantly studied in temperate regions. Here, green-up typically follows snowmelt and warming. Grazers, such as large ungulates (Aikens et al., 2020; Bischof et al., 2012; Geremia et al., 2019; Merkle et al., 2016; Middleton et al., 2018) or birds (Kelly et al., 2016; Kölzsch et al., 2015; Shariatnajibadi et al., 2014; Si et al., 2015; van Wijk et al., 2012), directly feed on the resource being measured by the normalized difference vegetation index (NDVI), a common remote sensing measure of greenness, and its derivatives. In less seasonal, tropical regions, these patterns are less well understood (Abernathy et al., 2019; Adamescu et al., 2018; Chapman et al., 2018), and phenological surfing is likely uncommon or at least under-explored in frugivorous tropical species, whose food availability is only indirectly linked to greenness (Branco et al., 2019; Giles et al., 2016, 2018; Holdo et al., 2009). This may be because tropical phenologies are not as well studied (Abernathy et al., 2018), and the seasonality in the landscape is less pronounced (Feng et al., 2013).

Perhaps at least partly as a consequence of reduced intensity of seasonal changes, the migration of terrestrial animals in the tropics remains understudied. This is particularly true for bats, where, despite the large numbers of tropical species, migration is rare. However, in those species that do migrate, movement does appear to be resource driven and occurs along food resource gradients or between seasonally ephemeral resource patches (Fleming, 2018; Fleming et al., 1993; Giles et al., 2016; Thomas, 1983). For example, nectar-feeding bats migrate along 'nectar' corridors in Mexico (Burke et al., 2019). The earliest evidence for fruit bat migration comes from seasonal variations in Straw-coloured fruit bats *E. helvum* colonies across Africa (Bernard & Cumming, 1997; DeFrees & Wilson, 1988; Huggel-Wolf & Huggel-Wolf, 1965; Jones, 1972; Kingdon, 1974; Lang & Chapin, 1917; Thomas, 1983). The size of these seasonal colonies can range from thousands to millions of individuals to a few or none at other times of the year (DeFrees & Wilson, 1988; Hayman et al., 2012; Peel et al., 2013, 2017; Sørensen & Halberg, 2001; Webala et al., 2014). Only two other African fruit bat species (*Myonycteris leptodon* [previously *M. torquata*] and *Nanonycteris veldkampii*) have been suggested to migrate to date (Thomas, 1983). Like *E. helvum*, both of these much less gregarious fruit bat species seasonally move from the rainforest to the savanna woodlands (Thomas, 1983). However, long-term tracking has been limited due to the small size of all bat species. In *E. helvum*, migration has been confirmed by short-term satellite tracking (Richter & Cumming, 2008), stable isotope analysis (Ossa et al., 2012), and

indirectly through colony counts (data shown here) showing that these bats can travel at least 2,000km, although the route, timing and drivers of migration across the continent remain unclear.

Here we investigated whether this abundant tropical frugivore behaves similarly to temperate-zone grazers, matching seasonal aggregations with remote sensing measurements of phenological events. Thomas (1983) proposed that migratory fruit bats move to regions where the amplitude of seasonal resource surplus is greatest, and this could be determined by both the phenological response of plants to climatic patterns and the amount of resources consumed by resident fruit bats. In highly seasonal savanna environments, resident populations would be limited by plant resources during the dry season, hence leading to a resource landscape favourable for immigrating fruit bats during the wet season. At one location in the woody savanna of Zambia, *E. helvum* match their arrival and departure from a colony with the fruit and flowering phenologies in the region (Richter & Cumming, 2005). We monitored colony sizes at 17 sites across Africa over several years and hypothesized that timing of peak colony numbers will be associated with peaks in resource availability. Specifically, these peaks will be associated with vegetation phenology, such as greenness or precipitation. Finally, colonies may work as extended sensory networks, allowing for social information about upcoming food resources away from the current roosting site to be transmitted (Marshall, 1983; Ward & Zahavi, 1973). We thus also hypothesized that *E. helvum* integrate social information when deciding when and where to migrate and larger colonies should be better able to match peak vegetation phenology.

The results of this study are not only of scientific interest for the understanding of the evolution and mechanisms of migration, but also for the conservation of the species. *Eidolon helvum* is a keystone seed disperser which provides important cross-boundary ecosystem services. At the same time, it is increasingly under threat from

hunting, direct prosecution and deforestation. It is of urgent importance to understand their seasonal colony dynamics and drivers of migration at a continental scale (Abedi-Lartey et al., 2016; Fahr et al., 2015; Richter & Cumming, 2008; van Toor et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Colony Counts

Colonies of *Eidolon helvum* bats were counted by members of the Eidolon Monitoring Network (www.eidolonmonitoring.com) at 17 sites across Africa (Figure 1; Table S1). We did not require ethical approval or permits for colony counts. Most colonies were counted by observing the bats at their roost site and multiplying the average number of bats in a cluster, with the average number of clusters on a branch, the average number of occupied branches in a tree and the number of occupied trees at the roost site (Fahr et al., 2015; Hayman et al., 2012). For roosts that were inaccessible without disturbing the colony, observers would count passing bats during evening emergence and extrapolate their numbers by the area monitored (Sørensen & Halberg, 2001). We calculated the ratio of the colony size as the fraction of the maximum colony size for that site across a moving window of all counts within a year, before and after each count.

2.2 | Peak colony month

As fruiting and flowering typically have one annual peak in the tropics (Adamescu et al., 2018), we defined colony peaks as roughly annual as well. We used a simple peak finding algorithm, which detects

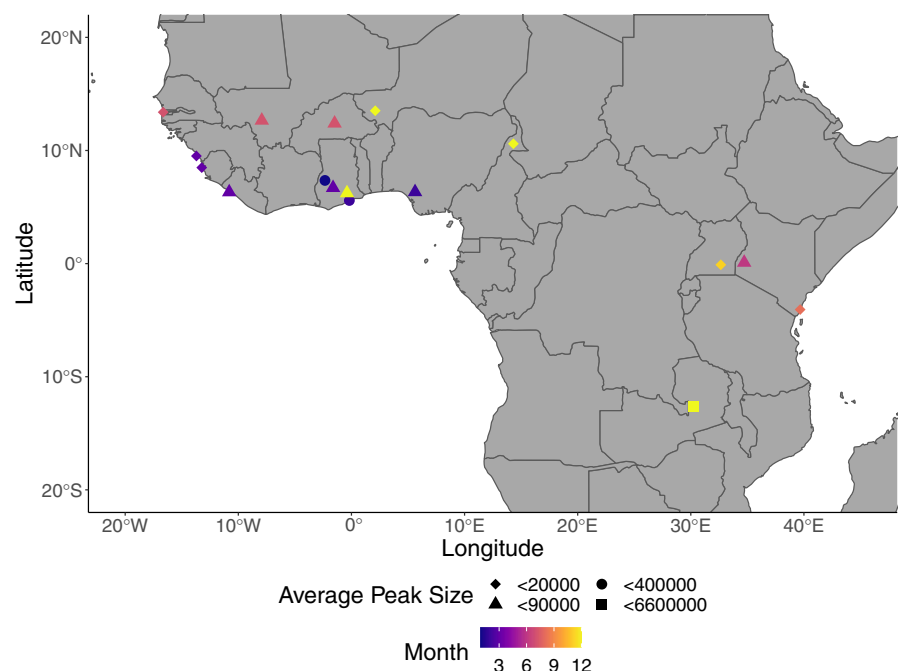


FIGURE 1 Monitored straw-coloured fruit bat colonies across Africa. Colour of the points indicates the average month of the year in which colonies reach their peak size and the shape of the points represents the average size of the colony at peak size

when counts transition from increasing to decreasing, to search for all potential peaks in the count data for each site. Additionally, we included counts in which the colony size ratio was at least 0.59, the third quartile of count ratios, to include isolated counts which would not be detected as a peak. This allowed us to include peaks in colony size even when we did not have counts before and after a peak as long as the peak size was consistent with the peak counts from surrounding years. For any peaks within 6 months of another peak, the smaller peak was removed to keep peaks roughly annual. For colonies that had multiple consecutive counts with a ratio of one, we took the middle count or just before the middle in cases with even numbers of counts. As colony counts were typically conducted monthly, we rounded all peak counts to the nearest start of the month. Given the high variability of many colony dynamics and occasional missing count data, the thresholds for time between peaks or minimum peak size were estimated to correspond with visual approximation of peak colony months. Because these thresholds are not strictly linked to independent predictions for peak colony timings, we also calculated more conservative estimates of peak colony month using a threshold of 10 months between colonies to determine whether a more restrictive set of peaks would also show similar environmental correlations.

2.3 | Environmental data

Phenological changes in the landscape were monitored using the enhanced vegetation index (EVI) and precipitation (PRP). EVI was designed to detect vegetation change in tropical regions from remote sensing images (Huete et al., 2002; Xiao et al., 2006). We extracted EVI (Terra-MODIS 250m 16-day VI product MOD13Q1.006) from Google Earth Engine using 'geeDataExtract' for all dates between 18 February 2000 and 18 December 2020 for locations of each monitored bat colony (Freidl et al., 2021; Schwantes & Nuñez, 2019). Values were extracted with a 67 km buffer around each colony location, matching the average distance bats flew from the roost during foraging (Calderón-Capote et al., 2020; Fahr et al., 2015; van Toor et al., 2019). Additionally, we filtered out low-quality pixels and fit a smoothing spline to the EVI measurements for each colony for all 20 years of data to adjust for any outliers or missing data (2% of points omitted). PRP was estimated for all colonies from 1 January 2000 to 1 December 2019 from Tropical Rainfall Measuring Mission (TRMM 3B43, resolution 0.25°), a merged microwave/IR precipitation estimate (in mm/month) accessed from Google Earth Engine using 'geeDataExtract' (Huffman et al., 2007; Schwantes & Nuñez, 2019). We estimated the instantaneous rate of green up (IRG), a measure of the seasonal rate of plant growth, by calculating the first derivative of the smoothed spline of EVI for each location (Bischof et al., 2012). Estimated instantaneous rate of precipitation (IRP) was also calculated as the first derivative of the smoothed spline of precipitation for each location.

We identified the annual maximum values of each phenological event (EVI, IRG, PRP and IRP), rounded to the nearest start of the

month and matched the values closest in time with the peak colony size months for each location (Figure 2). Peaks in IRG are associated with the start of the growing season. While onset of the wet season is typically measured by threshold estimates of precipitation (Ryan et al., 2017; Tadross et al., 2005), high variability in precipitation between sites required alternative estimates. Peaks in IRP indicate the highest rise in the rate of precipitation for each year, although further work is needed to determine if this metric is associated with the onset of the wet season more broadly. Average months of phenological estimates were generally consistent with phenologies derived from other datasets, although annual EVI and IRG peak months were statistically different for several locations (see Table S2).

2.4 | Statistical analyses

2.4.1 | Difference in timing

We explored the difference between peak colony month and month of peak EVI, IRG, PRP and IRP for all colony site years. First, we converted months into radians, by dividing the numerical month by 12 and multiplying by pi and then calculated the circular correlation using the function 'cor.circular' from the R package 'CIRCULAR' (Lund et al., 2017). Additionally, we calculated the months from peak colony size to peak phenological event for all colony sites years. We used a Wilcoxon signed-rank test to investigate whether months from peak colony size were significantly different between phenological events.

2.4.2 | Modelling

To understand the variation among colonies matching the overall closest phenological event, we used a linear mixed-effects model to predict the absolute value of the difference in months between peak colony date and peak phenological event. Due to small sample sizes for some colonies leading to model singularity, we used a Bayesian linear mixed-effect model from the R package 'BLME' (Chung et al., 2013), which adds a particular form of weak prior to avoid singularity. We considered landscape and colony size factors as predictor variables. We extracted the yearly maximum value of smoothed phenological events for each colony location (Figure 2). Additionally, we looked at the seasonality of phenological events by calculating its entropy, a metric that quantifies its concentration throughout the year (Feng et al., 2013). To calculate entropy first, we calculated the mean annual value for each location using $E = \sum_{m=1}^{12} r_m$ in which r_m was the average value for that month over all years. The relative entropy (D) with respect to the uniform distribution ($q_m = 1/12$ for all m) was then calculated using $D = \sum_{m=1}^{12} p_m \log_2(p_m/q_m)$. Entropy then provided a comparison to a uniform distribution signifying no seasonality. For example, low entropy occurs at a continuous level of greenness throughout the year with little variation for a location, while high entropy occurs when a location has greenness clustered

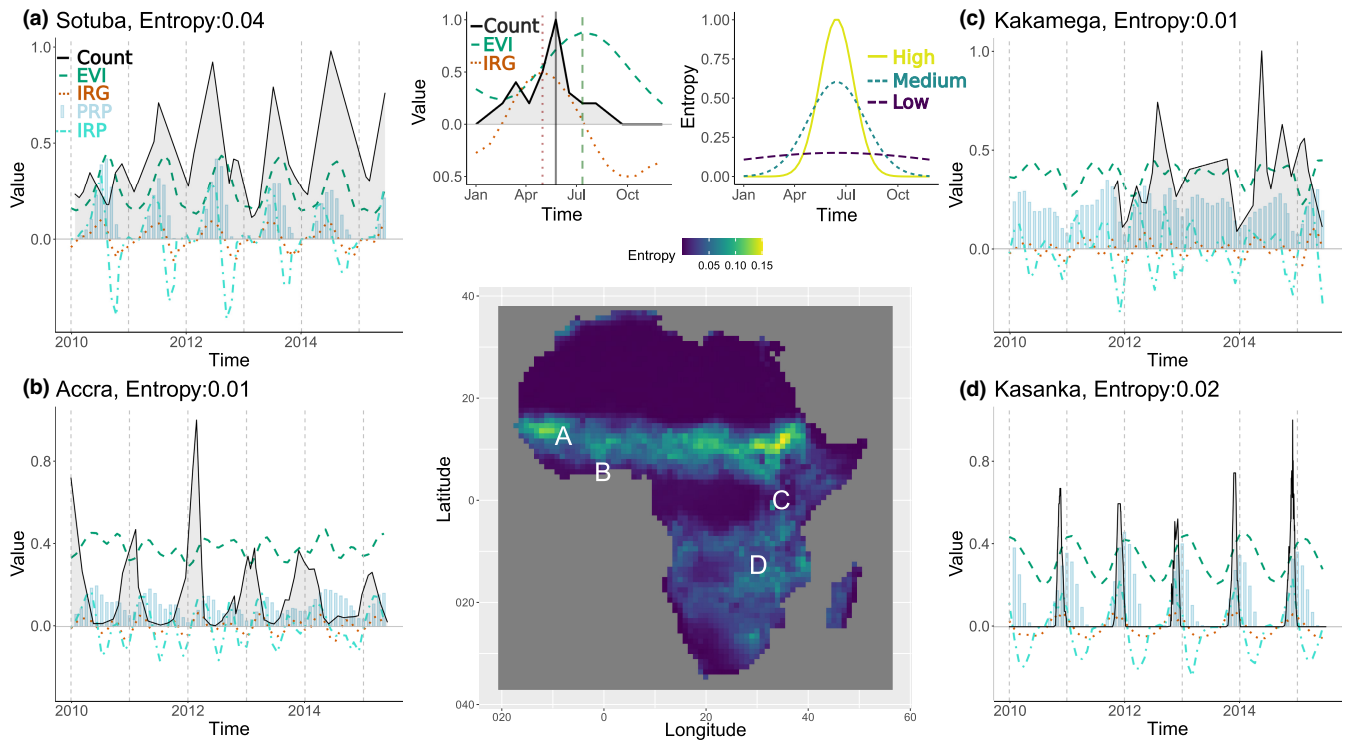


FIGURE 2 (a–d) Example of remote sensing values of enhanced vegetation index (EVI), instantaneous rate of green-up (IRG), precipitation (PRP), instantaneous rate of precipitation (IRP), and colony counts (shown in green dashes, red dots, blue columns, turquoise dot dashes, and black lines with grey area, respectively) for four monitored Eidolon colonies across Africa. These colonies were selected to show the variation in seasonality between sites, with sites such as Accra and Kasanka showing clear annual peaks while Sotuba and Kakamega sites are less regular. Middle figures demonstrate how peaks in remote sensing variables (EVI and IRG, shown in green and red, respectively) and colony size and entropy, the degree of temporal concentration of EVI, are estimated for each year. A map of the example colony locations with a 20-year average (2000–2019) EVI entropy across Africa is shown in the bottom centre

in a short period of the year (Figure 2). For colony size, we included the natural log transformation of peak colony size. All predictor variables were scaled and centred to aid comparison. To evaluate the predictive power of the models, we ran leave-one-colony-out cross-validation, in which we systematically omitted one colony and then used the resulting model to predict the match between peak phenological event and peak colony size for that model. R code for all analyses is available at <https://github.com/ehurme/EidolonGreenWave>.

3 | RESULTS

3.1 | Colony seasonality

We identified 65 colony size peaks across the 17 colonies. Four colonies (Accra, Ghana; Benin City, Nigeria; Sotuba, Mali; and Sunyani, Ghana) each had 1 year with two distinct peaks. Peak colony size occurred across the year in the different colonies (Figure 1). All colonies showed fluctuations in colony size and generally showed a clear peak in colony size during part of the year (Figure 2a–d). Minimum colony size varied between colonies with some colonies disappearing completely, while others maintained low populations during portions of the year (Table S1).

3.2 | Time to peak colony size

We investigated whether the timing of peak colony size was closely matched with peaks in four phenological events: EVI, IRG, PRP and IRP. Month of peak IRG showed the strongest circular correlation with month of peak colony size (cor: 0.55), when compared with month of peak EVI (cor: –0.08), month of peak precipitation (cor: –0.06) and month of peak increase in rate of precipitation (cor: 0.40; Figure 3a–d; Table S3). The sum of the absolute difference in months between peak colony month and peak phenology months were 112, 122, 178 and 226 for IRG, IRP, EVI and PRP respectively (Figure 3e). Months to peak IRG from peak colony size month was significantly different between months to peak EVI (Wilcoxon rank sum test, $W = 1,322$, $p < 0.001$, $N = 65$) and months to peak PRP (Wilcoxon rank sum test, $W = 1,638$, $p = 0.03$, $N = 65$). However, months to peak IRG were not significantly different from months to peak IRP (Wilcoxon rank sum test, $W = 2,321$, $p = 0.33$, $N = 65$; see Figure 3e for full pairwise comparison).

We used a Bayesian linear mixed-effects model to investigate which landscape variables best predicted the absolute difference in months between peak IRG month and peak colony month. The model included EVI_{max} , entropy of EVI and colony size. We excluded minimum EVI and amplitude of EVI from the model as they were each

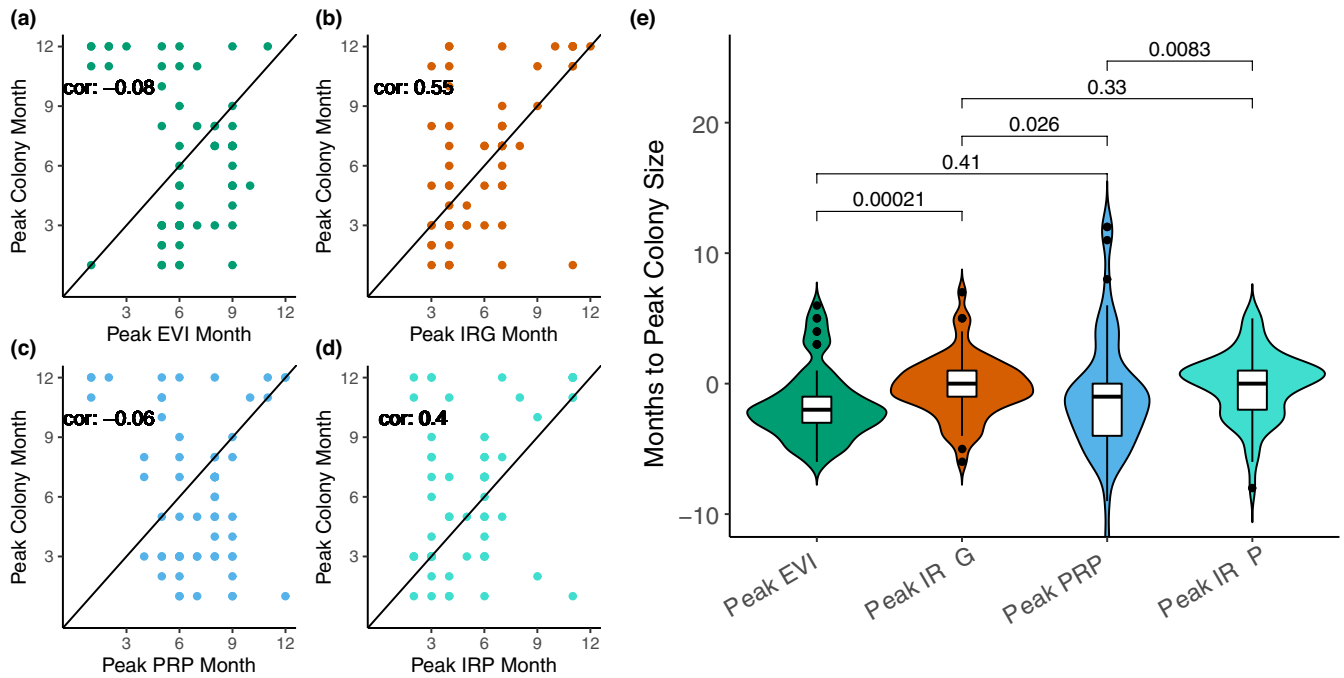


FIGURE 3 Match between phenological events and timing of peak colony size. (a–d) Peak colony month is plotted against the month peak phenological events, EVI (enhanced vegetation index), IRG (instantaneous rate of green-up), PRP (precipitation) and IRP (instantaneous rate of precipitation). A one-to-one line is provided for reference of a perfect match in timings and circular correlation coefficients are shown in the top left of each panel. (e) Violin plots of the difference in months between peak colony month and the peak month of each phenology for all colonies. Horizontal brackets above violin plots represent paired Wilcoxon signed-rank tests and the resulting *p*-values

Fixed effects	Estimates	95% CI	<i>t</i> value	<i>p</i> value
Intercept	1.72	1.28 to 2.16	7.84	<0.001
Maximum EVI	-0.62	-1.06 to -0.18	-2.84	0.006
Entropy	-0.76	-1.24 to -0.27	-3.13	0.003
Log(colony size)	-0.55	-1.01 to -0.09	-2.40	0.020
Random effects				
σ^2	1.77			
τ_{00}	0.28			
ICC	0.14			
N_{colonies}	17			
Observations	65			
Marginal/Conditional R^2	0.29/0.39			

TABLE 1 Mixed-effects model results on the variation in timing between peak IRG and peak colony size

highly correlated with entropy (-0.87 and 0.66 respectively; Table 1). The predictors suggested a closer match in timing between peak IRG and peak colony size when locations had a larger peak EVI, higher entropy and larger colony size (Figure S1). A model for absolute difference in months between peak IRP month and peak colony month including PRP_{max} , entropy of PRP, and colony size showed similar effect patterns; however, none of the effects were significant (Table S4).

Leave-one-colony-out cross-validation was fairly consistent across all colonies, with predicted months from peak colony size showing a positive slope of 0.6 (Figure S2) and resulting models having a consistent fit (Figure S3). However, omitting Kasanka did result in a substantially

reduced model fit, suggesting a disproportionate influence of this giant colony on overall model fit. Using a more restrictive set of colony peaks (minimum ratio of at least 0.6 and peaks must be more than 10 months apart) produced similar results for correlation with phenological peaks (Figure S4) and modelled time to peak IRG (Table S5).

4 | DISCUSSION

Seasonal peaks in the size of straw-coloured fruit bat colonies corresponded with the peak in the instantaneous rate of green-up (IRG)

for the majority of colonies monitored (Figure 3). The match between colony peak and peak IRG timing remained robust to stricter criteria for colony size peaks (Figure S5; Table S5) and alternative methods of estimating the start of the season (Table S2). This alignment was strongest in locations with higher maximum enhanced vegetation index (EVI_{max}) and greater entropy of EVI, indicating locations with a highly seasonal landscape. Additionally, larger colonies had a closer match with IRG peaks (Table 1; Figure S1), suggesting a possible role of collective sensing that coordinates *E. helvum* migration (Guttal & Couzin, 2010). Overall, these results support the hypothesis that seasonal aggregations of frugivorous straw-coloured fruit bats are timed to match the phenological peaks in the seasonal landscapes similar to what has been found in grazers. While previous green wave studies explored species that directly consumed new plant growth (Bischof et al., 2012), these bat migrations likely follow fruiting events, something currently not directly detectable from remote sensing measurement. In Africa, a clear wave of greenness annually moves up and down the tropics (Figure 4), likely driven by rains influenced by the movement of the intertropical convergence zone (Liu et al., 2020; Schneider et al., 2014). Our results suggest that bats are matching the green wave or some trait unknown to us which coincides with the green wave during their migration, and further work needs to confirm how the timing of the green wave represents relevant fruiting and flowering phenologies across Africa.

Eidolon helvum colonies matched the green wave closest in seasonal environments (Figure 4). The link between peak colony size and the start of the growing season suggests that plants in seasonal environments not only grow new leaves, but also provide valuable resources to bats during this time. The more northern and southern latitudes with highly seasonal environments showed a closer match between peak colony size and peak rate of green-up. These woody savanna environments can only support large populations of bats for a portion of the year due to their contracted fruiting and flowering seasons (Thomas, 1983). *Eidolon helvum* migrate to take advantage of peaks in fruiting and flowering with low levels of competition from local bats. This appears to be linked to peak IRG, yet extensive ground truthing is needed to understand what plant species are being consumed and their phenological patterns. The largest known *E. helvum* colony, in Kasanka National Park, co-occurs with the local peak in fruit availability (Richter & Cumming, 2005) as well as with peak IRG. Other phenological events, such as IRP, are also closely linked with peak colony size in Kasanka and peak EVI and PRP follow soon after (Figure 2d). Colonies likely match the timing of arrival and duration of stay at any given site based on what the local environment can support.

Rainfall is often a limiting resource for plant growth; however, several contrasting accounts depict colonies overlapping with wet (Cosson et al., 1996; Richter & Cumming, 2005) or dry season (Hayman et al., 2012; Lang & Chapin, 1917) depending on location. While our results found no significant correlation between timing of peak precipitation and peak colony size, there was a positive correlation with timing of IRP and peak colony size. This peak in the first derivative of precipitation mirrors the calculation of IRG

and provides a standardized approach to determining the month in which rainfall increases the most. Alternatively, onset of rain defined by a standard threshold approach revealed a low circular correlation with peak colony size month (Table S2). High variability in precipitation between sites limits the effectiveness of a uniform threshold and individual thresholds are likely needed for each location. An increase in the rate of precipitation often preceded peaks in IRG by roughly 1 month (Table S2), although these phenologies may not always be tightly coupled. In southern tropical Africa, green-up precedes the start of the wet season by roughly 1 month (Ryan et al., 2017). This precocious vegetation phenology is likely linked to access to groundwater (Do et al., 2008) or stored water in plants (Borchert, 1994) and could explain why IRG and IRP show slightly different phenological patterns. Despite a closer correlation between the timing of peak IRG and peak colony size, we cannot exclude a possible link between colony phenology and precipitation based on these results. When modelling the variation in time to IRP, we find similar but non-significant trends as with variation in time to IRG, with increases in max PRP, entropy of precipitation and colony size leading to closer matches with peak colony size (Figure S1). This suggests that IRG and IRP capture much of the same information and that these environmental variables are fundamentally linked with colony dynamics. The transition from dry to wet season may simply be a more easily observable seasonal pattern than peak IRG, leading previous studies to attribute precipitation to colony dynamics (Cosson et al., 1996; Hayman et al., 2012; Lang & Chapin, 1917; Richter & Cumming, 2005). Alternatively, other colony dynamics such as arrival or departure could be more closely tied with rainfall patterns. However, we could not accurately estimate these colony-level phenomena for all sites with this data, as many colonies show irregular fluctuations in size or partial migrations throughout the year.

In fact, roughly half of the monitored colonies showed partial migration (Table S1; Abedi-Lartey et al., 2016), demonstrating that some regions have resources that can support a smaller population of fruit bats year-round. Partial migration may result in some colonies being larger when migratory individuals return, yet it is unlikely that resident bats influence our result that larger colonies better match peak colony size. The remaining minimum colony sizes that do not reach zero, are typically 1,000–5,000 individuals, which is substantially less than most maximum colony sizes (see min-max Table S1). While several bat species segregate to give birth and raise pups (Levin et al., 2013), it is currently unknown if this species displays differential migration, in which age or sex classes show different migration patterns (Cristol et al., 1999; Lehnert et al., 2018). Fahr et al. (2015) caught similar numbers of adult males and females during the wet season when only about 5,000 bats remained. During the time, most of the Accra colony is absent, the remaining bats rely heavily on human-grown and introduced species. It may well be that partial migration is an increasing phenomenon, as supported by anecdotal reports from people at the colony sites. While many aspects of their migration are yet to be fully understood, it is unlikely that they have a major impact on our results.

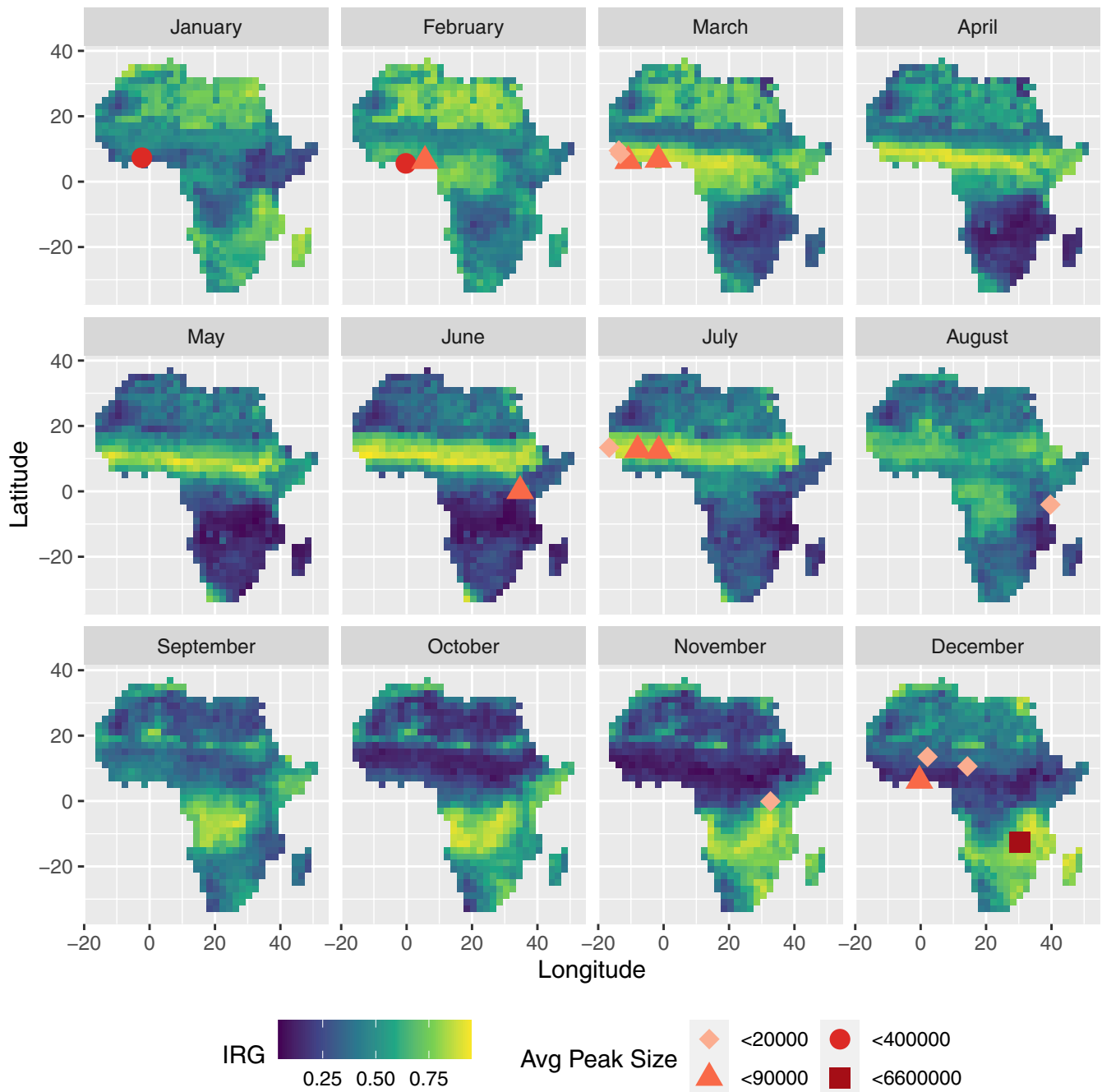


FIGURE 4 Average instantaneous rate of green-up (IRG) calculated for each month of the year with colonies overlaid on their corresponding average peak month. IRG values were averaged per pixel by month from 2000 to 2020. Colony size is represented by colour and shape

What will likely influence these migration patterns are the effects of climate change. In green wave surfing animals, a broken wave can halt a migration (Aikens et al., 2020). While we are limited in the number of colonies monitored, we find some months with no colony peaks which may be a result of a diffuse resource wave that may lead to different aggregation behaviours (Figure 4). As phenological timings shift with climate change, phenological waves could become weakened or disrupted (Butt et al., 2015). Climate change may also impact fruit availability, as

evidenced by the linked decline in fruiting and body condition of forest elephants over the past 30 years in Lopé National Park, Gabon (Bush et al., 2020). Phenological timings and length of the growing season in Africa have been changing over the past few decades (Adole et al., 2018; Vrieling et al., 2013). North Africa has a significant negative trend in entropy and positive trend in date of peak greenness (Ye et al., 2021). More work is needed to understand whether species can adapt to these changing patterns fast enough.

Our data show that colony counts provide crucial information for monitoring large-scale population fluctuations, even if they only provide approximate estimates of the total population size. Bats may not always roost in one central area and in areas where bats are hunted, counting is further complicated by bats flying and switching roosts when observers approach the colonies (Costa et al., 2020). *Eidolon helvum* form dense clusters on trees, making it nearly impossible to manually count all individuals. We provide a method that gives reliable colony counts within an order of magnitude of the true population size. A simulation of monitoring fruit bat colonies to detect population declines found that estimating the proportion of the population being counted was the most influential parameter for statistical power (Westcott et al., 2012). For *Eidolon helvum*, which roost in large numbers and are commonly referred to by locals as the 'noisy bat', we can have high confidence that our counts covered the majority of individuals in a colony. Techniques to more accurately count bats during fly out require researchers to film the emergence from several locations and substantial computation time to detect and track bats within the videos. The manual colony counts by volunteers employed in this study provide a low-cost and efficient method to monitor populations. In Accra, Ghana, we have seen annual peak colony counts decrease substantially from 1,000,000 in 2007 to 85,000 in 2015 (subsequent recent counts not included in this study have shown a decline to roughly 20,000; <https://www.eidolonmonitoring.com/monitoring/ghana>; Hayman et al., 2012). It is currently unclear whether these declines are a larger trend across Africa. Declining population sizes would impact the behaviour and migration of these bats due to possible Allee effects as indicated by the effect of colony size on accuracy of timing.

Collective sensing can increase the benefit of joining larger groups (Berdahl et al., 2013). While migratory decisions among individuals are often tied to local conditions and fat stores (Dechmann et al., 2017; Tøttrup et al., 2010), social factors may also play a large role. *Eidolon helvum* are adapted to large aggregations and due to accurate migration timing may not suffer the increased foraging duration costs that are expected with increased colony size (Calderón-Capote et al., 2020). This may be because colonies function as exploded sensory networks, where individuals scout out the wider landscape, and inadvertent, likely olfactory, information about upcoming resources is then shared at the central roost. With increasing colony sizes, fewer individuals with accurate information about the status of resources in any given direction are needed to identify when bats should migrate to the next location (Guttal & Couzin, 2010). This is supported by long-distance return movements of up to 150km one way by single individuals (Fahr et al., 2015; O'Mara et al., 2019). Alternatively, similar to many migratory birds, bats may be using personal knowledge or genetic cues to time migrations, which would then lead to phenological mismatch with climate change (Clausen & Clausen, 2013; Lameris et al., 2018; Shipley et al., 2022). Collective sensing may then help to make precise decisions about timing. Extreme group size, a roosting pattern not matched by any other African fruit bat, may be limited to species that can adequately track

and exploit these rich seasonal resources. More work is needed to understand how *E. helvum* may benefit from social information in the roost or during foraging or migration. Inversely, the observed widespread decreases in colony sizes across Africa may jeopardize environmental sensing in collectives and should be counteracted to avoid a potential scenario of extinction similar to the passenger pigeon (Hung et al., 2014).

Continued and increased monitoring of colonies but also tracking of individual migration will aid in understanding potential threats to the species. The counts provide crucial insight into population size and migration dynamics. *Eidolon helvum* often roost in large human settlements, where natural predation may be low but hunting and persecution can be very intense. With increasing persecution of bats around the world, disturbance at large colony sites may become more common. *Eidolon helvum* are very vocal during the day, leading to people trying to scare away bats from roost sites or removing roosting trees in populated areas (Costa et al., 2020; Webala et al., 2014). Perhaps, as a result of these disturbances, colony locations often occur where bats suffer less from harassment, such as hospital or embassy grounds, when in well-populated areas. Our results show the first quantitative link between colony size changes and landscape variables. Migratory behaviour in straw-coloured fruit bats has been inferred from annual cycles in population size consistent with seasonal migration (Peel et al., 2013; Richter & Cumming, 2005; Thomas, 1983). First partial satellite tracks of migration have shown bats flying distances of up to 1,400km from these large aggregations (Richter & Cumming, 2008). Our counts now support the hypothesis that bats leave the equatorial zone, not due to a shortage of food locally, but due to the larger surge in food in other more seasonal areas. For example, in Accra bats arrive during the peak flowering season yet leave the region before peak fruiting to likely forage further north in more seasonal areas such as Ouagadougou (Abedi-Lartey et al., 2016; Calderón-Capote et al., 2020; Fahr et al., 2015). Long-term tracking of individuals during migration as technologies become more miniaturized and battery lifetimes increase would aid in determining the drivers of migration, such as are bats anticipating or reacting to these resource peaks. As remote sensing analyses for determining fruiting and flowering phenology improve, we may see how bats match their movements to the fruit wave directly. Combined with more refined models of the drivers of migration, this would enable predictions of colony dynamics and even where currently undescribed colonies may occur.

AUTHORS' CONTRIBUTIONS

E.H., M.T.O., D.K.N.D., J.F. and M.W. conceived of the study; J.F. coordinated the collection of the data through the EMN and members of the EMN collected the data; E.H. performed the analysis; E.H. wrote the first draft of the paper and all authors contributed to editing and revisions of the paper.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code are available from Dryad Digital Repository [10.5061/dryad.z08kprdb](https://doi.org/10.5061/dryad.z08kprdb) (Hurme et al., 2022) and future counts will be available at <http://www.eidolonmonitoring.com>.

ORCID

Edward Hurme  <https://orcid.org/0000-0002-2936-2449>

Jakob Fahr  <https://orcid.org/0000-0002-9174-1204>

Bakwo Fils Eric-Moise  <https://orcid.org/0000-0001-7878-8158>

C. Tom Hash  <https://orcid.org/0000-0003-3138-9234>

M. Teague O'Mara  <https://orcid.org/0000-0002-6951-1648>

Iroko Tanshi  <https://orcid.org/0000-0002-0226-4929>

Natalie Weber  <https://orcid.org/0000-0003-0390-1229>

Martin Wikelski  <https://orcid.org/0000-0002-9790-7025>

Dina K. N. Dechmann  <https://orcid.org/0000-0003-0043-8267>

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