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Assessing roost disturbance of straw-coloured fruit bats (*Eidolon helvum*) through tri-axial acceleration

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RESUMO ALARGADO

A perturbação humana em animais selvagens é uma ameaça que causa crescente preocupação. Apesar da perturbação poder ter causas naturais (e.g. eventos climáticos), esta está mais frequentemente relacionada com actividades humanas, como lazer, caça, ruído associado a centros urbanos e alterações ao nível da paisagem. O rápido crescimento da população humana, consequente expansão de meios urbanos e urbanização de meios rurais, leva a que o contacto entre seres humanos e animais selvagens seja mais frequente, aumentando o risco de perturbação da fauna.

A perturbação pode desencadear respostas fisiológicas e comportamentais, podendo causar alterações no comportamento alimentar, sucesso reprodutivo, condição corporal, ou mesmo levar à morte dos indivíduos. Desta forma, a perturbação pode conduzir mudanças na abundância, distribuição e riqueza das espécies.

Apesar da ameaça que representa, o estudo da perturbação em animais selvagens continua a revelar-se um desafio para a comunidade científica. Em parte, porque as respostas à perturbação tendem a ser específicas de cada espécie, mas também devido a limitações metodológicas. Actualmente, muitos dos estudos sobre perturbação da fauna, avaliam a perturbação através de alterações comportamentais nos indivíduos, uma vez que as respostas comportamentais à perturbação são as mais comuns e facilmente identificáveis. Dentro das respostas comportamentais, a fuga - que em morcegos e aves se traduz em voo - é a resposta mais frequentemente utilizada. Este comportamento é muitas vezes identificado através de observação directa, ainda que seja reconhecido que a presença do observador pode também causar perturbação, enviesando os resultados.

Novos desenvolvimentos tecnológicos permitem identificar e quantificar as reacções à perturbação através de telemetria e detectores de movimento por infravermelhos, removendo assim o impacto da presença do observador. Além disso, o contínuo desenvolvimento dos dispositivos e tecnologia de *bio-logging* permite a recolha remota de dados, num grande leque de espécies e em habitats que de outra forma seriam inacessíveis. Os dispositivos utilizados permitem a recolha de dados de GPS e aceleração tri-axial, e a integração destes dois tipos de dados permite contextualizar espacialmente os dados de comportamento, fornecendo informação sobre os uso de habitat e a identificação de áreas importantes para as espécies, como as áreas de alimentação, abrigo e reprodução. Dado que os voos são uma resposta comum à perturbação em aves e morcegos, e dada a capacidade da aceleração tri-axial para discriminar este comportamento, é possível fazer uso desta tecnologia para identificar voos e utilizá-los como *proxy* de perturbação.

A perturbação pode afectar especialmente animais nocturnos e gregários, uma vez que o pico da actividade humana ocorre durante o dia, que corresponde ao período de repouso destes animais, e também porque estes tornam mais conspícuos quando agregados em colónias. *Eidolon helvum* (Kerr, 1792) é uma espécie de morcego frugívoro da família Pteropodidae, que se distribui amplamente pela África subsariana. Esta espécie forma colónias com milhares, em alguns casos milhões, de indivíduos, e tem actividade crepuscular e nocturna, sendo por isso um bom modelo para avaliar perturbação em abrigos diurnos. É capaz de grandes migrações e de percorrer longas distâncias para se alimentar, sendo uma espécie-chave para a dispersão de sementes em África. Actualmente, encontra-se classificada como "Quase Ameaçada" pela IUCN, em grande parte devido à sua caça.

Este estudo tem como principal objectivo identificar as principais causas de perturbação de *E. helvum* nos seus abrigos, utilizando voos diurnos, identificados a partir de aceleração tri-axial, como *proxy* de

perturbação. Além disto, espera-se avaliar a influência da perturbação no comportamento alimentar e utilização de locais de repouso diurno.

Para concretizar estes objectivos, foram estudados morcegos em cinco colónias em África continental - duas em Kibi (Gana), uma em Accra (Gana), uma em Ouagadougou (Burkina Faso), e uma no Parque Nacional de Kasanka (Zâmbia). Os morcegos foram capturados nos abrigos, quando regressavam de se alimentar, e foi-lhes aplicado um *datalogger* que recolhia dados de GPS e aceleração tri-axial. No total, foram obtidas 167 observações a partir de 46 indivíduos.

Os dados de aceleração tri-axial foram utilizados para identificar voos durante o dia, em detrimento de outros comportamentos. Os voos diurnos foram transformados numa variável binária, de presença/ausência de voos durante o dia, usada como *proxy* de perturbação. As localizações exactas dos abrigos foram obtidas através dos dados GPS, que permitiram identificar 25 novos abrigos (abrigos secundários) para além dos cinco abrigos principais, onde os morcegos foram capturados. Um conjunto de variáveis ambientais, climáticas e intrínsecas aos animais, assim como o tipo de abrigo (principal ou secundário), e a ocorrência de sessões de captura de morcegos para instalação de *dataloggers*, foram extraídas e utilizadas para modelar a presença de voos diurnos nos abrigos de *E. helvum*.

O tipo de abrigo, principal ou secundário, mostrou ser um importante preditor para a presença de perturbação, e a probabilidade de voos diurnos foi maior nos abrigos principais. É possível que este resultado se deva a diferenças de conspicuidade entre tipos de abrigo. Embora nada se saiba sobre os abrigos secundários descobertos, é possível que estes locais sirvam de abrigos temporários para pequenos grupos, perto das áreas de alimentação. Em contraste, os abrigos principais albergavam grandes colónias de *E. helvum,* muito conspícuas e consequentemente mais susceptíveis a predação e perseguição humana.

As sessões de captura para aplicação dos *dataloggers* nos abrigos principais também revelaram ser um bom preditor da presença de perturbação, sendo que a probabilidade de voos diurnos foi maior nos dias em que decorreram capturas. Este resultado é esperado, uma vez que as capturas podem causar uma perturbação directa nos morcegos, o que simultaneamente valida a abordagem metodológica usada neste estudo.

O vento e a energia solar têm também algum poder preditivo na presença de voos diurnos, embora este seja mais evidente quando o efeito das sessões de capturas é removido da análise. O vento teve um efeito negativo e a energia solar um efeito positivo na presença de voos diurnos. Menor velocidade do vento pode levar a que os morcegos não consigam dissipar energia de forma tão eficiente, da mesma forma que maior energia solar pode aumentar o ganho de energia por radiação. Desta forma, a maior probabilidade de voos diurnos pode dever-se a comportamentos de termorregulação, em que os morcegos mudam de posições no abrigo, de forma a encontrarem refúgio em partes com maior ensombramento.

Ao contrário do esperado, a perturbação (i.e., presença de voos diurnos) não parece ter efeito na distância percorrida na noite seguinte, nem parece explicar as mudanças de abrigo registadas neste estudo. Tanto a mudança de abrigo como a distância percorrida podem estar relacionadas com a disponibilidade de recursos, nomeadamente de áreas de alimentação, uma vez que parece haver uma relação entre a localização dos recursos alimentares e a localização dos abrigos noutras espécies de morcegos e de aves. Contudo, isto não significa que a perturbação não tem efeitos negativos nestes morcegos. A perturbação pode provocar outros efeitos nos indivíduos, como alterações no metabolismo, sistema imunitário ou reprodução, que não são identificáveis pelos parâmetros testados.

Este estudo fornece uma avaliação da perturbação em abrigos diurnos de *E. helvum* e dos seus principais preditores, e revela 25 novas localizações de abrigos diurnos. Desta forma, os resultados deste estudo podem ser utilizados para aumentar a vigilância em abrigos principais, e servem de base para aumentar o conhecimento sobre a perturbação em abrigos de *E. helvum* e contribuir para a sua protecção.

Por fim, este estudo fornece uma nova abordagem metodológica para identificar perturbação em abrigos diurnos, que pode ser aplicada em outras espécies de Pteropodidae ou mesmo noutras espécies coloniais, e assim avaliar uma das maiores ameaças que enfrentam: a perturbação.

Palavras-chave: Perturbação de fauna silvestre; *Bio-logging*; Aceleração tri-axial; *Eidolon helvum*; Pteropodidae.

ABSTRACT

Disturbance of wildlife is a threat of growing concern. It can be caused by natural effects, such as climatic events and by human related activities. It can negatively impact wildlife, causing changes in body condition, activity patterns, foraging behaviour, and can lead to changes in species distribution and richness.

Assessing disturbance on wildlife has proven to be challenging, as different species can have different responses to disturbance. However, behavioural responses are the most common and have been widely used to assess disturbance in birds and bats. This has been done mostly through direct observation, which may result in disturbance caused by the observer. Advances in bio-logging allow the remote collection of GPS and tri-axial acceleration data, removing the effect of the observer. Tri-axial acceleration can provide valuable information on behaviour, and its integration with GPS data may be used to identify important habitat areas (e.g. foraging and roosting areas).

As flight is a common response to disturbance in bats and birds, and tri-axial data can discriminate flight behaviour, daytime flights may be used as a proxy for disturbance. Therefore, this study aims to assess disturbance of straw-coloured fruit bats (*Eidolon helvum*) in day roosts across continental Africa and its most important predictors, using daytime flight as a proxy of disturbance. Tri-axial acceleration and GPS data was retrieved from 46 bats captured in five different colonies, located in Ghana, Burkina Faso and Zambia.

In addition to the five main roosts where bats were captured, 25 other roosting locations were found and classified as secondary roosts. The results show that main roosts are good predictors of daytime disturbance, possibly due to increased conspicuousness and consequent human predation. Capture events for bat sampling were also good predictors, and the probability of daytime flight was higher in days when captures were conducted. Wind speed had a negative effect, and solar energy a positive effect on presence of daytime flights. Lower wind speed and higher solar energy may lead bats to exhibit thermoregulatory behaviours, translated in flights to change towards more shaded positions in the roost. Disturbance, as measured, appears to have no effect on the distance travelled by the bat in the following night, nor could it explain the changes of roost recorded.

This study was able to successfully identify day roost disturbance in *E. helvum*, using daytime flights as a proxy, and to identify important predictors of disturbance. Ultimately, it provides a new methodological approach to assess day roost disturbance, which can be applied to other Pteropodidae or other colonial species.

Keywords*:* Wildlife disturbance; Bio-logging; *Eidolon helvum*; Pteropodidae.

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1. INTRODUCTION

Disturbance of wildlife is a threat of growing concern (e.g. Kunz 1982; Riddington et al. 1996; Blanc et al. 2006). It can be related to natural events (e.g. climatic events, fire, drought), or result from human activities (Riddington et al. 1996; Blanc et al. 2006). As human population grows and urbanisation increases (Bradley & Altizer 2006), human-wildlife interactions become more likely to occur (Soulsbury & White 2015). These interactions may rise in rural areas as well, as pressure of urbanisation intensifies (Patterson et al. 2003), increasing the chance of human driven disturbance to wildlife.

Human related disturbance can be direct (e.g. when animals at roosting or nesting location are disturbed (Scobie et al. 2014; Edson et al. 2015; Pearse et al. 2017)) or indirect (e.g. when landscape level changes due to human activities will impact long term survival of animals (Phelps et al. 2018)) and can differ in frequency and intensity (Cayford 1993). It can be either intentional - such as hunting (Anderson 1995; Madsen 1998; Cardiff et al. 2009), or not - such as non-consumptive recreational activities (Taylor & Knight 2003; Lou et al. 2013), noise related to human structures (Scobie et al. 2014), or even by research activities (Lewis 1995).

Negative impacts of disturbance in wildlife have been widely reported, and include changes in body condition (Phelps & Kingston 2018), activity patterns (Mann et al. 2002; Gaynor et al. 2018), energy expenditure (Speakman et al. 1991; Riddington et al. 1996), foraging behaviour (Blanc et al. 2006), breeding success (Beale & Monaghan 2004), roosting preferences and locations (Giroux 1991; Ho & Lee 2003; Ferrara & Leberg 2005) and can lead to roost abandonment and death (Knight & Cole 1995; Kunz et al. 2011). Ultimately, disturbance can drive changes in species distribution and richness (Finney et al. 2005; Blanc et al. 2006; Mckinney 2008).

Despite its negative effects, assessing and measuring wildlife disturbance imposes many challenges, mostly because responses to disturbance can vary between species (Cayford 1993) and can be species-specific (Cunto & Bernard 2012). At individual level, disturbance has been measured through physiological parameters, such as stress hormones, cardiac response and immunocompetence (Tarlow & Blumstein 2007). However, changes in behaviour are the most frequent and noticeable responses to disturbance in wildlife (Blanc et al. 2006), and assessment through direct observation is still the most prevalent approach described in the literature (Taylor & Knight 2003). Animal's escape reaction is among the most common parameters of disturbance, particularly in birds (e.g. Riddington et al. 1996; Fernández-Juricic and Tellería 2000; Tarlow and Blumstein 2007), and bats (e.g. Thomas 1995; Mann et al. 2002; Edson et al. 2015).

The use of automated methods to identify escape reactions has become more common in recent years, as they provide larger amounts of data and cancel the disturbance induced by the observer (Ferrara & Leberg 2005), more so when humans are perceived as predators (Beale & Monaghan 2004). These methods include infrared motion detectors (Thomas, 1995), telemetry (Preisler et al. 2006), and more recently a wide variety of bio-loggers deployable directly on the animals, mainly due to technological breakthroughs in electronic sensors miniaturization (GPS in particular)(Cooke 2008; Nathan et al. 2012; Kays et al. 2015). Data collection using dataloggers can provide a continuous record of data, over habitats that may be difficult to access otherwise, and can be important to gain information on species' geographic range, demography, reproduction, population's connectivity (Cooke 2008), activity levels and habitat use (Pacheco 2019), that can ultimately aid species' conservation (Cooke 2008).

Commonly these devices combine the collection of GPS and acceleration data (Moreau et al. 2009; Nathan et al. 2012), but can also be used to collect data on parameters such as travel speed, altitude or light levels (Cooke 2008; Brown et al. 2013). Acceleration data can be used to classify behaviour

(Nathan et al. 2012) and to assess energy expenditure (Wilson et al. 2006), providing information over different temporal and spatial scales, allowing the record of important ecological and biological events and removing some of the limitations of direct observation (Nathan et al. 2012; Brown et al. 2013). The integration of GPS and tri-axial acceleration data allows a deeper understanding of habitat use, providing spatial context for behavioural data (Brown et al. 2013; Resheff et al. 2014). This information can help identifying foraging and reproductive areas (Cooke 2008), and roosting locations (e.g. (De Jong et al. 2013), improving the knowledge on bats' spatial ecology and supporting informed management measures to protect the habitat (Cooke 2008).

Considering flight behaviour has been greatly used to assess disturbance (e.g. Thomas 1995; Mann et al. 2002; Edson et al. 2015), and that acceleration data allows the discrimination and identification of behaviour, it seems reasonable that daytime flights, detected through tri-axial acceleration, can be used as a proxy to study disturbance. Nocturnal animals may be more subjectable to human disturbance, as human activities able to cause disturbance are higher during the day, overlapping with their resting periods (Scobie et al. 2014). More so when concentrated over specific locations, such as roosts (Sheffield et al. 1992), making the straw-colour bat, *Eidolon helvum* (Kerr, 1792), a good model to assess disturbance.

The straw-coloured fruit bat (*E. helvum*), is a large species of Old World fruit bat (Pteropodidae) (Thomas & Henry 2013). It occurs across sub-Saharan Africa (DeFrees & Wilson 1988) and can migrate up to 2000 km (Richter & Cumming 2008; Ossa et al. 2012), likely in response to changes in food availability (Richter & Cumming 2006). This frugivore feeds on a large variety of fruits and flowers (Wilson 1973; Webala et al. 2014) and can travel long distances to forage (Fahr et al. 2015), features that make this species a keystone seed disperser in Africa, especially in fragmented landscapes (Abedi-Lartey et al. 2016).

E. helvum roosts in trees, preferably in bare branches (Mickleburgh et al. 1992), forming colonies from hundreds of bats up to several millions (Peel et al. 2017). The largest known roost of this species is located at Kasanka National Park with a colony of 5 to 10 million bats (Richter & Cumming 2006). This species his highly adaptable (Mickleburgh et al. 1992), able to forage in cities and suburb areas (Fahr et al. 2015) and forms large colonies in urban areas, including the city centre of major cities, such as Accra (Abedi-Lartey et al. 2016; Peel et al. 2017). The species is extensively hunted, leading to populations' decrease (Mickleburgh et al. 2009; Kamins et al. 2011) and to its classification as Near Threatened by the IUCN (Mickleburgh et al. 2008). Additionally, these bats may be threatened by loss of roosting trees and disturbance (Perpetra & Kityo 2009; Webala et al. 2014).

New and exact information on disturbance levels of the colonies of this species is crucial to inform conservation actions and protection regulations. Particularly because the high abundance of this species and its use of humanized areas can be misleading on its true conservation status. In order to address this information gap, 46 straw-coloured fruit bats we tagged in five colonies of three countries of continental Africa (Ghana, Burkina Faso and Zambia) with GPS-Accelerometer devices. Daytime roost flights, identified from accelerometer signatures, were used as a proxy of roost disturbance. The occurrence of daytime roost flights was then modelled against several variables previously considered in the literature to have caused disturbance in different animals. I predicted that:

1. Disturbance is potentiated by several bat intrinsic parameters and environmental factors;
2. Human direct intervention at the colonies is a source of bat disturbance;
3. Bat disturbance at the day roost will result in changes in bat foraging and roosting behaviour.

2. METHODS

2.1. Study area

Data for this study was collected in colonies of four different locations across continental Africa: Accra and Kibi, in Ghana, Ouagadougou in Burkina Faso, and Kasanka National Park, in Zambia (Fig. 2.1).

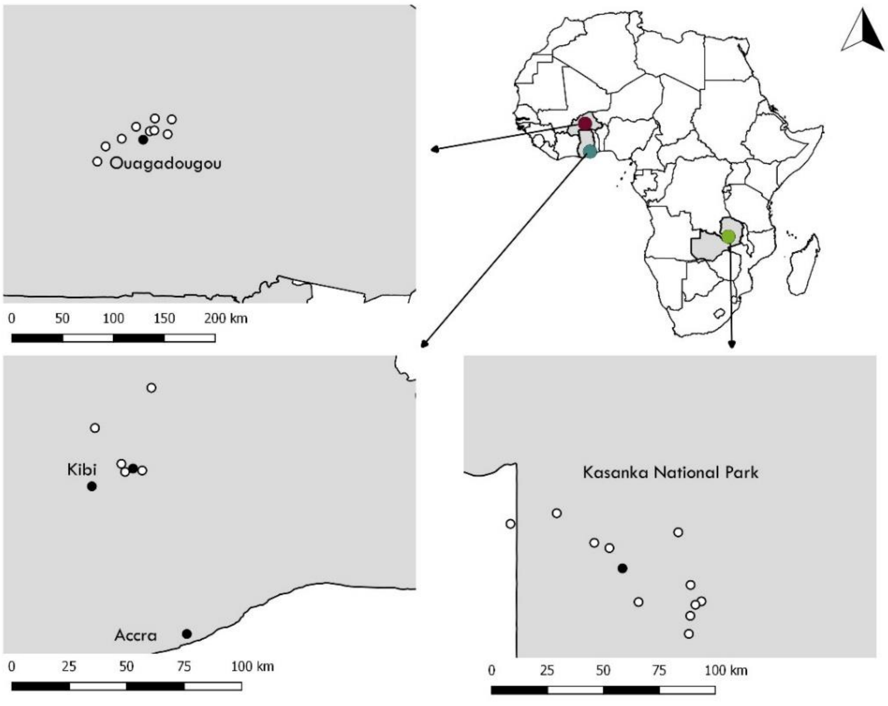

Figure 2.1 – Map of the study areas at Burkina Faso (top left), Ghana (bottom left), and Zambia (bottom right). Roosts where bats were captured are represented by black dots, and white dots represent other roosts used during the period bats were tracked.

Accra

The city of Accra belongs to the Greater Accra Region, located near the coast of the Atlantic. Densely populated with almost two million people, it is home to nearly half of the Region's human population (Ghana Statistical Service 2012).

It exhibits a bimodal climate with two rainfall peaks: the first between March and June, and the second from September to October, with the dry seasons in-between. Average annual rainfall is 810 mm (Abedi-Lartey et al. 2016), and average monthly temperatures vary between 26 ºC and 29 ºC (The World Bank Group 2018).

In Accra, the colony where Straw-coloured fruit bats (*E. helvum*) were captured is located in the area of the 37 Military Hospital (5.586°, -0.185°), near the city centre. The colony fluctuates in size across seasons: it peaks during the dry season, reaching over 250 thousand individuals, and reaches its low, of only a few thousand individuals, during the wet season (Hayman et al. 2012; Fahr et al. 2015; Abedi-Lartey et al. 2016).

Kibi

Kibi is a rural area located ca. 76 km North from Accra, in the East Akim District of the Eastern Region of Ghana. This district has lower population count and density than Accra Metropolitan Area, with nearly 168 thousand people (Ghana Statistical Service 2012). The landscape includes areas of moist semi-deciduous forests (Hall & Swaine 1976), farmlands and degraded forests (Abedi-Lartey et al. 2016).

Just like Accra, the climate in Kibi is bimodal, but precipitation peaks in slightly different periods: between May and July, and then between September and November. Here average annual rainfall is nearly double than in Accra (with 1600 mm) (Abedi-Lartey et al. 2016) and average monthly temperatures range from 25 ºC to 28 ºC (The World Bank Group 2018).

In Kibi, bats where captured in two roosting sites: one in Old Tafo (6.235°, -0.394°) and the other in Kibi Palace (6.165°, -0.555°). These have been previously considered as sub-colonies of a single interaction colony (Abedi-Lartey et al. 2016; Capote 2018), but for the purpose of this study they were considered separately. The population size of the two colonies together reaches its peak during dry season (51,500 individuals, in 2013) and its low during the wet season (523 individuals, in the same year) (Abedi-Lartey et al. 2016).

Ouagadougou

The city of Ouagadougou is the capital of Burkina Faso, West Africa. Located in the Centre Region, the city itself contains 85% of the Region’s population with nearly one and a half million people (Institut National de la Statistique et de la Démographie 2008). The high population density in the Region has led to overexploitation of natural resources and environmental degradation (Ministère de l’environnment et de l’eau 1999).

Ouagadougou belongs to the savanna biome (Kangoyé et al. 2015) and is situated in the Sudanian climatic zone, exhibiting two seasons of different duration: one short wet season from May to September, and a long dry season in the remaining months (Ministère de l’environnment et de l’eau 1999). Both rainfall and temperature are unimodal, with annual precipitation varying between 600 mm and 1000 mm (Abedi-Lartey 2016) and average monthly temperatures ranging from 25 ºC and 33 ºC (The World Bank Group 2018).

Bats were captured in a colony located in the Parc Urbain Bangr Weogo (12.398º, -1.489º), in downtown Ouagadougou. In monthly counts undertaken in 2013 and 2014, the colony showed two population peaks during the wet season, one of over 670000 individuals (between June and July) and other of over 37000 individuals (between August and September), and the roost was vacated during the dry season (Abedi-Lartey 2016).

Kasanka National Park

Kasanka National Park (KNP) is located on the northern part of Central province of Zambia, near the border with Democratic Republic of Congo. This province has low population density, of 14 individual/km^2, and about 85% of its population lives in rural areas (Central Statistical Office 2012).

KNP was previously a game reserve, and was gazetted as a National Park in 1972 (Himoonde 2007), currently under public-private management. The Park extends for 420 km^2 mainly composed by Miombo woodlands (Smith & Fisher 2001) and includes small patches of *Mushitu* evergreen swamp forests, where *E. helvum* roosts (Richter & Cumming 2006; Byng et al. 2010).

Zambia has three seasons throughout the year: a hot dry season from August to October, a warm wet season from November to April, and a cool dry season from May to August (Himoonde 2007). The region where the park is located has above Zambia's average rainfall, with a mean of 1200 mm (Goldspink et al. 1998), falling from November to April (Richter & Cumming 2006). Throughout the year average monthly temperatures vary between 17 and 25 ºC (The World Bank Group 2018).

KNP roost where bats where captured (-12.587º, 30.242º) is used by *E. helvum* from October to January (Richter & Cumming 2006). It is estimated that during this time the colony can reach 5 to 10 million individuals (Richter & Cumming 2006), and the roost is left vacated during the rest of the year (Richter & Cumming 2008).

2.2. Bat capture and tracking

Bats were captured in the morning, as they returned from foraging, using canopy nets and 10 m high macro nets. Individuals were weighted with a Pesola spring scale and the length of the forearm was measured. Dataloggers were deployed to adult males, except for two young males (270g and 290g) and an adult female (280g) that were large enough to safely sustain the devices (Table S1.1). In 12 bats the datalogger was attached with glue, and in the remaining 34 the device was attached to a collar closed with degradable suture thread, to allow the logger to be dropped after a few weeks of tracking (O'Mara et al. 2014) (for detailed description see Fahr et al. 2015 and Abedi-Lartey et al. 2016) (Table S2.1). Captures were conducted between 2009 and 2014 covering different sampling years for all locations and different seasons for Kibi and Accra (Table 2.1).

Dataloggers recorded GPS location, height and speed between 18h00 and 6h00 (local time) and tri-axial acceleration was recorded continuously, day and night. The frequency of GPS fixes varied from 2.5 to 30 min depending on the dataset, and acceleration bursts of 14 or 15s per minute at 18.74 or 20 Hz were recorded (Table S2.1).

Data was retrieved from 46 individuals, weighing 276.5 ± 18.3 g. Dataloggers weighed 21.7 ± 1.8 g, corresponding to 7.9 ± 0.9% of the bats' body mass (ranging from 6.5 to 10.5%) (Table S2.1). The maximum tag load recommended for bats is 10% according to O'Mara et al. 2014.

Table 2.1 – Information regarding bat data collection, including location, year, season and the periods during which bat behaviour was tracked.

Location	Year	Season	Dates of collection
Accra	2009	Wet	26/08 – 31/ 08
	2011	Dry	02/02 – 09/02
Kibi	2011	Wet	27/08 – 31/08
	2012	Wet	28/08 – 16/09
	2013	Dry	25/01 – 01/02
	2013	Wet	20/09 – 29/09
Ouagadougou	2013	Wet	19/08 – 31/08
	2014	Wet	17/06 – 24/06
Kasanka	2013	Wet	04/12 – 11/12
	2014	Wet	29/11 – 08/11

2.3. Measure of roost disturbance

We used events of flight during daylight (7h00 to 17h00) as a proxy of roost disturbance. Flight events have been used before to identify disturbance level in bats (e.g. Thomas 1995; Edson et al. 2015) and birds (e.g. Riddington et al. 1996; Rogers et al. 2006). Flights were detected from acceleration readings with high variation in heave as compared with surge and sway (see Fig. 2.2). This is related to the fact that in flight the animal body shows regular vertical oscillation of high amplitude and not so much torsion on the lateral and longitudinal body axis (Fig. 2.2 b). Specifically, acceleration bursts were classified as "flying" if the standard variation of heave was higher than 4.3 and at least 1.5 times the standard variation of surge and sway, otherwise they were considered "not flying". Although flight behaviours classifications were obtained for every minute, these were grouped for each day. Thus, for each day, a bat was considered as "not disturbed" if no flight events were recorded, otherwise it was considered "disturbed". This procedure was necessary due to the very large amount of "not flying" classifications.

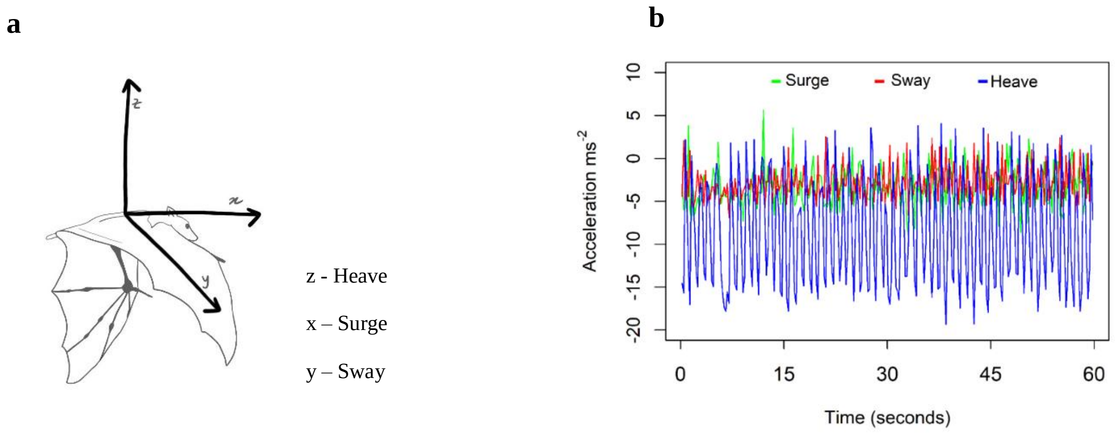

Figure 2.2 – Representation of tri-axial accelerometer attached to a bat and respective axes (z – heave, x – surge, y – sway) (a) and acceleration signatures during fight events (b).

2.4. Predictors of roost disturbance

A set of potential predictors of roost disturbance were tested. This included weather, landscape and intrinsic (biometrics or behaviour related) variables, roost type (main roost or secondary) and the occurrence of bat capture sessions undertaken by the data collectors (Table 2.2).

Sites where bats stayed at least for an entire day, i.e. showing morning and evening GPS fixes within distances up to 500 m, were considered roosts. Each roost was given an ID and their location was set as the centroid of GPS fixes recorded while the bats were stationary. In addition to the five roosts where the captures took place, 25 other roosts were identified from the GPS data collected. The first five roosts were considered "main roosts" as they were known from studies before to hold a large number of bats (Richter & Cumming 2006; Fahr et al. 2015; Abedi-Lartey 2016), while the remaining 25 were considered "secondary roosts". It was not confirmed if these had large colonies. However, it is unlikely that they have gone unnoticed in earlier studies if they sustained colonies as large as the ones in the “main roosts”, and it is possible that these roosts are used by single individuals or small groups (e.g. Roberts et al. 2012).

Weather variables were extracted for each of the study sites rather than for each roosting location, due to the coarse spatial resolution of the data available. Landscape variables were extracted for each of the 30 roosts.

Landscape variables were measured at two different scales. Land-cover and Normalized Difference Vegetation Index (NDVI) were measured within a 76 km radius from the roost (the maximum distance travelled by the bats in a single night), as these variables are expected to influence foraging primarily (Fahr et al. 2015), and as landscape variables may influence disturbance on bats (Phelps et al. 2018). Human and road densities were measured within a 1.5 km radius from the roost, as I expect these variables to influence roost disturbance more directly.

All GIS processing was done using QGIS software, version 2.18.23 (QGIS Development Team 2018).

Table 2.2 – Summary table of all weather, landscape, intrinsic, and other variables used to model roost disturbance, including their type, range, units, source, and temporal and/or spatial resolution. *Data sets: 1 – Accra 2009; 2 – Accra 2011; 3 – Kibi 2011; 4 – Kibi 2012; 5 – Kibi 2013 dry season; 6 – Kibi 2013 wet season; 7 – Ouagadougou 2013; 8 – Ouagadougou 2014; 9 – Kasanka 2013; 10 – Kasanka 2014.

	Variable	Type, range and units	Source	Spatial/temporal resolution
Weather variables	Mean temperature	Continuous: 17.494 – 34.203 (ºC)	1 – 9*: CFRS at https://globalweather.tamu.edu/ 10*: Weather station at http://www.sasscalweathernet.org/weatherstat_daily_we.php (Table S3.1)	1 day
	Precipitation	Continuous: 0 – 86.988 (mm)		
	Wind	Continuous: 0.52 – 4.0366 (m/s)		
	Solar energy	Continuous: 2.5186 – 30.6920 (MJ/m^2)		
	Humidity	Continuous: 0.3971 – 0.9804 (fraction)		
Landscape variables	Land cover	Land cover of Africa, in 10 categories: tree cover areas, shrub cover areas, grassland, cropland, vegetation aquatic or regularly flooded, lichen mosses/sparse vegetation, bare areas, built up areas, snow and/or ice, open water. Categorical	CCI Land Cover Available at European Space Agency 2017	2016, 20 m
	NDVI	Normalized Difference Vegetation Index Continuous: 0.2401 – 0.7898 (median)	2, 5, 7 – 10*: MODIS Terra (Didan 2015a) (Table S3.2) 1, 3, 4, 6*: MODIS Aqua (Didan 2015b) (Table S3.2)	16 days, 250 m 1 month, 1 km
	Human population density	Density of humans. Continuous: 5.289 – 11416.408 (individuals/km^2, 1.5 km radius)	Derived from Center for International Earth Science Information Network - CIESIN (2017)	2010, 1 km
	Road density	Density of roads. Continuous: 0 – 0.605798 (km/km^2, 1.5 km radius)	Derived from Center for International Earth Science Information Network - CIESIN (2013)	1980–2010
Intrinsic variables	Weight	Continuous: 239 – 321 (g)	Field measurements	
	Forearm	Continuous: 103.67 – 131.2 (mm)	Field measurements	
	Colony size	Number of individuals in roosts Continuous: 4017 – 13440000	Field observations	Available for main roosts only
	Distance flown the previous night	Cumulative distance flown from and to the roost Continuous: 814 – 164570 (m)	Derived from GPS points	1 day
Others	Roost type	Binary: 1 – main; 0 – secondary		1 day
	Capture day	Capture of bats for deployment of dataloggers Binary: 1 – yes; 0 – no		1 day

2.5. Data analysis

2.5.1. *Modelling predictors of roost disturbance*

The effects of the potential predictors of roost disturbance (Table 2.2) were tested through Generalized Linear Mixed Models (GLMMs), using the occurrence of daytime flights as the dependent variable, and the individual bat identifier as a random effect. Models were fitted with binomial distribution and "logit" link function, using "lme4" package in R software (Bates et al. 2015).

Continuous predictors were tested for collinearity through Spearman's correlation test. In each pair of variables with correlation values > 0.7 (Tabachnick & Fidell 2014), one of them was excluded from further analysis. Exclusion of variables took into consideration their ecological value, based on biological relevance and literature (Table S4.1 and S4.2). The land cover class "vegetation aquatic or regularly flooded" was excluded from analysis due to lack of biological relevance. In total, 12 predictors were used to model the data.

A set of multivariate models was produced with different combinations of predictors, using "dredge" function from R package "MuMIn" (Barton 2018), and models were ranked based on Akaike's information criterion (AIC). The assumption of linearity with the logit was tested by modelling the logarithmic and squared forms of the selected variables (Hosmer & Lemeshow 2000).

Ranked models with $\Delta\text{AIC} \leq 2$ (Burnham & Anderson 2002) were compared considering their complexity and biological meaning. Reduced models produced from these top models were also considered and final model selection took into consideration AIC value and biological relevance of variables. Model performance was evaluated by the area under the ROC curve (AUC), produced using "pROC" package in R (Robin et al. 2011).

Three data subsets were modelled with different aims: 1) testing all potential predictors of disturbance, except colony size; 2) excluding the effect of disturbance due to capture events; and 3) including colony size as a model predictor of disturbance. For (1) I included all 167 observations and 46 individuals, but the variable colony size could not be modelled, as the colony size was unknown for the "secondary roosts". For (2) I used 131 observations from 44 individuals, as the 36 remaining observations were recorded during days of bat capture in the colonies. For (3) I used 92 observation from 38 individuals, using only data from the "main roosts" for which the colony size was known and excluding observations with bat captures in the colonies.

2.5.2. *Modelling bat responses to roost disturbance*

As disturbance may affect energy expenditure on bats (Speakman et al. 1991), due to the increased energetic cost of daytime flights (Voigt & Lewanzik 2011), I expected roost disturbance could affect distance flown to forage. This was tested with a Linear Mixed Model (LMM), where the cumulative distance flown in each night was set as the response variable, the roost disturbance in the previous day (disturbed vs not disturbed) was set as fixed effect, and Animal ID was set a random effect. The model produced with presence/absence of disturbance as a predictor was then compared with the null model using AIC as measure of goodness of fit. Both models were fitted with normal distribution, "identity" link function and by Maximum Likelihood, using 142 observations from 43 bats.

Disturbance may also affect roosting behaviour, by leading bats to change roosts in response to disturbance (Lewis 1995; Peel et al. 2017). Thus, I expected bats might change roost following disturbance events, to avoid further disturbance. This was tested using GLMM, with change of roost each day (0/1) set as the dependent variable, roost disturbance in the previous day (disturbed vs not disturbed) set as fixed effect and animal ID set as a random effect. The model produced with the predictor (presence/absence of disturbance) was compared with the null model, using AIC to evaluate goodness of fit. Both models were fitted with binomial distribution, using 121 observations from 35 bats.

All models were adjusted using "lme4" package (Bates et al. 2015) in R environment (R Core Team 2018). The significance level was set at 0.05.

3. RESULTS

Daytime flight data was successfully retrieved from 46 individuals, providing 167 observations (Table 3.1), with a median of 4 days per bat. Of these, 129 were at the main roosts, and the remaining 38 at secondary roosts.

Table 3.1 – Summary table of datalogger data collected for *E. helvum*. Number of individuals, days of data (observations), and days with flight events collected per location and year.

Dataset	Number of individuals	Number of days	Number of days with flight events
Accra 2009	6	10	1
Accra 2011	4	8	3
Kibi 2011	2	3	2
Kibi 2012	4	14	3
Kibi 2013	3	8	1
Kibi 2013	1	4	0
Ouagadougou 2013	4	18	2
Ouagadougou 2014	6	20	6
Kasanka 2013	3	14	3
Kasanka 2014	13	68	17
Total	46	167	38

3.1. Predictors of roost disturbance

Modelling all observation

The best model from the set of candidate models fitting all observations (Table 3.2), showed that the probability of daytime flights was higher at the main roosts and in the days when bat captures took place at the roost. Wind showed a negative effect on daytime flight probability, although this effect was not statistically significant. (Table 3.3, Fig 3.1). This model shows a high predictive value with an AUC value of 0.78, showing adequate ability to discriminate between the two possible outcomes (Table 3.3).

Table 3.2 – Set of candidate GLMM models considering all observations (approach 1). Parameters of each model, Log-likelihood, AIC, difference from lowest AIC values (ΔAIC), Akaike weights (ω) and AUC are presented. Interaction between parameters is represented by "*". The best model is presented in bold.

Model	Parameters	Log-likelihood	AIC	ΔAIC	ω	AUC
1	**Capture day + roost type + wind**	-80.810	171.6	0.00	0.339	0.7772
2	Capture day + roost type	-81.853	171.7	0.09	0.325	0.8095
3	Capture day + roost type + solar energy + wind + solar energy*wind	-79.280	172.6	0.94	0.212	0.7711
4	Capture day + roost type + wind+ weight	-80.808	173.6	2.00	0.125	0.7791

Table 3.3 – Parameters for the best *E. helvum* disturbance GLMM model considering all observations (approach 1) (AUC = 0. 7772). Capture day and roost type are categorial variables, having presence of capture events and main roosts, respectively, as reference classes. Significance levels: *** p<0.001, ** p<0.01, * p<0.05, ns – non-significant.

	Estimate ± SE	z value	*P* value	significance
(Intercept)	-2.3472±0.8625	-2.722	0.0065	**
Capture day (1)	1.2772±0.5219	2.447	0.0144	*
Roost type (1)	1.6413±0.7897	2.078	0.0377	*
Wind	-0.3093±0.2201	-1.405	0.1600	ns

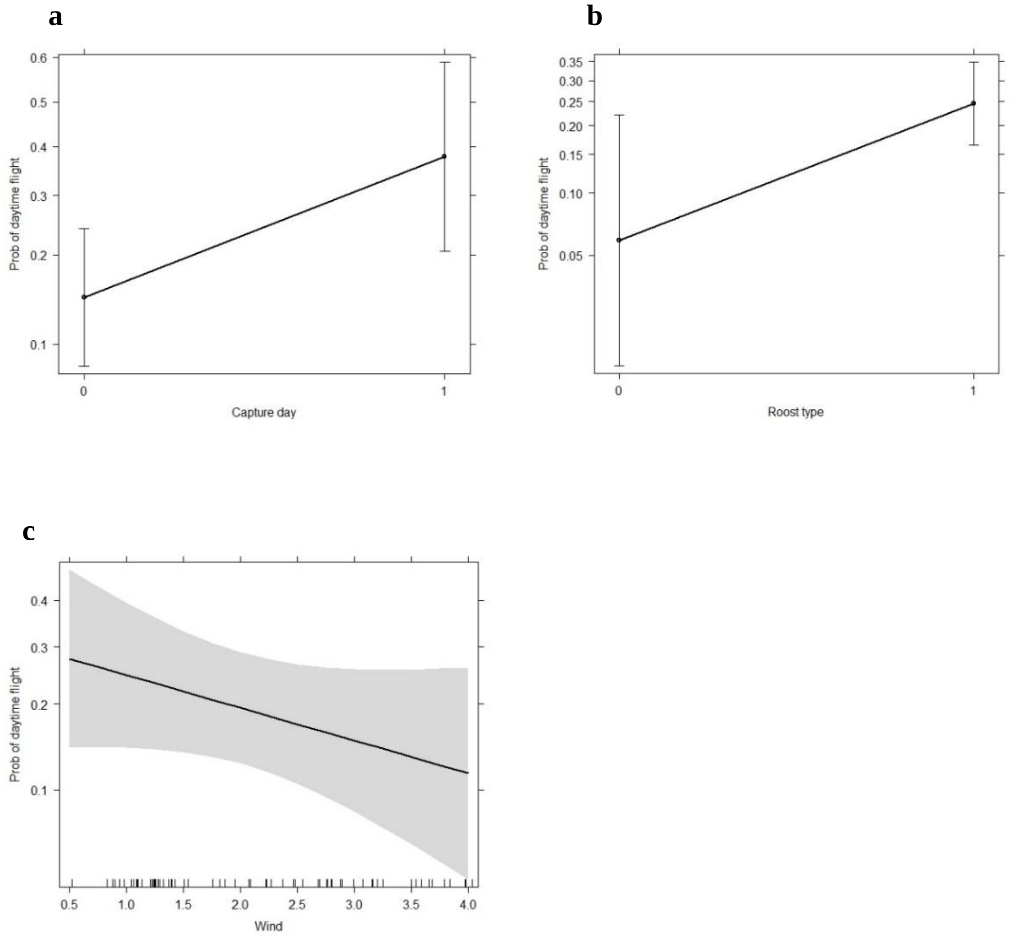

Figure 3.1 – Partial effects plots for the best *E. helvum* disturbance GLMM model considering all observations (approach 1). Plots of the effect of capture sessions (a), roost type (b), and wind (m/s) (c) on probability of daytime flight, represented with 95% confidence intervals. Days when bat captures took place are represented by 1, and 0 otherwise (a). Main roosts are represented by 1 and secondary roosts represented by 0 (b).

Excluding disturbance from capture events

When excluding the days when bat captures took place in the colonies, the best fitted model from the set of candidate models (Table 3.4) included roost type, wind and solar energy as predictors. As in the previous model, bats showed a higher probability for daytime flying at their primary roosts compared with the secondary roosts, and when wind was lower. Solar energy showed a positive effect on daytime flight probability, although this effect was not statistically significant (Table 3.5, Fig. 3.2).

Table 3.4 – Set of candidate GLMM models considering all observations except the ones associated to bat capture sessions (approach 2). Parameters of each model, Log-likelihood, AIC, difference from lowest AIC values (ΔAIC), Akaike weights (ω) and AUC are presented. Interaction between parameters is represented by "*". The best model is presented in bold.

Model	Parameters	Log-likelihood	AIC	ΔAIC	ω	AUC
1	**Roost type + solar energy + wind**	-54.649	119.3	0.00	0.282	0.7709
2	Roost type + solar energy + wind + solar energy*wind	-53.719	119.4	0.14	0.263	0.7903
3	Roost type + wind	-55.889	119.8	0.48	0.222	0.7858
4	Roost type	-57.454	120.9	1.61	0.126	0.8752
5	Roost type + solar energy + wind + weight	-54.606	121.2	1.91	0.108	0.7927

Table 3.5 – Parameters for the best *E. helvum* disturbance GLMM model considering all observations except the ones associated to bat capture sessions (approach 2). AUC = 0.7709. Roost type is a categorical variable having main roosts as reference class. Significance levels: *** p<0.001, ** p<0.01, * p<0.05, ns – non-significant.

	Estimate ± SE	z value	P value	Significance
(Intercept)	-3.50315±1.30507	-2.684	0.00727	**
Roost type (1)	1.80138±0.80817	2.229	0.02582	*
Wind	-0.71773±0.35179	-2.04	0.04133	*
Solar energy	0.08864±0.06011	1.475	0.14031	ns

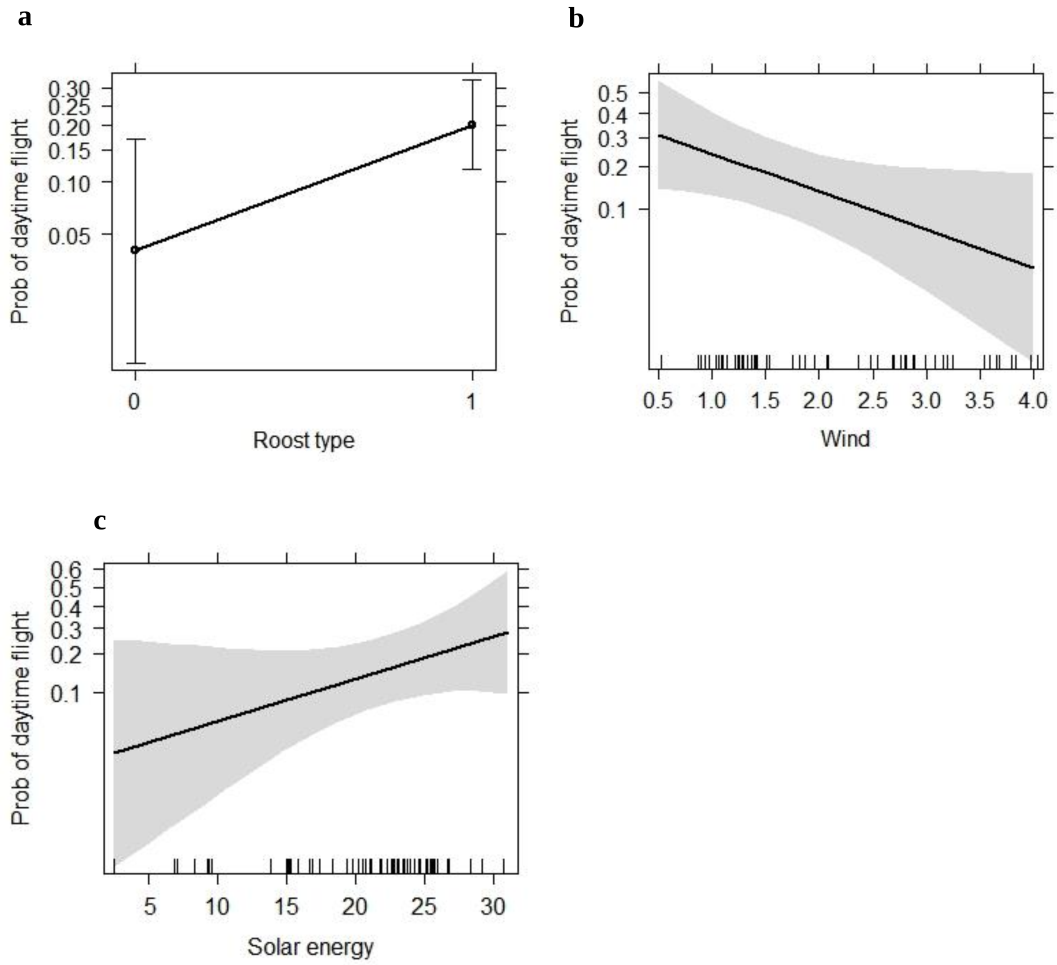

Figure 3.2 – Partial effects plots for the best *E. helvum* disturbance GLMM model considering all observations except the ones associated to bat capture sessions (approach 2). Plots of the effect of roost type (a), wind speed (m/s) (b), and solar energy (MJ/m^2) on probability of daytime flight, represented with 95% confidence intervals. Main roosts are represented by 1 and secondary roosts represented by 0 (a).

Colony size as a predictor of disturbance

The best fitted model from the set of candidate models used to test the effect of colony size on roost disturbance (Table 3.6), showed a negative effect of wind and solar energy on probability of daytime flight, and interaction between these predictors showed a positive effect. These effects were not statistically significant. Colony size was not amongst the predictors for the best model (Table 3.7).

Table 3.6 – Set of candidate GLMM models considering observations of main roosts and excluding the ones associated to bat capture sessions (approach 3). Parameters of each model, Log-likelihood, AIC, difference from lowest AIC values (ΔAIC), Akaike weights (ω) and AUC are presented. Interaction between parameters is represented by "*". Colony size is represented by "bat population" and was modelled in its logarithmic form. The best model is presented in bold.

Model	Parameters	Log-likelihood	AIC	ΔAIC	ω	AUC
1	**solar energy + wind + solar energy*wind**	-44.516	99.0	0.00	0.278	0.758
2	Solar energy + wind	-45.551	99.1	0.07	0.269	0.7312
3	Solar energy + wind + bat population	-45.298	100.6	1.56	0.127	0.7056
4	Wind	-47.429	100.9	1.83	0.112	0.799
5	Solar energy	-47.456	100.9	1.88	0.109	0.7076
6	Solar energy + wind + weight	-45.489	101.0	1.95	0.105	0.7611

Table 3.7 – Parameters for the best *E. helvum* disturbance GLMM model, modelling colony size (approach 3). AUC = 0.758. Significance levels: *** p<0.001, ** p<0.01, * p<0.05, ns – non-significant.

	Estimate ± SE	z value	P value	Significance
(Intercept)	1.63336±3.08058	0.530	0.596	ns
Wind	-3.31830±2.05492	-1.615	0.106	ns
Solar energy	-0.09563± 0.16451	-0.581	0.561	ns
Wind*solar energy	0.12515±0.09254	1.352	0.176	ns

3.2. Bat responses to roost disturbance

Roost disturbance, as measured by the occurrence of daytime flights did not show any predictive power for the distance bats flew during the following night (Table 3.8).

Table 3.8 – Parameters for the GLMMs models for *E. helvum* distance flown during the following night. These models consider all observations containing night data (142 observations). The null model corresponds to the models with no predictors, and "Disturbance" corresponds to the model with presence or absence of disturbance as the predictor, with presence as reference class. Values of Log-likelihood, AIC, difference from lowest AIC values (ΔAIC) and Akaike weights (ω) are presented.

Model	(Intr)	df	Log-likelihood	AIC	ΔAIC	ω
Null	50.52	3	-671.108	1348.2	0.00	0.698
Disturbance	49.89	4	-670.946	1349.9	1.68	0.302

Similarly, roost disturbance (i.e. daytime flights) did not show any predictive power for bat change of roost in the following day (Table 3.9).

Table 3.9 – Parameters for the GLMMs models for *E. helvum* change of roost. These models consider all observations containing information on roost change (121 observations). Null model corresponds to the models with no predictors, and "Disturbance" corresponds to the model with presence or absence of disturbance as the predictor, with presence as reference class. Values of Log-likelihood, AIC, difference from lowest AIC values (ΔAIC) and Akaike weights (ω) are presented.

Model	(Intr)	df	Log-likelihood	AIC	ΔAIC	ω
Null	-1.683	2	-60.135	124.3	0.00	0.638
Disturbance	-1.558	3	-59.703	125.4	1.14	0.362

4. **DISCUSSION**

With this study I was able to identify important predictors of day roost disturbance in colonies of straw-coloured fruit bats (*E. helvum*) from a range of landscape, weather, and intrinsic variables. Contrary to what was expected, day roost disturbance in *E. helvum* does not seem to be directly related to level of urbanisation: factors such as road density, human density and land use in surrounding areas of roosts had no measurable effect on roost disturbance, measured as the occurrence of daytime flights. Similarly, colony size at the main roosts, appeared to have no traceable influence on roost disturbance. As expected, roost disturbance was higher when captures were conducted at the roosts, validating this methodological approach of using daytime flights as a proxy of disturbance and of identifying them through tri-axial acceleration. Roost disturbance was also higher in main roosts when compared to secondary roosts, and wind and solar energy showed some relevance to explain roost disturbance. The effect of solar energy was only traceable when capture days were removed from the analysis.

Roost disturbance, however, had no identifiable effect on distance travelled in the following night, nor could it explain the changes of roost observed.

Main predictors of disturbance

Landscape factors related to level of urbanisation (i.e. human and road densities, land use) had no measurable effect on bats while in the roost. These results depart from what was expected, as several bat species are known to be sensitive to urbanisation (Russo & Ancillotto 2014), and studies with some bird species have shown that urbanisation related variables (e.g. roads, bridges, presence of pedestrians) can cause disturbance as well as affect roost site selection, space use and cause changes on energy expenditure (Riddington et al. 1996; Rogers et al. 2006b; Scobie et al. 2014; Pearse et al. 2017). Although this was unexpected, it is not completely unforeseen, as many bat species are well adapted or can thrive in urban environments (Jung & Kalko 2011; Russo & Ancillotto 2014) and other species of Pteropodidae have been shown to be able to roost, or even prefer to roost near human settlements (Hahn et al. 2014; Kumar et al. 2015). Furthermore, the effects of urbanisation on bats are considered species-specific (Russo & Ancillotto 2014; Jung & Threlfall 2016), and may change with the scale of analysis (Russo & Ancillotto 2014). Thus, the lack of a measurable behavioural response to urbanisation variables found in this study may be related to the species' specific response to this type of disturbance, that may be manifested in ways other than behavioural.

The type of roost used by bats during the day, either main or secondary, had a significant effect on presence of disturbance, and that effect was significantly higher on main roosts. To better understand the role of main roosts in disturbance, we should consider the differences between them and secondary roosts. Since landscape features in the surrounding area of roosts could not explain differences in observed bat disturbance, other hidden or untested factors may be making main roosts more prone to disturbance.

The main roosts in this study sheltered large colonies of straw-coloured fruit bats. On the other hand, there is no information about the secondary roosts discovered in this study, besides the fact that they were used by one (in one situation by two) tracked bats, in one or more nights. The species is considered conspicuous (Peel et al. 2017), more so when roosting in large numbers (Webala et al. 2014), such as the ones found in these main roosts. Bat in larger aggregations may be easier to detect by hunters (Mickleburgh et al. 1992, 2009) and hunting methods used on *E. helvum*, such as shooting, use of slingshots and capture in nets (Mickleburgh et al. 2009; Kamins et al. 2011; Peel et al. 2017) may be a cause of roost disturbance (Cardiff et al. 2009). In contrast, roosts considered secondary may have less bat abundance, and serve as temporary roosts for individuals or small groups near foraging areas, as it has been suggested for another Pteropodidae species (Roberts et al. 2012). A reduced number of bats at secondary roosts could suggest these bats have lower predation risk (Hebblewhite & Pletscher 2002), and are less prone to human persecution (Webala et al. 2014). Therefore, level of conspicuousness in main and secondary roosts, may explain differences in bat disturbance observed.

This study would have benefited from incorporating hunting information to assess day roost disturbance. Moreover, ground-truthing of secondary roosts would have been important to truly understand if these are at haphazardly locations, related to the location of their foraging areas (e.g. (Roberts et al. 2012)), containing smaller groups, and thus less conspicuous, or if these are roost with established and larger colonies. Although the accidental discovery of a large colony of *E. helvum* in Ghana using tracking devices has happened before (Hayman et al. 2012), it is unlikely that all 25 secondary roosts contain well established colonies that have gone unnoticed.

As expected, bats were more disturbed in the days of capture and tagging, and this was well reflected in the increased probability of diurnal flight. Even though captures were done at a single location each night, it is likely that disturbed individuals disturbed others while flying or perching in new trees for roosting, causing a propagation of disturbance. This sort of disturbance is likely similar to that of hunters (e.g. use of capture nets (Peel et al. 2017)).

Even though capture sessions were a source of disturbance, its unwanted consequences can never be entirely avoided (Kenward 2001), and studies using tracking devices and implying bat captures can deepen our knowledge of the species. For instance, data from the bats tracked in this study has already provided valuable information on their foraging behaviour (Fahr et al. 2015; Capote 2018), habitat use (Fahr et al. 2015), and their ability for long distance seed dispersal (Abedi-Lartey et al. 2016). With such information, conservation efforts and management actions can be specific and consider the species' ecology.

Wind had a negative effect on presence of daytime flight in the model including all observations and the model excluding days of capture, but its effect was only significant in the latter. Solar energy, although not significant, had a positive effect on presence of daytime flight, that was only identifiable when observations of days of capture were removed.

Bats roosting in trees, as is the case of *E. helvum*, are exposed to environmental variables and sunlight, and thus not protected from solar radiation (Norris & Kunz 2012). It is plausible that higher solar energy may increase the heat gain, as well as reduce heat loss through convection (Voigt & Lewanzik 2011).

Decreased wind may also affect heat loss through convection (Norris & Kunz 2012) and solar heat gain can be higher when wind speed is lower (Walsberg & Wolf 1995).

Mammals have a range of behavioural responses to solar radiation exposure, used to balance heat gain (Norris & Kunz 2012), and in some bats these include wing fanning, body licking (Ochoa-Acuña and Kunz 1999; Welbergen et al. 2008), shade-seeking (Welbergen et al. 2008), and change of position within the roost (Licht & Leitner 1967). As different positions in the roost may be exposed differently to solar radiation, and thus have different temperatures (Snoyman et al. 2012), changes in positions can be sought by bats to refuge in cooler parts of the roost (Licht & Leitner 1967). Therefore, flights observed during the day associated with higher solar energy and lower wind speed, may be a thermoregulatory behaviour, used to change positions within the roost or seek shade, and consequently decrease heat gain.

Contrary to what was expected, colony size had no identifiable effect of roost disturbance. The main roosts in this study sheltered colonies of different sizes, that ranged from just a few thousands to several millions of straw-coloured fruit bats, and as group size can be related to increased sensitivity to disturbance (larger group size may be related to larger response distances) (Taylor and Knight, 2003), I expected colony size could help explain differences in roost disturbance. However, colony size had no expressed effect on daytime flights.

Responses to day roost disturbance

Roost change is common in this dataset. In fact, the 25 new roosting locations found were used by bats tagged in the five main roosts. One could think bats changed roosts in response to disturbance, as higher disturbance would lead to lower roost fidelity (Lewis 1995), and as *E. helvum* bats have been reported to flee roosts in response to hunting (a probable cause of disturbance) (Peel et al. 2017). However, the results showed that roost change was unrelated to roost disturbance.

Roost change has been documented for *E. helvum* before (Hayman et al. 2012) and for other pteropodid bat species as well (Banack 2002; Roberts et al. 2012). It may entail benefits for bats, allowing bats to maintain proximity to foraging areas (Kunz 1982) and serving as stopovers for bats commuting longer distances, or may be simply related to changes in food resources' availability (Roberts et al. 2012).

When analysing possible impacts of disturbance on distance flown while foraging, no identifiable effects were found. Bat flight is energetically costly, more so during the day (Voigt & Lewanzik 2011). Thus, I expected roost disturbance to have an effect on distance flown during the night, either negative, due to increased energy expenditure (Speakman et al. 1991), or positive, in order to reach more advantageous foraging locations (Rainho & Palmeirim 2011). However, no such effect was detected.

Differences in distance flown may be better explained by other factors, such as the location of bat roosts and their foraging areas. If secondary roosts found were located closer to foraging areas, as it has been suggested for other species (e.g. Roberts et al. 2012), commuting distances could be shorter when bats leave to forage from those roosts. A relationship between location of foraging and roosting areas in order to minimize commuting distance and energy expenditure has been suggested for bird species (Dias et al. 2006; Rogers et al. 2006a) and bats as well (Kunz 1982), and thus is not farfetched for this species.

In this case, change of roost and distance flown seem to not be related to disturbance. Yet, this does not mean disturbance had no negative effect on bats. Disturbance can affect bats' body condition (Phelps & Kingston 2018) and energy expenditure (Speakman et al. 1991), and can have negative effects at physiological and cellular levels, impacting animals' immune system, metabolism and reproductive success (Knight & Swaddle 2011), which are not reflected by the parameters tested. Furthermore, this study focused on male adults, and susceptibility to disturbance may differ for females and young (Kunz 1982; Edson et al. 2015).

Importance of detecting disturbance through tri-axial acceleration

Roost disturbance is among the major threats faced by bats (Mickleburgh et al. 2002) and methods to detect and assess disturbance are still lacking. Disturbance is often hard to quantify and most published studies on this topic using bats rely on qualitative assessments (e.g. Edson et al. 2015), or identify disturbance by its effects at a population or community level. In those cases, disturbance is identified by changes in abundance (Ferrara & Leberg 2005), bat diversity (Medellín et al. 2000), species richness (Lou et al. 2013) or colony size (Cardiff et al. 2009).

Bat studies using tracking devices have been conducted for at least the last 50 years (O'Mara et al. 2014) and are important tools to study bat movements (Smith et al. 2011). As various studies with pteropodid bats already integrate GPS and acceleration technology (e.g. De Jong et al. 2013; Weber et al. 2015; Oleksy et al. 2017) there is great potential in using this method to identify and possibly quantify roost disturbance. Furthermore, this method can be applied to data that has already been collected and can be integrated into new studies collecting GPS and acceleration data.

Identifying disturbance through tri-axial acceleration data does not require the presence of researchers in the roosts after attachment of devices and release of bats. This method can thus help detect events of disturbance that may be discouraged if researchers are in the vicinity of the roost, allowing a truer depiction of what goes on in the roost. Furthermore, using daytime flights and identifying them through tri-axial acceleration provides a uniform measure of disturbance allowing comparisons within the same roost and between roosts.

Despite its ability to identify daytime flights as day roost disturbance, this method would benefit from being tested in a more controlled environment. The setting of a baseline for disturbance has been suggested (e.g. Bowles 1995), and done before (e.g. (Thomas 1995), and understanding what can cause bats to fly during the day, considering the specie's natural behaviour, would further validate this method. For instance, the method could be tested in bats from a roost known to be undisturbed, and in roosts where causes and levels of disturbance can be assessed through direct observation. In this way, it would be possible to create a baseline of flights during the day, and to understand how different levels of disturbance are reflected in presence and amount of daytime flights.

Notwithstanding this limitation, this study is pioneer in identifying day roost disturbance in bats using tri-axial acceleration data and can greatly improve knowledge of disturbance in this species and other pteropodid bats.

Implications for conservation

As *E. helvum*, many other pteropodid bats face risk of extinction (Mickleburgh et al. 2002), and roost disturbance is one of the main threats to these species (Mickleburgh et al. 1992). This study successfully assessed roost disturbance and was able to identify important predictors of disturbance.

In this study, disturbance was higher in *E. helvum* main roosts. This information can be used to increase monitoring in main roosts, and investigate the causes making them more vulnerable to disturbance. In the future, this method may be used in comparative studies including a wider range of colonies, possibly allowing to identify roosts that are more highly disturbed and to increase monitoring at those roost. Additionality, information on causes of roost disturbance can be used to develop protection measures that can be integrated into wildlife management policies (e.g. Riddington et al. 1996; Blanc et al. 2006; Pearse et al. 2017).

This study also allowed the unveiling of 25 new roosting locations for *E. helvum*. It is not known if some of these are established roosts, but this information alone provides a starting point to better understand this species roosting requirements and preferences, which can be important to integrate into sustainable management plans (Tidemann & Nelson 2004), and help identify protection needs and measures for roosts (Banack 2002; Weber et al. 2015).

As this species is able to migrate for over 2000 km (Richter & Cumming 2008; Ossa et al. 2012), travel long distances to forage (Fahr et al. 2015), change roosts (this study; Hayman et al. 2012; Peel et al. 2017), and is thought to have a fission-fusion social structure (Peel et al. 2017), understanding roost disturbance and identifying new roosting location is even more important, as its conservation cannot be limited to their known main roosts.

The conservation of the straw-coloured fruit bat is important not only because its population is declining, in response to great hunting pressure (Mickleburgh et al. 2009; Kamins et al. 2011), but also because this species provides valuable ecosystem services as an important seed disperser (Abedi-Lartey et al. 2016). This species is able to disperse large seeds possibly up to 560 meters, and small seeds up to 75 km from the parent tree (Abedi-Lartey et al. 2016), and due to its migration ability, it can be a keystone species for seed dispersal across continental Africa (Richter & Cumming 2008; Ossa et al. 2012). Therefore, conservation actions should aim to protect the species itself and the ecosystem services it can provide.

This study provides a useful starting point to better identify and understand roost disturbance in *E. helvum* bats. Hopefully, it can be used to advance the increase knowledge on roost disturbance of this and other pteropodid bats, in which this methodological approach can be applied, ultimately contributing to their conservation.

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SUPPLEMENTARY MATERIALS

SECTION 1: Metadata of study subjects

Table S1.1 – Metadata of bats: animal identification (Animal ID), first day of data (Day 1), number of data days (Days), sex (m – male, f – female), age (ad – adult, yg-ad – young adult), forearm length (mm), and body mass (BM, in g).

Animal ID	Location	Season	Year	Day 1	Days	Sex	Age	Forearm	BM
1079	Accra	wet	2009	27-08	2	m	ad	118.1	284
1080	Accra	wet	2009	27-08	1	m	ad	113.9	244
1081	Accra	wet	2009	27-08	2	m	ad	123.5	274
1084	Accra	wet	2009	29-08	3	m	ad	115.1	239
1086	Accra	wet	2009	29-08	1	m	ad	118.2	277
1088	Accra	wet	2009	29-08	1	m	ad	120	247
1607	Accra	dry	2011	04-02	5	m	ad	124.7	321
1616	Accra	dry	2011	06-02	1	m	ad	121	292
1620	Accra	dry	2011	07-02	1	m	ad	119.7	255
1626	Accra	dry	2011	03-02	1	m	ad	119.1	280
1875	Kibi	wet	2011	28-08	2	f	ad	119.1	280
1870_2	Kibi	wet	2011	30-08	1	m	ad	117.5	275
2394	Kibi	wet	2012	10-09	1	m	ad	118.8	275
2396	Kibi	wet	2012	29-08	5	m	ad	121.6	270
2402	Kibi	wet	2012	07-09	5	m	ad	120.3	272
2404	Kibi	wet	2012	14-09	3	m	yg-ad	121.9	270
2608	Kibi	dry	2013	26-01	3	m	ad	117.9	275
2612	Kibi	dry	2013	26-01	3	m	ad	125.6	250
2772	Kibi	dry	2013	31-01	2	m	ad	122	245
2609	Kibi	wet	2013	21-09	4	m	ad	122.5	290
1618	Ouagadougou	wet	2013	20-08	5	m	ad	103.7	250
1619	Ouagadougou	wet	2013	20-08	6	m	ad	118.9	275
1621	Ouagadougou	wet	2013	29-08	3	m	ad	124.0	260
1624	Ouagadougou	wet	2013	22-08	4	m	ad	124.8	280
3967	Ouagadougou	wet	2014	18-06	2	m	ad	121.4	280
3969	Ouagadougou	wet	2014	19-06	4	m	ad	116.6	270
3970	Ouagadougou	wet	2014	19-06	4	m	ad	122.4	300
3971	Ouagadougou	wet	2014	19-06	5	m	ad	121.3	315
3972	Ouagadougou	wet	2014	20-06	1	m	ad	122.0	255
3973	Ouagadougou	wet	2014	20-06	4	m	ad	123.7	265
3359	Kasanka	wet	2013	05-12	5	m	yg-ad	126.1	290
3364	Kasanka	wet	2013	06-12	5	m	ad	118.1	285
3370	Kasanka	wet	2013	06-12	4	m	ad	124	298
4148	Kasanka	wet	2014	30-11	4	m	ad	131.2	306
4149	Kasanka	wet	2014	30-11	6	m	ad	116.4	278
4151	Kasanka	wet	2014	30-11	7	m	ad	125.4	275
4154	Kasanka	wet	2014	30-11	6	m	ad	122.3	269
4155	Kasanka	wet	2014	30-11	6	m	ad	120.6	282
4156	Kasanka	wet	2014	01-12	6	m	ad	125.1	278
4157	Kasanka	wet	2014	01-12	6	m	ad	126.4	315
4158	Kasanka	wet	2014	01-12	6	m	ad	121.4	274
4160	Kasanka	wet	2014	30-11	6	m	ad	127.3	286
4161	Kasanka	wet	2014	30-11	1	m	ad	122.9	272
4162	Kasanka	wet	2014	01-12	1	m	ad	124.6	293
4163	Kasanka	wet	2014	01-12	7	m	ad	121.7	273
4164	Kasanka	wet	2014	01-12	6	m	ad	121.2	281

SECTION 2: GPS and acceleration settings

Table S2.1 – Datalogger settings by bat: bat's body mass (BM, in g), datalogger mass (DLM, in g), weight percentage of the datalogger by bat (% BM), attachment method, GPS frequency of fixes (min), acceleration frequency (ACC freq, in Hz) and bursts duration (ACC burst in s/min).

Animal ID	Location	Year	Season	BM	DLM	% BM	Attachment method	GPS	ACC freq	ACC burst
1079	Accra	2009	wet	284	19.5	6.9	glue	10	18.74	15
1080	Accra	2009	wet	244	19.5	8.0	glue	10	18.74	15
1081	Accra	2009	wet	274	19.5	7.1	glue	10	18.74	15
1084	Accra	2009	wet	239	19.5	8.2	glue	10/5	18.74	15
1086	Accra	2009	wet	277	19.5	7.0	glue	10/5	18.74	15
1088	Accra	2009	wet	247	19.5	7.9	glue	10/5	18.74	15
1607	Accra	2011	dry	321	24	7.5	glue	30/10	18.74	15
1616	Accra	2011	dry	292	24	8.2	glue	30/10	18.74	15
1620	Accra	2011	dry	255	24	9.4	glue	30/2.5	18.74	15
1626	Accra	2011	dry	280	24	8.6	glue	30/2.5	18.74	15
1875	Kibi	2011	wet	280	21.1	7.5	glue	30/2.5	18.74	15
1870_2	Kibi	2011	wet	275	22	8.0	glue	30/2.5	18.74	15
2394	Kibi	2012	wet	275	25.4	9.2	collar	30/2.5	18.74	15
2396	Kibi	2012	wet	270	24.3	9.0	collar	30/2.5	18.74	15
2402	Kibi	2012	wet	272	23	8.5	collar	30/2.5	18.74	15
2404	Kibi	2012	wet	270	23.5	8.7	collar	30/2.5	18.74	15
2608	Kibi	2013	dry	275	26.2	9.5	collar	30/2.5	18.74	15
2612	Kibi	2013	dry	250	25.9	10.4	collar	30/2.5	18.74	15
2772	Kibi	2013	dry	245	25.8	10.5	collar	30/2.5	18.74	15
2609	Kibi	2013	wet	290	22.2	7.7	collar	30/2.5	18.74	15
1618	Ouagadougou	2013	wet	250	20.5	8.2	collar	30/2.5	18.74	15
1619	Ouagadougou	2013	wet	275	20.5	7.5	collar	30/2.5	18.74	15
1621	Ouagadougou	2013	wet	260	20.5	7.9	collar	30/2.5	18.74	15
1624	Ouagadougou	2013	wet	280	20.5	7.3	collar	30/2.5	18.74	15
3967	Ouagadougou	2014	wet	280	22	7.9	collar	30/2.5	18.74	15
3969	Ouagadougou	2014	wet	270	22	8.1	collar	30/2.5	18.74	15
3970	Ouagadougou	2014	wet	300	22	7.3	collar	30/2.5	18.74	15
3971	Ouagadougou	2014	wet	315	22	7.0	collar	30/2.5	18.74	15
3972	Ouagadougou	2014	wet	255	22	8.6	collar	30/2.5	18.74	15
3973	Ouagadougou	2014	wet	265	22	8.3	collar	30/2.5	18.74	15
3359	Kasanka	2013	wet	290	22	7.6	collar	30/2.5	20	15
3364	Kasanka	2013	wet	285	22	7.7	collar	30/2.5	20	15
3370	Kasanka	2013	wet	298	22	7.4	collar	30/2.5	20	15
4148	Kasanka	2014	wet	306	20.5	6.7	collar	30/2.5	20	14
4149	Kasanka	2014	wet	278	20.5	7.4	collar	30/2.5	20	14
4151	Kasanka	2014	wet	275	20.5	7.5	collar	30/2.5	20	14
4154	Kasanka	2014	wet	269	20.5	7.6	collar	30/2.5	20	14
4155	Kasanka	2014	wet	282	20.5	7.3	collar	30/2.5	20	14
4156	Kasanka	2014	wet	278	20.5	7.4	collar	30/2.5	20	14
4157	Kasanka	2014	wet	315	20.5	6.5	collar	30/2.5	20	14
4158	Kasanka	2014	wet	274	20.5	7.5	collar	30/2.5	20	14
4160	Kasanka	2014	wet	286	20.5	7.2	collar	30/2.5	20	14
4161	Kasanka	2014	wet	272	20.5	7.5	collar	30/2.5	20	14
4162	Kasanka	2014	wet	293	20.5	7.0	collar	30/2.5	20	14
4163	Kasanka	2014	wet	273	20.5	7.5	collar	30/2.5	20	14
4164	Kasanka	2014	wet	281	20.5	7.3	collar	30/2.5	20	14

SECTION 3: Complementary information on variables collection

Table S3.1 – Weather data collection information: study site, year, source (Climate Forecast System Reanalysis – CFSR, or weather station), geographic location of the data (latitude, longitude), elevation (m), and access date to the data. Data temporal resolution of one day.

Study site	Year	Source	Location (lat, long)	Elevation (m)	Access date
Accra	2009, 2011	CFSR	5.776º, 0.000º	80	02 Aug 2018
Kibi	2011, 2012, 2013	CFSR	6.088º, - 0.625º	593	02 Aug 2018
Ouagadougou	2013, 2014	CFSR	12.333º, -1.562º	307	02 Aug 2018
Kasanka	2013	CFSR	-13.270º, 30.312º	1481	02 Aug 2018
Kasanka	2014	Weather station	-13.227º, 30.215º	1395	02 Aug 2018

Table S3.2 – Summary table of MODIS images used to extract NDVI, including type of MODIS image (Aqua or Terra), temporal resolution, spatial resolution (m), dates of the images, overall cloud cover (%, this includes two values when study area overlapped over two MODIS images).

Location	Year	Bat tracking dates	Modis image	Temporal resolution	Spatial resolution	Date of image	Cloud cover
Accra	2009	27 – 31 Aug	Aqua	1 month	1000	01-31 Aug	31; 37 %
Accra	2011	03 – 08 Feb	Terra	16 days	250	02-17 Feb	1; 21 %
Kibi	2011	28 – 30 Aug	Aqua	1 month	1000	01-31 Aug	27; 42 %
Kibi	2012	29 Aug– 16 Sept	Aqua	1 month	1000	01-30 Sept	13; 30 %
Kibi	2013	26 Jan – 01 Feb	Terra	16 days	250	17 Jan- 01 Feb	1; 13 %
Kibi	2013	21 – 24 Sept	Aqua	1 month	1000	01-30 Sept	17; 29 %
Ouagadougou	2013	20 – 31 Aug	Terra	16 days	250	29 Aug - 13 Sept	12%
Ouagadougou	2014	18 – 23 Jun	Terra	16 days	250	10 - 25 Jan	1%
Kasanka	2013	5 – 10 Dec	Terra	16 days	250	17 Nov - 02 Dez	2; 4%
Kasanka	2014	30 Nov – 7 Dec	Terra	16 days	250	17 Nov - 02 Dez	2; 2 %

SECTION 4: Spearman correlation results and variable exclusion

Table S4.1 – Spearman correlation table for the different variables considered for the analysis of day roost disturbance. Correlations higher than 0.7 are presented in bold.

	Precip	**Wind**	**Humidity**	**Solar energy**	**Forearm**	**Weight**	**Colony size**	**Dist prev night**	**Human density**
Precip	1.00	-0.17	**0.76**	-0.29	-0.13	-0.04	-0.46	-0.03	0.32
Wind	-0.17	1.00	-0.35	0.50	0.01	0.14	-0.11	0.02	0.03
Humidity	0.76	-0.35	1.00	-0.55	-0.11	-0.04	-0.36	0.07	0.24
Solar energy	-0.29	0.50	-0.55	1.00	0.02	0.07	-0.12	-0.14	0.04
Forearm	-0.13	0.01	-0.11	0.02	1.00	0.36	0.40	0.33	-0.31
Weight	-0.04	0.14	-0.04	0.07	0.36	1.00	0.27	0.37	-0.14
Bat population	-0.46	-0.11	-0.36	-0.12	0.40	0.27	1.00	0.51	**-0.81**
Dist prev night	-0.03	0.02	0.07	-0.14	0.33	0.37	0.51	1.00	-0.26
Human density	0.32	0.03	0.24	0.04	-0.31	-0.14	-0.81	-0.26	1.00

(Table S4.1 cont.)

	NDVI	Road density	Trees cover	Shrub cover	Grassland	Cropland	V. aquatic	Lichen Mosses	Bare areas	Built up	Open water	T med
Precip	0.66	0.20	-0.10	-0.44	-0.26	0.12	-0.02	-0.55	0.05	0.38	0.45	-0.20
Wind	-0.17	-0.04	-0.12	0.06	0.01	-0.13	0.13	0.17	0.13	-0.09	-0.07	0.06
Humidity	0.68	0.09	0.06	-0.64	-0.19	-0.04	0.10	-0.67	-0.11	0.38	0.43	-0.33
Solar energy	-0.29	0.10	-0.21	0.29	-0.06	0.13	-0.15	0.34	0.19	-0.06	-0.05	0.33
Forearm	-0.17	-0.29	0.30	-0.01	0.28	-0.31	0.27	-0.02	-0.25	-0.29	-0.28	-0.22
Weight	-0.27	-0.07	0.17	-0.01	0.22	-0.30	0.33	-0.01	-0.10	-0.31	-0.24	-0.24
Colony size	-0.35	**-0.80**	**0.79**	0.25	**0.81**	**-0.80**	**0.80**	0.26	**-0.79**	**-0.84**	**0.84**	-0.52
Dist prev night	-0.19	-0.36	0.35	-0.24	0.31	-0.54	0.51	-0.09	-0.35	-0.34	-0.25	-0.39
Human density	0.12	**0.80**	**-0.81**	-0.22	**-0.84**	**0.72**	-0.41	-0.27	**0.78**	**0.81**	**0.89**	0.66
NDVI	1.00	0.09	0.12	-0.45	-0.20	0.09	-0.11	-0.56	-0.15	0.36	0.31	-0.25
Road density	0.09	1.00	-0.61	-0.06	**-0.73**	**0.76**	-0.58	-0.12	0.65	0.65	0.63	0.58
Trees cover	0.12	-0.61	1.00	-0.25	0.60	**-0.72**	0.41	-0.12	**-0.94**	-0.54	-0.68	**-0.74**
Shrubs cover	-0.45	-0.06	-0.25	1.00	0.17	0.25	-0.29	**0.83**	0.30	-0.38	-0.44	0.28
Grassland	-0.20	**-0.73**	0.60	0.17	1.00	**-0.82**	0.68	0.16	-0.62	**-0.92**	**-0.79**	**-0.70**
Cropland	0.09	**0.76**	-0.72	0.25	**-0.82**	1.00	**-0.86**	0.15	**0.72**	**0.75**	0.64	**0.79**
V. aquatic	-0.11	-0.58	0.41	-0.29	0.68	**-0.86**	1.00	-0.31	-0.38	-0.61	-0.36	-0.62
Lichen Mosses	-0.56	-0.12	-0.12	**0.83**	0.16	0.15	-0.31	1.00	0.11	-0.36	-0.48	0.20
Bare areas	-0.15	0.65	**-0.94**	0.30	-0.62	**0.72**	-0.38	0.11	1.00	0.52	0.60	**0.74**
Built up	0.36	0.65	-0.54	-0.38	**-0.92**	**0.75**	-0.61	-0.36	0.52	1.00	**0.88**	0.58
Open water	0.31	0.63	**-0.68**	-0.44	**-0.79**	0.64	-0.36	-0.48	0.60	**0.88**	1.00	0.55
T med	-0.25	0.58	**-0.74**	0.28	**-0.70**	**0.79**	-0.62	0.20	**0.74**	0.58	0.55	1.00

Table S4.2 – List of variables excluded and kept after analysis of spearman's correlation test.

Excluded variables	Included variables
Precipitation	Mean temperature
Human density	Wind
Road density	Solar energy
Tree cover	Humidity
Grassland	Forearm
Cropland	Weight
Lichen mosses	Distance previous night
Bare areas	NDVI
Built up	Shrub cover
Open water	Colony size