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SHORT COMMUNICATION

The effect of rainfall on population dynamics in Sahara-Sahel rodents

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Abstract
In arid and semi-arid regions, rainfall is scarce, limiting primary productivity and animal reproduction. As long-term population monitoring is limited in remote arid areas, indirect and remote technicals are needed. We investigated if and how populations of rodents in Sahara-Sahel responded to past events of rainfall. Using short field surveys and remotely sensed rainfall data, spanning between years 2010 to 2015, we tested if rainfall prior to field surveys affected populations of *Gerbillus* rodents. Generalized additive analysis showed that amount of moonlight (the effect of number of days away from full moon) negatively correlated with number of trapped animals. When controlling for moonlight and geographic and temporal variation, rainfall up to 1 year prior to surveys positively and rainfall 2 years prior to surveys negatively correlated with number of trapped gerbils. We suggest that the effect of increased number of gerbils resulted from reproduction and population density increase after bursts of primary productivity. Negative correlation with rainfall could be related to increased predation or other ecological effects (e.g., resource collapse, pathogens spread) on prey population densities and activity levels. Our results suggest multiphase delayed effect of gerbils population response to rainfall implying interactive model of population regulation in rodent communities on Sahara-Sahel. Presented indirect method and results are readily applicable to population monitoring and management of remote and understudied areas.

Keywords Desert · Climate · North Africa · Population dynamic · Primary productivity · Precipitation

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Introduction

Rodents are key species in many ecosystems, having a great influence on plant communities (Olofsson et al. 2014; Gordon and Letnic 2016) and on mammalian and bird predators (Millon et al. 2014; Korpela et al. 2014). Many species are characterized by multi-annual cycles and fluctuations in population densities, related to dynamics in primary productivity and predation pressure (Hanski et al. 1991; Hanski and Korpimäki 1995; Cornulier et al. 2013). Rodents are important pests in agricultural and forestry production and as source of zoonotic diseases, sometimes causing severe economic losses (John 2014; Cayol et al. 2017; Imholt et al. 2017). Thus, ability to predict high densities of rodents is of economical and health importance (Huitu et al. 2009; Korpela et al. 2013).

Variation in rainfall affects primary productivity (Fay et al. 2003; Mowll et al. 2015) and agriculture yield (Prăvălie et al. 2014; Ray et al. 2015) and influences occurrence of crop pests

(Dickman et al. 1999; Lima et al. 1999). Fluctuating climatic conditions can shape available food resources that affect population densities and individual activity patterns (Granjon et al. 2005). But in areas exposed to relatively high degree of stochasticity in rainfall, it is challenging to forecast dynamics of natural populations. Yet water is a limiting resource in arid ecosystems and its sporadic availability shapes phenology of arid-adapted species, sometimes causing rapid population explosions (Beatley 1969; Brown and Ernest 2002). Changes in rainfall patterns are also major concerns for mitigating negative effects of climate change (Weltzin et al. 2003; Lawrence and Vandecar 2015; Pittelkow et al. 2015). In the dry and semi-dry areas, like Sahara-Sahel, primary productivity is determined by rainfall (Mowll et al. 2015). The lack of water (the annual mean rainfall in the Sahara is below 25 mm per year) and the extreme variation in temperature make this region as one of the least productive (Huxman et al. 2004), and due to its remoteness one of the least studied (Brito et al. 2014, 2018), on Earth. Yet, the region is highly heterogeneous and host-rich biodiversity (Vale et al. 2016; Brito et al. 2016, including up to 40 *Gerbillus* rodent species (Abiadh et al. 2010). Sahara-Sahel passed repeatedly through wet and dry climatic phases (Drake et al. 2011; Tierney et al. 2017), resulting in fluctuation of extension of desert in North Africa (Kröpelin et al. 2008). Consequently, the magnitude and the velocity of the climatic changes are major concerns in this and other arid areas, threatening already vulnerable biodiversity but also hampering food production for increasing human population (Loarie et al. 2009; Vale and Brito 2015).

In this work, we proposed method to study how variation in rainfall affects population dynamics of species in remote and hard to access areas. We specifically asked if and how occurrence of past rainfall affected population status of West Sahara-Sahel *Gerbillus* rodents. Rainfall can have indirect positive effect on gerbils abundance, affecting primary production and emergence of insects, the main food sources for rodents on Sahara-Sahel (Aulagnier et al. 2009; Yan et al. 2016). Increased prey densities can attract predators, due to occurrence of localized food resources (Greenville et al. 2014), but also deplete resources and promote spread of pathogens (Cayol et al. 2017). Those effects can decrease gerbils abundance, but also activity (Kotler 1984). Thus, two delayed phases of rodent population dynamics are expected in response to rainfall, faster and positive, signaling rodent population grow, and longer and negative, related to population decrease (Hanski et al. 2001; Krebs and Berteaux 2006). To overcome the lack of long-term population monitoring on the Sahara-Sahel, but to assess gerbils population dynamics, we developed analysis based on the short-term spatial and temporal field surveys accompanied with remotely sensed data.

Materials and methods

Field surveys

Gerbillus rodents were life trapped with Sherman traps (XLK, extra large folding kangaroo rat traps) placed in lines of ten traps every 10 m in two to four lines. Traps were set before sunset, baited with standard dry pellets, and collected around sunrise. Surveys were conducted only one night in a single location (in total of 149 locations) to detect the presence of any of the *Gerbillus* individuals. Field surveys were conducted between 2010 and 2015, across the Sahara-Sahel of Mali, Mauritania, and Morocco (Fig. 1, Electronic Supplemental Material: Table S1; (Boratyński et al. 2013; Moutinho et al. 2015; Guerreiro et al. 2016). During field surveys, we have detected the presence of nine *Gerbillus* species in the study region (*G. amoenus*, *G. campestris*, *G. gerbillus*, *G. henleyi*, *G. nancillus*, *G. occiduus*, *G. pyramidum*, *G. tarabuli*, and *Gerbillus* sp., a species awaiting formal taxonomic description; Ndiaye et al. 2016; Boratyński et al. 2017). Due to difficulties in distinguishing between some of the species and because, e.g., agricultural management does not necessarily need particular species information, we have pooled all

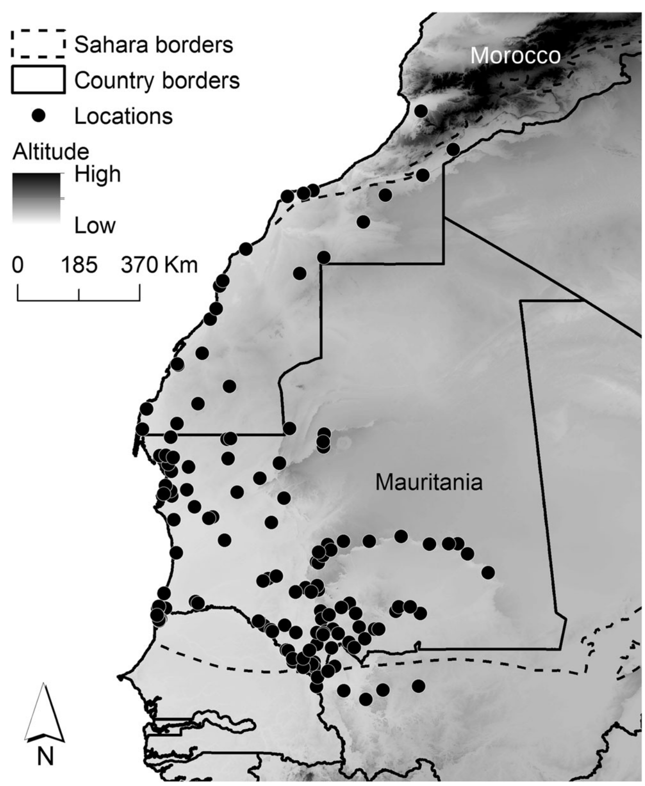

Fig. 1 Map of field survey locations of *Gerbillus* rodents in the West Sahara-Sahel

species data to one statistical test. From pooled number of *Gerbillus* individuals, we calculated an index, relative number of trapped individuals divided by the number of traps set in given location, and used it in statistical analyses as response variable. All animals were released in their capturing locations after surveys.

Rainfall data and vegetation indexes

Rainfall data (monthly averages) for each of the 149 trapping locations was downloaded from the publicly available Tropical Rainfall Measuring Mission and Other Sources Rainfall Product dataset (TRMM 3B43; Kummerow et al. 2000). It has been shown that TRMM 3B43 monthly values are good predictors of ground measures of monthly rainfall levels (Fleming et al. 2011; Karaseva et al. 2012; Ouatiki et al. 2017). Monthly averages on a 0.25° by 0.25° global spatial resolution from 50° S to 50° N latitude (Macritchie) were obtained from January 2007 to August 2015 for all surveyed locations (Fig. 1, Table S1). Thus, 27 monthly averages prior to the earliest field survey were collected spanning over the expected lifespan of *Gerbillus* species (Aulagnier et al. 2009). We used vegetation indexes to validate that occurrence of rainfall affected availability of resources in the environment. Vegetation indexes (monthly averages; collected by the MODIS, Moderate Resolution Imaging Spectroradiometer, Terra satellite; https://terra.nasa.gov/) for randomly selected 50 trapping locations (Table S1) were downloaded from the publicly available Land Processes Distributed Active Archive Center (LP DAAC; https://lpdaac.usgs.gov). Monthly averages (for the years 2010–2015) of normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI; Didan 2015) were included on a 0.25° by 0.25° global spatial resolution for a month of survey and for 3 months following field surveys.

Statistical analyses

Pearson's product-moment correlation coefficient was used to test the associations between monthly averages of rainfall during field surveys and monthly averages of vegetation indexes during and following 1, 2, and 3 months after surveys, and average for those. We tested the relationship between response variable (relative number of trapped individuals, Poisson distribution) and predictors (year and season of surveys, moon phases, and 3-month averages of rainfalls) using a generalized additive model (GAM, "mgcv" package in R). To account for variation in sampling effort among study sessions, we calculated an index of relative number of trapped individuals: number of trapped individuals divided by number of traps used in a given trapping location. We calculated 9 averages (log transformed) of rainfalls during three following months (trimesters, e.g., during and 1 and 2 months prior to surveys, 3–6 months prior to surveys) for a given location (unimportant trimesters were excluded from final model by stepwise elimination of insignificant terms: $p > 0.1$). We included a variable describing amount of moon light, number of days away from full moon (referring to number of days before or after full moon, 0–15 days), to control for *Gerbillus* activity patterns related to amount of light in the habitat (Kotler et al. 2010). To control for seasonal variability in number of captured animals, we included fixed factor: season of survey (winter, summer, or fall). Rainfall trimesters, moon light, and season were fitted as parametric terms in the GAM model. We accounted for spatial autocorrelation between surveyed locations by including latitude and longitude as a smoothed, interaction term (i.e., $s(x,y)$) and for variation between years as a random, smoothed factor [i.e., *s*(year, bs = "re"); Dormann et al. 2007; Wood 2017]. Finally, we partitioned data by size of the trapped individuals referring to size classes of *Gerbillus* species (small species 7 to 16, medium 17 to 27, and big 28 to 40 g) to test persistence of the detected in the main model effects. The effective degree of freedom (Edf) in GAM was estimated for smoothing parameter of geographic coordinates and its statistical significance was evaluated with the generalized cross validation method. The output of the GAM included the percentage of explained deviance by the model. All statistical analyses were performed using the "R" platform, version 3.4.3 (R Core Team 2016).

Data availability statement Field survey data collected during this study are included in supplementary information file.

Results

We trapped 97 *Gerbillus* specimens in 32 out of 149 (21%) surveyed locations (Fig. 1). We found substantial variation in monthly rainfall averages in surveyed locations that referred to rainfall variation between rainy and dry seasons (overall rainfall average 0.078, median 0.173, maximum 0.677, minimum 0.010, standard deviation 0.102; Fig. 2). We found positive significant Pearson's product-moment correlations between rainfall measured during surveys and both, NDVI and EVI, vegetation indexes measured during and up to 3 months after surveys (Figs. 2 and 3; Table S2).

The variation in the relative number of captured individuals was affected by geographic coordinates of locations, suggesting significant spatial autocorrelation ($Edf = 28.21$, $F = 2.96$, $p < 0.001$) (Fig. 4). We found that significantly higher number of gerbils was captured during winter than

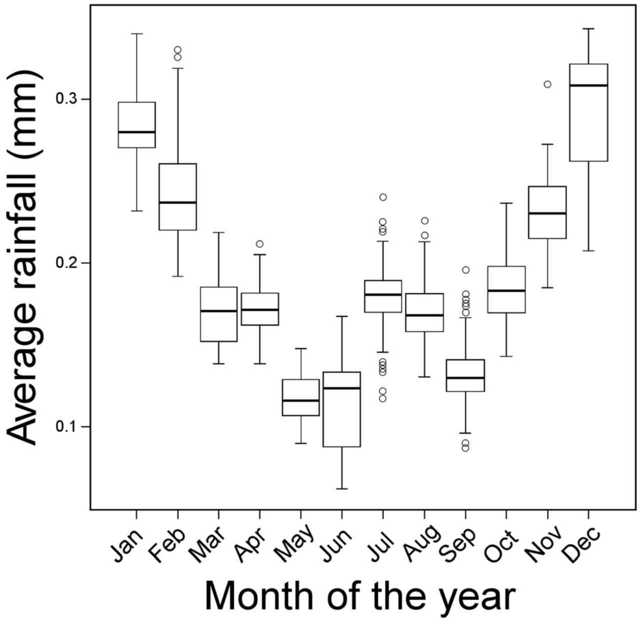

Fig. 2 Seasonal variation in rainfall (Tukey boxplots) in surveyed locations in the West Sahara-Sahel

during summer and autumn (Table 1). When controlling for geographic and temporal variation in the GAM model, we found that a higher number of animals were captured during nights with less moon light in comparison to full moon and waxing moon nights (the effect of number of days

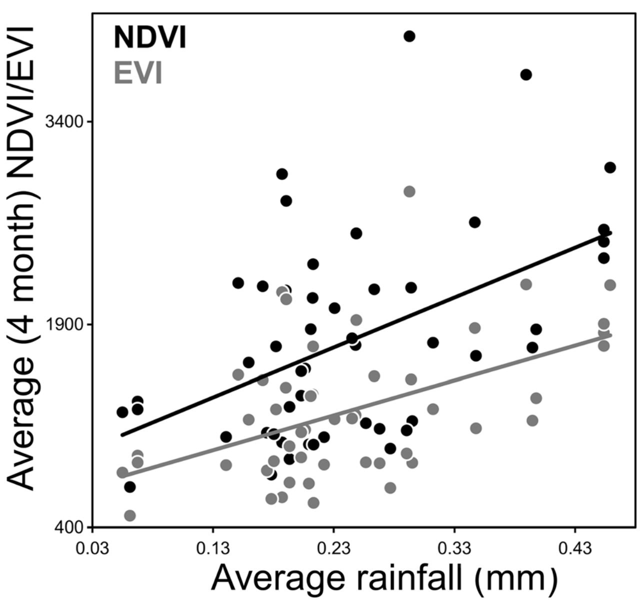

Fig. 3 Association (Pearson's product-moment correlations) between monthly averages of rainfall during survey and mean normalized difference vegetation indexes (NDVI; $r = 0.49$, df = 48, $t = 3.89$, $p = 0.0003$) and enhanced vegetation index (EVI; $r = 0.50$, df = 48, $t = 4.01$, $p = 0.0002$) derived for month during and 3 months after surveys

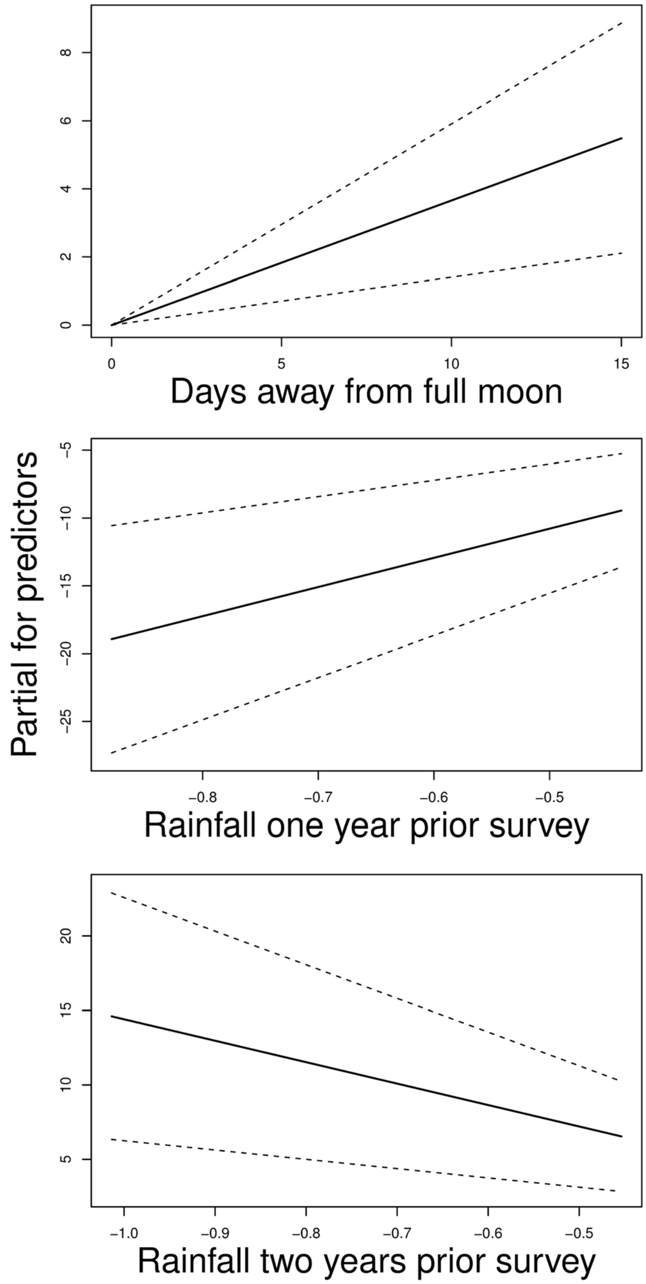

Fig. 4 Regression between relative number of trapped individuals (number of individuals divided by number of traps; partial values for a given predictor and its standard errors) and moonlight (number of days before or after full moon "0"), and rainfall 1 and 2 years prior to surveys, as derived from generalized additive model (Table 1)

away from full moon: $t = 3.25$, $p = 0.0015$; Table 1), confirming previous results for limited geographic extend (Kotler et al. 2010; Embar et al. 2011). Most importantly, our results highlighted significance of rainfall in shaping population dynamics of gerbils. We found that the amount of rainfall during trimesters up to 1 year prior to the field surveys positively correlated with relative number of trapped animals

Table 1 Results from generalized additive model analyses for relative number of trapped *Gerbillus* individuals, as explained by variation in rainfall prior to trappings (e.g., $Rain^{0–2}$ during and 1 and 2 months prior trapping); differences between years, seasons, and ecoregions; and number of days before/after full moon. The percentage of explained deviance by the model was 80.5% for R^2 adj = 0.86, GCV = 0.052, and n = 149. The approximate significance of smooth term, spatial autocorrelation, was Edf = 28.21, F = 2.96, p = < 0.0001. Variance for random, year, effect was 2.68e−05

	Est.	SE	*t*	*p*
Intercept	9.58	4.84	1.98	0.050
$Season^{summer}$	− 13.16	3.79	− 3.48	0.0007
$Season^{fall}$	− 6.69	1.92	− 3.48	0.0007
Moon light	0.37	0.11	3.25	0.0015
$Rain^{0–2}$	5.43	2.43	2.24	0.027
$Rain^{6–8}$	15.57	4.69	3.32	0.0012
$Rain^{9–11}$	21.56	4.77	4.52	< 0.0001
$Rain^{24–26}$	− 14.41	4.08	− 3.53	0.0006

($t \geq 2.24$, $p \leq 0.027$; Table 1). At the same time, the amount of rainfall during trimester 2 years prior to surveys negatively affected the number of trapped animals ($t = -3.53$, p = 0.0006; Table 1). When considering limited data that included only individuals belonging to middle-sized class of *Gerbillus* species (17–27 g; small and big species classes consisted too small data for confident statistical tests), we found similar positive effect of rainfall 9 to 11 months prior to survey on gerbils abundance ($t = 4.52$, $p = 0.011$), but the other rainfall effects were insignificant (Table S3). This reduced dataset also confirmed positive effects of moon light on gerbils abundance ($t = 2.52$, $p = 0.013$) and higher abundance of gerbils during winter comparing to fall ($t = -2.41$, $p = 0.017$).

Discussion

In this work, we presented a method to assess animal population dynamics in remote and inaccessible areas, by combining remotely sensed data with short-term field surveys. By spatial and temporal sampling of population relative densities, this method allowed us to test effects of environmental and geographic variation (i.e., rainfall level, spatial autocorrelation, moonlight intensity) on population dynamics in regions where large-scale and long-term monitoring is infeasible.

Rodent populations from arid and semi-arid regions can respond to occasional bursts of primary productivity by quick development of up to several generations (Beatley 1969; Brown and Ernest 2002; Letnic and Dickman 2009). Rainfall and following increase in primary productivity affect quantity of important food sources for rodents, which can trigger reproduction of desert species (Brown and Ernest 2002). Variation in rainfall can cause diet shift in gerbils (Degen et al. 1997), and it has been shown that in the communities of arid adapted animals, at least some of the species can respond to habitat productivity by breeding (Soliman and Mohallal 2009; Shenbrot et al. 2010; Sarli et al. 2015). Given the relatively fast reproduction of a typical gerbil (Aulagnier et al. 2009), it can be hypothesized that observed high densities in some populations are caused by reproduction and population grow following rainfall up to 1 year prior to the surveys (Table 1). Observed low numbers of gerbils found 2 years after rainfall might have been caused by increased presence of predators (Abramsky et al. 1996; Brown and Kotler 2004; Embar et al. 2011; Boonstra 2013), due to depletion of resources, or due to density-dependent mortality related to infectious diseases or other pathogens (Hanski and Korpimäki 1995; Hochachka and Dhondt 2000).

Indirect methods, like the one presented here, are critical in pursuance of understanding processes in remote and understudied regions exposed to environmental changes, and rodent populations can be a key tool in monitoring dynamics of desert and semi desert ecosystems (Shenbrot 2014). During historical dry climatic stages of the Sahara-Sahel, the steppe- and savanna-like habitats were replaced by hyper-arid bare areas (Le Houérou 1997). The historical regime shifts that caused changes in environmental conditions (Foley et al. 2003) can refer to currently observed extended drought events in the region (Dardel et al. 2013) that hamper biodiversity conservation (Brito et al. 2016). Multiphase effects of population responses to rainfall in rodents suggest interactive regulation of Sahara-Sahel animal communities, depending on habitat productivity and population dynamics (Brown and Ernest 2002). Desertification and land degradation pose challenges for animal population management and agricultural planning (Portnov and Safriel 2004; Falkenmark and Rockström 2008). Understanding model organism population dynamics is an important first step to predict effects of ongoing ecosystem changes.

Aridification and decrease of rainfall predictability are already a major concern in many regions, as arid and semi-arid zones suffer the fastest climatic changes. In this work, we have showed how publicly and freely available resources on rainfall data can be successfully applied to study population dynamics of common species. The method can be applied to manage fragile desert ecosystems; likewise, it can be translated to any system worldwide. Above results can be used to optimize effectiveness of rodent monitoring schemes, for preventing major crop losses and for mitigating exposure to rodent-borne pathogens. However, long-term population monitoring will add to understand ecosystem processes in climate-sensitive regions and validate above results.

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Compliance with ethical standards

All applicable international, national, and institutional guidelines for the care and use of animals were followed.

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

Ethical approval Capturing and handling of animals adhered to the guidelines and regulations approved by the local authorities (the Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification of Morocco, decisions 20/2013, 41/2014, 42/2014, and the Ministère de l'Environnement et du Développement Durable of Mauritania, decision 227/ 08.11.2012).

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