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ORIGINAL CONTRIBUTION

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Seasonal pattern in population dynamics and host plant use of non-swarming *Ruspolia differens* Serville (Orthoptera: Tettigoniidae)

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Abstract

The edible *Ruspolia differens* (Serville) (Orthoptera: Tettigoniidae) is an important source of food in East Africa, but the seasonality of its population dynamics and host plant use are not fully understood. We studied seasonal patterns in the population density and relative frequency of developmental stages, sexes, colour morphs and host plants of the non-swarming *R. differens* at two study sites in central Uganda over 15 months. Linear mixed models were used to study how precipitation and Enhanced Vegetation Index (EVI) predict population density and relative frequency of developmental stages, sexes, colour morphs and host plants. The results showed that all developmental stages of non-swarming *R. differens* were found in the field throughout the year. The population densities of *R. differens* were high in wet seasons and low in dry seasons and were best predicted by the EVI of the previous month. The sex ratio of the non-swarming *R. differens* populations was female biased. The proportion of males and green colour morphs increased during and after the rainy season. The use of host plants fluctuated seasonally so that during the greener seasons individuals used the more preferred host *Panicum maximum* more frequently. Overall, our work indicates that *R. differens* has a seasonal dynamic so that vegetation greenness can be used to forecast non-swarming *R. differens* population densities. Our results also suggest that source populations for swarming individuals might have a local origin. This is important for the management of habitats for reproduction and conservation of viable populations of *R. differens* in East Africa.

KEYWORDS

edible insects, population dynamics, rainfall, the edible grasshopper, Uganda, vegetation greenness

1 | INTRODUCTION

The edible *Ruspolia differens* (Serville) (Orthoptera: Tettigoniidae), “nsenene,” is an important source of food and nutrition for people in East Africa, for example, in Uganda, where it is harvested from natural populations during the two annual periods of swarming (Agea, Biryomumaisho, Buyinza, & Nabanoga, 2008). *Ruspolia differens* is mainly a nocturnal species (Bailey & McCrae, 1978) with a body length varying between 30 and 42 mm (Matojo & Yarro, 2013). The duration of the life cycle of *R. differens* is approximately 147 days (Brits & Thornton, 1981). The egg development typically takes 19 days (Brits & Thornton, 1981; Hartley, 1971) after which the developmental cycle includes six (male) or seven (female) nymphal stages with a nymphal duration of approximately 46 (male) or 56 (female) days at 30°C (Brits & Thornton, 1981). For adult females, pre-oviposition and oviposition periods last approximately 16 and 32 days, respectively, and in the laboratory, the adults can live 50–90 days (Brits & Thornton, 1981). The species has two typical colour morphs, green and brown, while morphs with purple stripes and purple head are found more rarely (Bailey & McCrae, 1978). In East Africa, *R. differens* lives in grassland habitats (Bailey & McCrae, 1978) and can feed on a large number of grass and sedge species (Valtonen et al., 2018). However, it is selective in its host use and prefers inflorescences to leaves (Valtonen et al., 2018). The species forms swarms which, in East Africa, typically occur during and after the two annual rainy seasons, usually with a preponderance of males (Bailey & McCrae, 1978). The swarms are thought to be associated with long-distance migration, but the areas where reproduction takes place and the origins of the swarms are unknown. In the swarming phase, the behaviour of individuals changes as they fly actively in high densities, mostly at night, and they are attracted to lights (Bailey & McCrae, 1978; McCrae, 1982).

The seasonal dynamics of non-swarming *R. differens* populations, where solitary individuals feed in grassland habitats, is currently poorly understood. Seasonal variation in population densities, colour polymorphism and sex ratio of these non-swarming *R. differens* has been reported in a short-term study in north-western Tanzania (Matojo & Njau, 2010; Matojo & Yarro, 2013). However, longer-term data on the seasonal dynamics of the population densities of either nymphs or adults in non-swarming populations, or seasonal patterns in sex ratio, proportions of colour morphs and host use are, to our knowledge, currently lacking. Yet, such information is necessary when understanding the basic ecology and biology of *R. differens*, and it is also essential for the conservation and long-term sustainable harvest of this species.

In this study, we report a long-term (15-month) survey conducted on the seasonal dynamics of a non-swarming *R. differens* population in Uganda. Specifically, we asked whether there is a seasonal pattern in population density, or relative frequencies of developmental stages, sexes, colour morphs and host plants used, and whether these patterns are associated with the two key variables describing the environmental conditions in the study area, that is, precipitation and vegetation greenness.

We hypothesized that, since the seasonal patterns in the populations of many tropical insects are typically related to precipitation (Davis, 1945; Dobzhansky & Pavan, 1950; Kasenene & Roininen, 1999; Nyeko, 2009; Valtonen et al., 2013; Wolda, 1980, 1988), non-swarming (local) *R. differens* populations should also be fluctuating in synchrony with precipitation, potentially with a short time lag. More specifically, we expected that the two annual rainy seasons in the study area lead to a rapid increase in the production of new grass foliage (increased vegetation greenness; Yan, Zhang, Yu, & Guo, 2017) and grass inflorescences. This, in turn, increases the availability of food for *R. differens*, which leads to their increased population density. Increased moisture during rainy seasons could also have a direct positive effect on *R. differens* by preventing mortality due to desiccation (Gehrken & Doumbia, 1996). Particularly, egg development of *R. differens* is known to require a high level of humidity (Brits & Thornton, 1981).

2 | MATERIALS AND METHODS

2.1 | Study area and the study sites

The study was conducted in the grazing farmlands at the Makerere University Agricultural Research Institute Kabanyolo (MUARIK; 0.46°N and 32.61°E; approx. 1,150 m a.s.l.) in Wakiso district, Uganda. The study area has two annual rainy seasons which are rather similar in their duration and intensity (WMO, 2018): The first is between March and May and the second is between September and November, with a mean annual rainfall of 1,170 mm (Nsubuga, Olwoch, & Rautenbach, 2011). The mean daily minimum temperature in the region is 17.6°C, and the mean daily maximum temperature is 27.8°C (WMO, 2018). The soil type is ferrallitic (Edema & Adipala, 1994).

The study was conducted in two study sites located 1.5 km apart. Both study sites represent open grasslands with solitary trees, shrubs and herbs. Study Site 1 was 5.2 ha and dominated by grass *Brachiaria ruziziensis* (Germ & Evrard). Study Site 2 was 11.0 ha and dominated by two grasses: *Panicum maximum* (Jacq.) and *Chloris gayana* (Kunth).

To describe the seasonal variation in the environmental conditions in our study area, we obtained information on precipitation and vegetation greenness. Estimates of daily precipitation (mm) were obtained using the IRI Rainfall Analysis Tool (IRI, 2018a). This data set represents satellite-estimated precipitation data generated by Climate Prediction Center Morphing Technique (CMORPH) (Joyce, Janowiak, Arkin, & Xie, 2004). The spatial resolution of the data set is 0.25 × 0.25° lat/long grid. For statistical analyses, we calculated the sum of precipitation (mm) for the studied months within the grid cell around MUARIK (covering approx. 28 × 28 km region). The satellite-estimated precipitation correlates well with the observed precipitation at the nearest weather station at Namulonge, 8 km north of MUARIK (Supporting Information Figure S1).

Vegetation greenness of the studied area was described using the Enhanced Vegetation Index (EVI) (derived from IRI, 2018b). This data set originates from United States Geological Survey, Land Processes Distributed Active Archive Center, Moderate Resolution Imaging Spectroradiometer (USGS LandDAAC MODIS) (Huete et al., 2002). The spatial resolution of the data set is 250 × 250 m. For statistical analyses, we calculated the mean EVI value for the studied months across an approx. 22 × 22 km region around MUARIK (ranging from 32.51°E to 32.71°E and 0.37°N to 0.57°N).

2.2 | Sampling of *Ruspolia differens*

The non-swarming populations of *R. differens* were sampled for 15 months between November 2015 and January 2017. All censuses were made by the same observer (R.O.). Each of the two study sites was visited one to six nights per month (in 83% of the cases, this involved 3–5 census nights per month). Each night, the study site was censused for 3.5 hr between 7:30 and 11:00 p.m. Data were collected by walking along a pre-defined trail, established on both study sites, and starting at a random point of the trail. During the walk, *R. differens* were searched for with the help of an insect binocular and an overhead light. From each encountered individual, we recorded the developmental stage, sex (when possible), colour morph and the host plant species on which the individual was encountered. *Ruspolia differens* males and females go through six and seven nymphal stages, respectively (Brits & Thornton, 1981), but, for simplicity, we classified the developmental stages as "small nymphs" (stages 1–3), "medium nymphs" (stages 4–5), "large nymphs" (stages 6–7) and "adults." The ovipositor was used to distinguish females from males (this was possible from the 4th nymphal stage onward). We classified the colour morphs as "green" and "brown"; light brown and purple striped brown were pooled with the brown colour morph, while purple light green, light green, pale green and purple striped green were pooled with the green colour morph. The mean number of *R. differens* recorded per night (per 3.5-hr sampling intensity; Supporting Information Table S1) in each studied month was calculated and used as an estimate of the *R. differens* population density. For each studied month, we also calculated the proportion of recorded individuals representing each developmental stage, sex or colour morph, and the proportion of individuals observed on the six most frequent host plant species of each site. The monthly values were used in all statistical analyses.

2.3 | Statistical analyses

We modelled the population density of *R. differens* with precipitation and EVI, using linear mixed models. Precipitation and greenness correlated positively and strongly with each other (Pearson's correlation coefficient = 0.65, $p = 0.006$) and could not be added to the same model as explanatory variables. For this reason, we

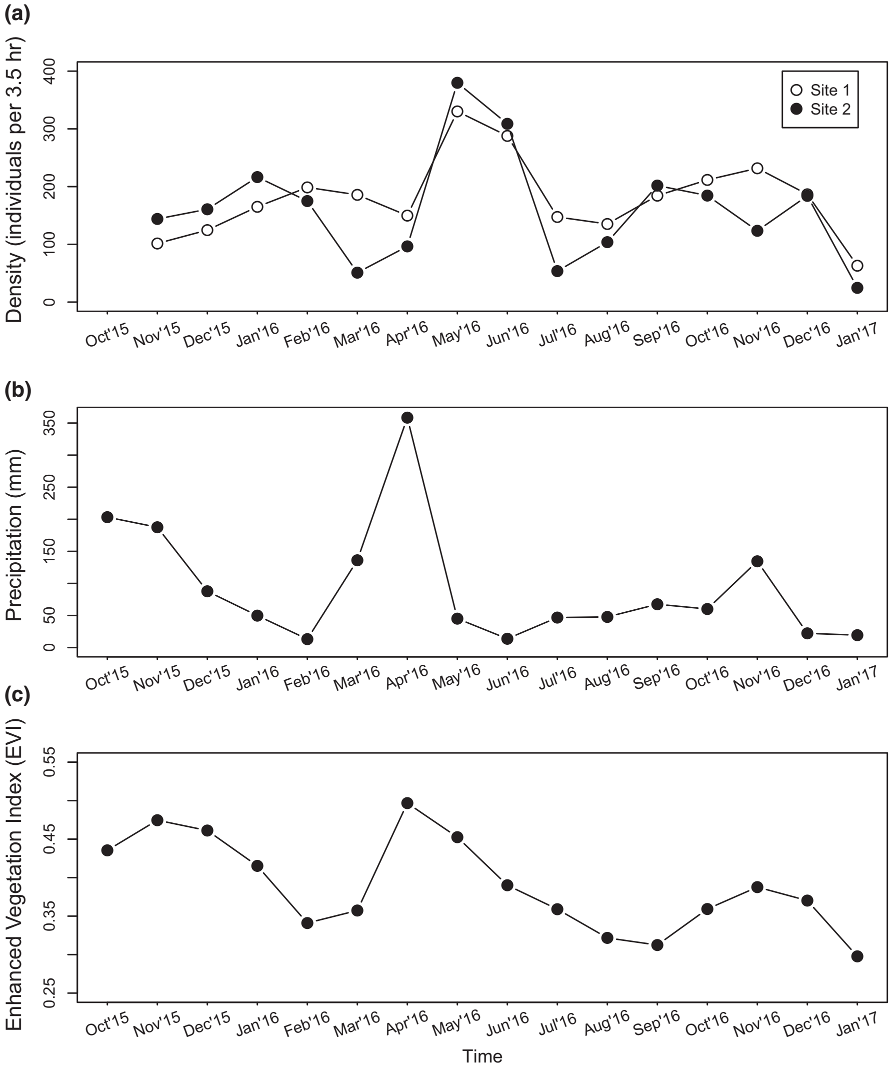


FIGURE 1 (a) Seasonal pattern of the population density of *Ruspolia differens* in the two study sites at MUARIK, Uganda. The population densities at the two sites correlated positively (Pearson's correlation coefficient = 0.79, $p < 0.001$). Seasonal pattern in (b) accumulated precipitation per month (mm) and (c) Enhanced Vegetation Index (EVI)

fitted four models where the population density (mean of Sites 1 and 2, as they correlated positively; Figure 1) was the dependent variable, and (a) precipitation, (b) EVI, (c) precipitation of the previous month (d) or EVI of the previous month, as the explanatory variables. In each model, we accounted for temporal autocorrelation by specifying residual correlation structure as an auto-regressive model of order 1 (package "nlme" in R; Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2018) following Zuur, Ieno, Walker, Saveliev, and Smith (2009; p. 143–150). The fit of the four models was compared based on the Akaike information criterion (AIC) (Burnham & Anderson, 2002).

Linear mixed models (as described above) were also fitted to model the proportion of adults and youngest nymphs, sex ratio, ratio of green and brown morphs and proportion of individuals observed on the two most This should be: "frequently used host" species of each site. All statistical analyses were conducted with program R version 3.3.2 (R Development Core Team, 2016).

3 | RESULTS

3.1 | Seasonal pattern in the population density of ***Ruspolia*** differens

In both study sites, the population densities of *R. differens* were low in the dry seasons and high in the rainy seasons (Figure 1a). Both precipitation (Figure 1b) and EVI (Figure 1c) showed a typical seasonal pattern for the study region, with two annual wet and greener seasons in around April and November. The population density of *R. differens* was best (and positively) predicted by the EVI of the previous month (linear mixed model; slope = 1,174 [*SE* ± 361], *t* = 3.25, *p* = 0.006; AIC = 151.6). EVI of the current month (AIC = 157.4), precipitation of the previous month (AIC = 168.5) and precipitation of the current month (AIC = 170.2) were poorer predictors of population density.

3.2 | Seasonal pattern in the relative frequencies of developmental stages

Nymphs of all stages and adult *R. differens* were present in the field throughout the study period (Figure 2; average densities shown in Supporting Information Figure S2). The proportion of adults (out of all observed individuals; mean of Site 1 and Site 2) was not predicted by either EVI or precipitation. The best-ranked model (according to AIC) showed no association between the EVI of the current month and the proportion of adults (linear mixed model; *p* = 0.18). Also, the proportion of small nymphs (out of all observed individuals; mean of Site 1 and Site 2) was not predicted by either EVI or precipitation. The best-ranked model (according to AIC) showed no association between the EVI of the current month and the proportion of small nymphs (linear mixed model; *p* = 0.69).

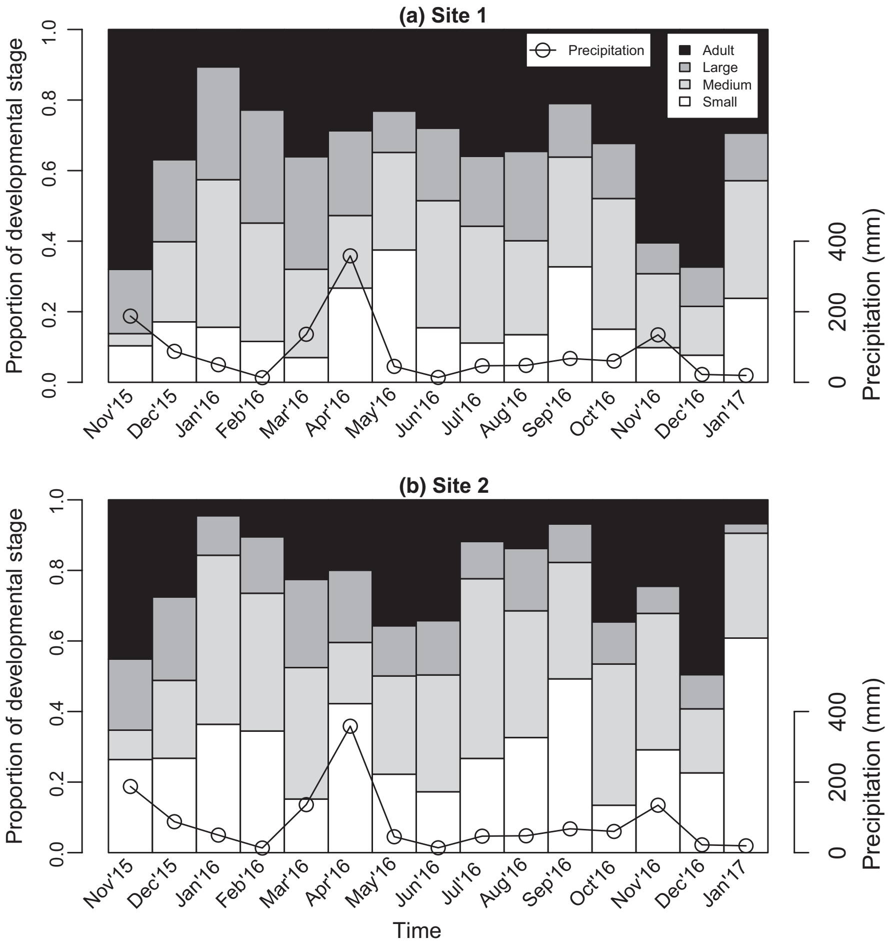


FIGURE 2 Seasonal pattern of the proportions of developmental stages of *Ruspolia differens* (a) at Site 1 and (b) at Site 2 at MUARIK, Uganda, shown with monthly precipitation

3.3 | Seasonal pattern in the sex ratio

At both sites, the sex ratio was biased towards females throughout the sampling period (the data from the first sampling month, November 2015, was excluded from analyses; Figure 3). The proportion of males (mean of Site 1 and Site 2) was best (and positively) predicted by the EVI of the previous month (linear mixed model; slope = 0.50 [*SE* ± 0.17], *t* = 3.0, *p* = 0.012; AIC = −43.9). EVI of the current month (AIC = −37.6), precipitation of the previous month (AIC = −25.3) and precipitation of the current month (AIC = −24.9) were poorer predictors of sex ratio.

3.4 | Seasonal pattern in the colour morphs

There was a strong seasonal fluctuation in the ratio of green and brown colour morphs, but the ratio was biased towards green morphs almost throughout the sampling period (Figure 4). The proportion of green morphs (mean of Site 1 and Site 2) was best (and positively) predicted by the EVI of the current month (linear mixed model; slope = 1.1 [*SE* ± 0.6], *t* = 2.0, *p* = 0.070; AIC = −13.9), although the relationship was quite not significant. EVI of the previous month (AIC = −11.2), precipitation of the previous month (AIC = 1.3) and precipitation of the current month (AIC = 2.9) were poorer predictors of colour ratio.

3.5 | Seasonal pattern in host plant use

Almost throughout the sampling period and at both sites, more than half of the *R. differens* observations were made on the dominant grass species at each site, namely, *B. ruziziensis* at Site 1 and *P. maximum* at Site 2 (Figure 5). At Site 1, the proportion observed on the dominant grass species *B. ruziziensis* was not predicted by either EVI or precipitation. The best-ranked model (according to AIC) showed no association between the EVI of the previous month and the proportion on *B. ruziziensis* (linear mixed model; *p* = 0.18). The proportion observed on the second most frequently used, *P. maximum*, was nearly equally well (and positively) predicted by EVI of the previous month (slope = 1.3 [*SE* ± 0.5], *t* = 2.7, *p* = 0.017; AIC = −21.0) and EVI of the current month (slope = 1.0 [*SE* ± 0.4], *t* = 2.6, *p* = 0.022; AIC = −19.3). Precipitation of the previous month (AIC = −13.0) and precipitation of the current month (AIC = −0.1) were poorer predictors.

At Site 2, the proportion observed on the dominant grass species *P. maximum* fluctuated positively with EVI. Based on AIC, the proportion of *P. maximum* was nearly equally well (and positively) predicted by EVI of the current month (linear mixed model; slope = 1.4 [*SE* ± 0.6], *t* = 2.3, *p* = 0.038; AIC = −9.5) and EVI of the previous month (slope = 1.4 [*SE* ± 0.7], *t* = 2.0, *p* = 0.067; AIC = −9.1), although the latter relationship was not quite significant. Precipitation of the previous month (AIC = 2.6) and precipitation of the current month (AIC = 9.3) were poorer predictors. The proportion observed on the second most frequently used host, *C. gayana*, was not predicted by either EVI or precipitation. The best-ranked model (according to AIC) showed no association between the EVI of the previous month and the proportion on *C. gayana* (*p* = 0.14).

4 | DISCUSSION

The population densities of non-swarming *R. differens* fluctuate seasonally, being low in the dry season and high during and immediately after the two annual rainy seasons. Also, the seasonal timing of *R. differens* swarming in Uganda typically takes place during and shortly after the two annual rainy seasons (Bailey & McCrae, 1978), suggesting that the build-up of non-swarming populations most likely ignites swarming behaviour. The two annual rainy

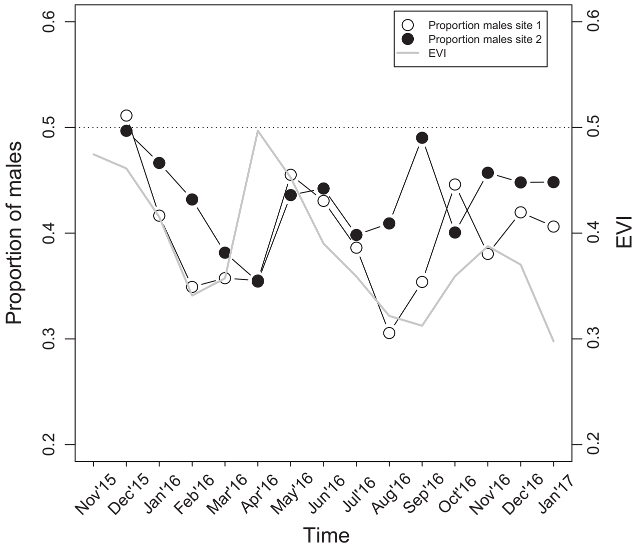


FIGURE 3 Seasonal pattern of the sex ratio of *Ruspolia differens* at MUARIK, Uganda, shown with EVI. The dotted line shows the equal proportion of females and males

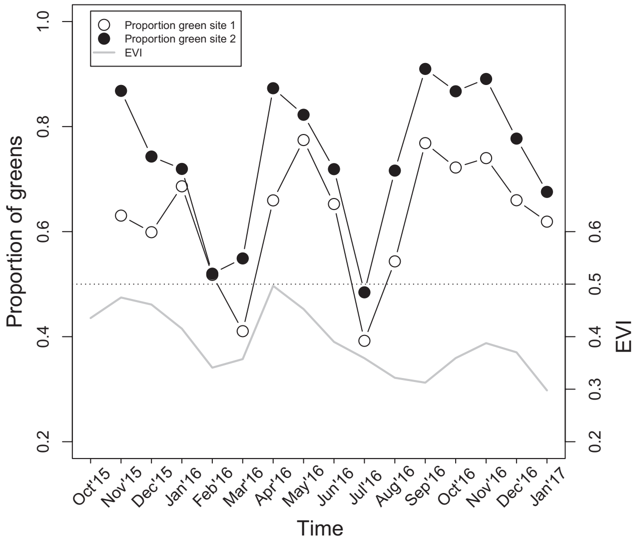
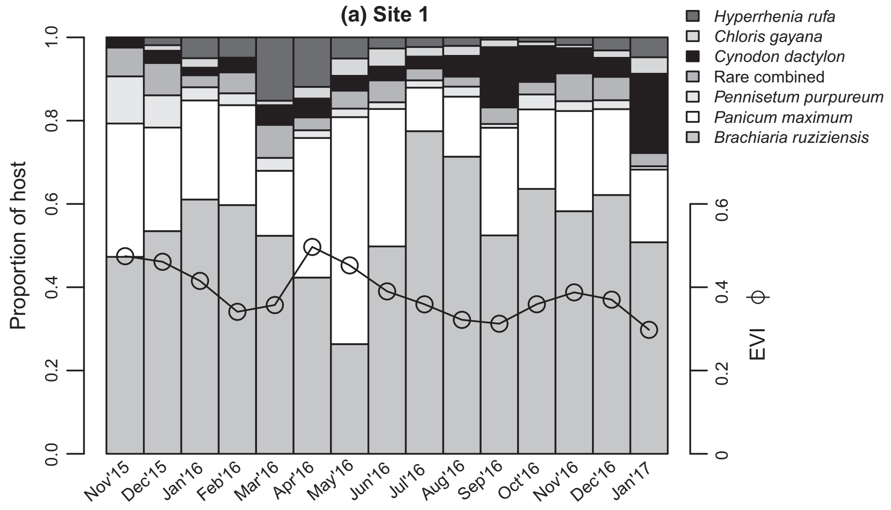


FIGURE 4 Seasonal pattern of the ratio of green and brown colour morphs of *Ruspolia differens* in MUARIK, Uganda, shown with EVI. The dotted line shows the equal proportion of green and brown colour morphs


(a) Site 1

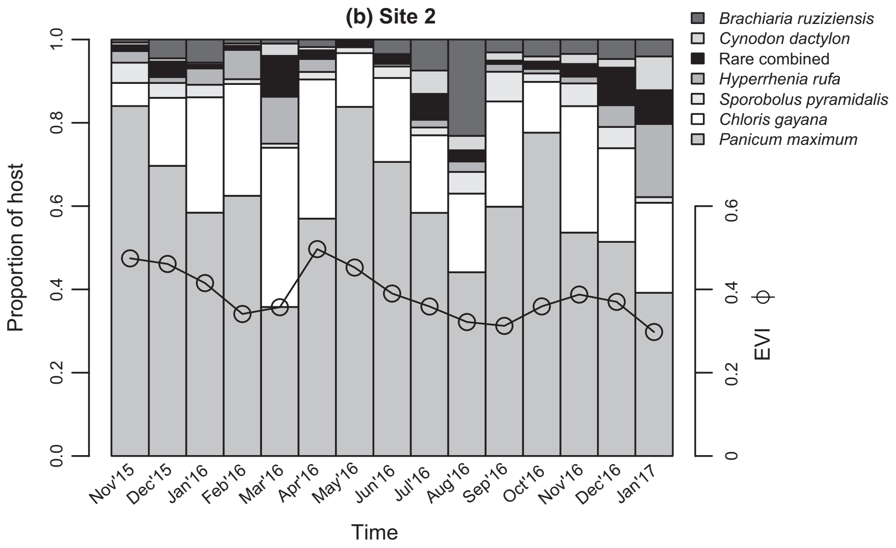

(b) Site 2

FIGURE 5 Seasonal pattern of host plants on which *Ruspolia differens* were observed (a) at Site 1 and (b) at Site 2 at MUARIK, Uganda, shown with EVI. The six most frequent host plants at each site are shown, while the rest of the species are pooled as "Rare combined"

seasons in our study area led to a rapid increase in production of new grass foliage (increased vegetation greenness) as well as the flowering of grasses. This, in turn, is likely to increase the availability and quality of food for *R. differens*, enabling the population densities to increase via increased egg production and faster development rate of nymphs. Corresponding increased reproduction due to increased host plant availability has been observed with other Orthopteran species (Branson, 2006). *Ruspolia differens* prefers grass inflorescences over leaves (Valtonen et al., 2018) and has been observed as a pest of developing seeds of crops (Swaine, 1964). Inflorescences and developing seeds are rich in protein (Bernays & Chapman, 1994; Roulston, Cane, & Buchmann, 2000; Sabelli & Larkins, 2009) and, in the laboratory, a protein-rich diet enhances the development rate of *R. differens* (Lehtovaara et al., 2017). The rainy seasons could also decrease egg mortality of *R. differens* due to decreased probability of desiccation (Bailey & McCrae, 1978; Brits & Thornton, 1981; Hartley, 1971). The population densities could respond quickly to improved conditions because when moistened and in optimal conditions, egg development of *R. differens* can take less than two weeks (Hartley, 1971). Conversely, the decline of the population densities of non-swarming *R. differens* during the dry seasons could be enhanced by an increasingly larger proportion of individuals recruited to swarms. Swarms are known to attract predators, particularly birds (Bailey & McCrae, 1978), and year on year, the swarms have become increasingly harvested by humans with commercial light traps in urban centres and villages of Uganda (Okia et al., 2017).

Our results support the idea that swarming populations could be recruited from local suitable reproductive habitats, and they are not necessarily produced by individuals migrating long distances. As a fact, until now, the specific reproductive areas for *R. differens* have not been identified and it is unknown if the swarms comprise individuals recruited from nearby local populations (reflecting the local environmental conditions), or if they are aggregates of individuals arriving from long distances. Our results also indicate that the population densities of *R. differens* can be roughly predicted by the amount of resources available: The greener the vegetation in the studied Ugandan grassland, the higher the population densities of non-swarming *R. differens* in the following month. Similarly, early observations in the 1960s showed that exceptionally high precipitation during the rainy season can, within one generation, give rise to exceptionally large *R. differens* swarms (Bailey & McCrae, 1978).

Prediction of population sizes may be possible in the future by developing prediction tools for *R. differens* population sizes based on precipitation and satellite-derived information on vegetation greenness. In Africa, sophisticated prediction tools are already available for the breeding and migration of the desert locust *Schistocerca gregaria* on the web (IRI, 2018c). The desert locust is a pest of crops, but it is also eaten by human (van Huis et al., 2013). However, it undergoes outbreaks (Despland, Rosenberg, & Simpson, 2004), and in this way, the ecology markedly differs from that of *R. differens*, populations of which fluctuate predictably with the season as shown in this work.

Based on our results, the sex ratio of the non-swarming population tended to be female biased, but after vegetation greenness increased the proportion of males tended to increase presumably due to the addition of young individuals (with equal sex ratio) to the population. The sex of *R. differens* can be determined from the 4th instar onwards and females have seven but males have only six instars (Brits & Thornton, 1981). In our data set, females represented 49% of medium-sized nymphs (4–5th instar), 77% of the large nymphs (6–7th instar) and 56% of the adults. Hence, it seems that the sex ratio in our non-swarming population is largely explained by the slower development of female nymphs and/or higher mortality of large-nymph stage males and to a lesser degree possibly by a higher recruitment rate of adult males from non-swarming populations to swarms or higher rate of (ovipositing) females returning to non-swarming populations from swarms (Bailey & McCrae, 1978). Interestingly, in the swarms of the Kampala region, the sex ratio has typically been male biased (Bailey & McCrae, 1978), while the opposite pattern has been recorded among non-swarming and swarming populations in Tanzania (Matojo & Yarro, 2013).

To some extent, environmental conditions influence the proportions of colour morphs, as also observed previously in Tanzania (Matojo & Yarro, 2013). The colour morph of *R. differens* can change during moulting (Robinson & Hartley, 1978). The role of colours in providing cryptic camouflage for *R. differens* nymphs can be debated, because in the non-swarming phase, the insects are nocturnal, hiding in grass tussocks during the day (Bailey & McCrae, 1978). However, the activity level of swarming individuals can remain high during the daytime, and aggregated swarms can be observed in grasslands, thickets or woodlands (Bailey & McCrae, 1978). Birds (e.g., pied crows, cattle egrets and black kites) opportunistically gather to feed on *R. differens* in the morning following nocturnal swarms (Bailey & McCrae, 1978). For nymphs, the role of colour morphism in improving their survival during dim-light conditions should be studied experimentally (Meyer-Rochow & Teh, 1991), but at least for the adult stage, the colours could be related to camouflage (Valverde & Schielzeth, 2015). When vegetation becomes greener during and after the rainy season, it is likely to provide green individuals better camouflage than brown individuals, with the opposite pattern during the dry season.

The preference for the dominant grass species at each study site indicates that *R. differens* is an opportunistic feeder in the field, feeding primarily on the proportionally most abundant grasses available. However, no-choice and multiple-choice experiments in the laboratory have shown that this species can also be selective in its use of both leaves and inflorescences, and that it prefers inflorescences over leaves (Valtonen et al., 2018). Our results suggest that *P. maximum* is a favoured host, because *R. differens* prefers it even more during and after rainy seasons when it produces fresh foliage and inflorescences. Our previous laboratory experiment has also shown that *R. differens* benefits from mixing different foods in the diet, resulting in a shorter developmental time and higher fresh adult weight and female fecundity (Malinga et al., 2018). Overall, our results corroborate previous studies that have demonstrated that vegetation structure, quality and quantity are important predictors of Orthopteran population densities (Deveson, 2013; Lazar, Piou, Doumandji-Mitiche, & Lecoq, 2016; Uyehara, Sisanya, Hemp, & Rubenstein, 2016; Zhu et al., 2017). Our results, therefore, draw special attention to the availability of diverse grasslands in East Africa, in order to preserve viable natural populations of *R. differens* in the long term. In East Africa, threats to natural and semi-natural grassland habitats include, for example, overgrazing and expansion of croplands (Darkoh, 2003) and urban expansion (Seto, Güneralp, & Hutyra, 2012).

Another potential challenge for the persistence of viable *R. differens* populations includes climate change, which, in East Africa, is predicted to increase precipitation during the second annual rainy season between September and November, due to Indian Ocean warming (Stocker et al., 2013). Increased precipitation could lead to increased vegetation greenness, which positively correlates with population densities of *R. differens* as shown in this work and this should have positive consequences for the harvesting economy in the region. On the other hand, even small increases in temperature could lead to increased mortality, since *R. differens* are currently experiencing temperatures very close to their thermal optimum for survival (Lehtovaara, Roininen, & Valtonen, 2018; see also Deutsch et al., 2008). However, as shown in this work, the opportunistic and flexible use of host plants could protect *R. differens* to some degree from the adverse effects of climate change and habitat loss.

In conclusion, this study provides evidence that local non-swarming *R. differens* are present in all developmental stages year-round in central Ugandan grassland areas, but the population densities fluctuate following seasonal fluctuations in precipitation and production of lush grass foliage (vegetation greenness) and consequent grass flowering. The sex ratio of the non-swarming *R. differens* populations is female biased, with the proportion of males and green colour morphs increasing during and after the rainy season. The use of host plants seems to be opportunistic, that is, the locally most common grass species is used the most, but fluctuates seasonally so that when vegetation greenness increases, individuals more likely select the more preferred host *P. maximum*. This study highlights the need to conserve grasslands in East Africa that are available for *R. differens* throughout the year. Understanding how the populations of *R. differens* respond to seasonal fluctuations in precipitation and vegetation greenness can be used for forecasting its population densities and for planning conservation interventions by the natural resource managers. Such information is essential for conservation and sustainable harvest of *R. differens* in the long term.

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AUTHOR CONTRIBUTION

HR, PN and AV conceived research. RO contributed data. AV, PN and HR analysed data and conducted statistical analyses. RO, GMM, KR, PN, HR and AV wrote the manuscript. HR secured funding. All authors read and approved the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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