

Demographic response of the Gambian Gerbil to seasonal changes in Savannah fallow fields

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Abstract

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The Savannah gerbil, *Gerbilliscus gambianus* (Muridae: Gerbillinae) is important to the ecological relations of the dry grassland ecosystem of West Africa, as well as, being a zoonotic agent of human diseases and potential crop pest. We examined the impact of seasonal changes on the population dynamics of *G. gambianus* in northern Nigeria, by completing population estimates using capture–mark–recapture (CMR) and indirect population density indices (PDI) methods. The latter included fecal pellet counts and limited spotlighting. During 1990–1992 we collected both CMR and PDI data, and established their relationship by regression, thus calibrating the PDI values to CMR estimator. We also completed a separate, PDI only, study during 2015–2017, and estimated monthly densities indirectly by toning the PDI values to population sizes in the CMR estimator. The lowest declines (<20 gerbils ha^{-1}) were in mid rains (July–August), and highest increases (>90 gerbils ha^{-1}) were after the rains (October–January). Seasonal effects on densities were significant during 1990–1992 but not during 2015–2017. There were improved survival rates for both adults (0.95) and young (0.83), adult capture probability (0.56), and mean monthly recruitment of young (23) after the rains. There was no significant change in the overall population dynamic pattern of *G. gambianus* over a 25-year period. Because *G. gambianus* did not maintain colonies inside farmlands cultivated by rain or irrigation, and its tendency for large population drops in mid-rains, we are in doubt of its potential as crop pest in northern Nigeria.

Keywords

Gerbil, grassland, population, rodents, tropical, West Africa

Introduction

There is a good representation of the genus *Gerbilliscus* (Syn. *Gerbillurus*, GRANJON et al., 2012), across many regions of Africa (ARSLAN et al., 2013; COLANGELO et al., 2007; GRANJON and DOBIGNY, 2003; LÖTTER, 2010; MASSAWE et al., 2011; MUSSER and CARLETON, 2005; RABIU and ROSE, 1997; 2004; ZIEGLER et al., 2002), with the species of interest in the present study, *Gerbilliscus gambianus*, amongst the commoner ones in the grassland and

semi-arid belts, but also noted in forest clearings (IKEH et al., 1995) though, on the whole showing greater preference for drier savannah than the humid, derived savanna to the south of Nigeria (HAPPOLD, 1987). The species also shows considerable tendency towards seasonal reproduction in many regions, usually during the rains, e.g., in Nigeria (RABIU and ROSE, 1997), and in eastern Africa (DELANAY, 1986). Aside from being a potential crop pest (TAYLOR, 1984), *G. gambianus* along with other rodent species (MEERBURG et al., 2009) represents a reservoir of bacillus

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(*Yersinia pestis*) plague with transmission to other wild rodents (GRATZ, 1997; GRATZ and ARATA, 1975); of Phlebotomus fever virus (IKEH et al., 1995); and leishmaniosis parasites (DEDET et al., 1979; IKEH et al., 1995).

Perhaps, it is important to note some changes in the systematics of *Gerbilliscus* over the past 15 years or so. The savannah gerbil in the present study, *G. gambianus*, Thomas, 1910, is the same as *Tatera valida* in earlier works in the same area by RABIU and ROSE, (1997; 2004) and presumably in other contemporary publications at the time. The genus *Tatera* now belongs entirely to the Indian subcontinent, while *Gerbilliscus* includes all African species previously named with *Tatera* (MUSSEY and CARLETON, 2005). Across the African continent *Gerbilliscus* is systematically rich; in fact, has more than 10 species with many congeneric ones (COLANGELO et al., 2007; GRANJON et al., 2012). Indeed, the systematics of the genus *Gerbilliscus* remains a controversial issue (GRANJON et al., 2012).

In most African habitats gerbilline rodents tend to be less common than other species (GRANJON and DUPLANTIER, 2009; NEAL, 1982; O'FARRELL et al., 2008). This is also true for northern Nigeria (RABIU and ROSE, 1997). Percent relative abundance for *Gerbilliscus* sp. (= *Tatera* sp. in old literature) amongst insectivores and rodents in Alatish National Park, northwestern Ethiopia, was estimated at 2.40%, well below that of several murid species that included *Arvicanthis niloticus* and *Mastomys natalensis* (HABTAMU and BEKELE, 2008). Elsewhere in the Sudanian savannah of Guinea, West Africa, species of both *Gerbilliscus* and *Taterillus* represented fewer than 10% of all rodents captured, and showed evidence of population crash, losing over 90% of the individuals over a short period of time (BÂ et al., 2013). Also, NEAL (1982) describes the species as a slow breeder with a reproductive success rate of 8.5 young per adult female (HUBERT, 1977; HUBERT and ADAM, 1975). Breeding patterns, and hence population dynamics, in *G. gambianus* being seasonal in northern Nigeria, is influenced by climatic factors, especially rainfall (RABIU and ROSE, 2004). Interestingly, rodent populations in cold climates are similarly affected by climatic factors peculiar to a given region. For instance, both rodents and shrews had better reproductive and survival successes during the subsequent vegetation season that followed thick snow (HLÔŠKA, et al., 2016).

Although not specifically assessing population densities in his work, DEMETER (1981) recorded barely 20 gerbilline rodents, approximately 16% of all species collected within five kilometers over a period of two months at the Yankari Game Reserve, northern Nigeria. Working in the vicinity of Zaria, the same vegetation zone as that of DEMETER (1981), EZEIFEKA et al. (1987), reported only four captures for *G. gambianus* out of 183 rodents, representing 2% of all captures. Several measures of rodent population sizes have used one estimator method or the other, e.g., CMR or removal methods. In certain situations, however, when rapid population data is desired, indirect measures of estimating population size by counting indices of popu-

lation density may be deployed (MCKELVEY and PEARSON, 2001). In relation to this, KARELS et al. (2004), argues that such indices must be calibrated with known population sizes in order to serve a meaningful purpose.

Our objectives were to determine the influence of seasonal changes on the population dynamics of *G. gambianus* in natural, savannah grass fields, near Kano, Nigeria; compare the species monthly population sizes by means of a population estimator (standard CMR grid) and by indirect indices of population density; as well as, test the effect of moisture application (by rainfall and irrigation) on the demography of the species.

Materials and methods

Study sites

Study sites were in old fallow and pasture fields of northern Nigeria where the rainy season was from late May to mid-October, and dry season spanning from late October to early May or, even as late as June in years of drought. During the dry season some segments of the same fields that are within approximately 20 km of water reservoirs may come under irrigation. Three sampling grids were initially trapped in natural, old fallow vegetation at Karfi, Bagauda and Gwarmai settlements (11°03'00.69"N, 8°01'11.29"E; 11°03'48.39"N, 8°19'11.69"E and 12°03'22.96"N, 8°12'16.21"E, respectively) 50 to 110 km south-west of Kano, with an additional grid at Kadawa (12°07'N; 8°48'E) near the irrigated fields located in a citrus orchard surrounded by fields of rice or wheat. Given that one of our objectives was to determine the effect of seasonal changes on the population dynamics of *G. gambianus*, temperature and precipitation records for both 1990–1992 and 2015–2016 periods from a station eight kilometers northwest of the Bagauda study site are given in Figs 1 and 2.

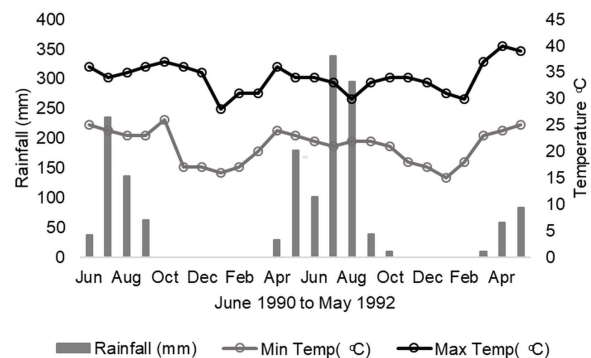


Fig. 1. Temperature and precipitation data for June 1990 to May 1992 from near Bagauda, 11°03'00.49"N, 8°06'41.21"E, south of Kano, Nigeria.

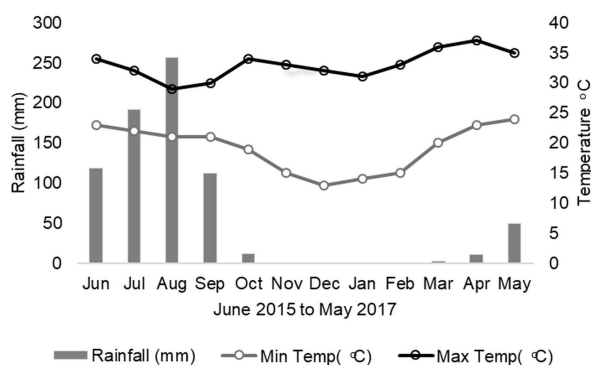


Fig. 2. Temperature and precipitation data for June 2015 to May 2017 from near Bagauda, 11°03'00.49"N, 8°06'41.21"E, south of Kano Bagauda, south of Kano, Nigeria.

There were also surveillance trap lines in the margins near cultivated farms outside grid areas. Monthly trapping began in July 1990, but we experienced disruption in all the grids. Field work was seriously disrupted early in 1991 when, rather suddenly regional agricultural exhibitions were initiated at the Bagauda site. There were also occasions of trap vandalism, when we were forced to relocate and seek other, alternative sites. However, a few months later, the Bagauda site made remarkable recovery in terms of vegetation, and trapping was resumed. Because of infrequent suspension of trapping, we gave up on the Karfi site, and present this data as average composite for Bagauda and Gwarmai; also leaving out Kadawa, where not a single gerbil was ever trapped.

Trapping and marking rodents

Essential trap components for Modified Fitch traps (ROSE, 1994) were shipped to Kano, and the traps were assembled there, using additional local materials. Rodents were collected by live trapping following the methods of ROSE and GAINES (1978), with traps placed at 10 m⁻¹ interval in a 10 × 10 grid. The Fitch trap, with a 62 × 58 mm opening, offers better ventilation than the oft used commercial Longworth trap, which has a smaller entrance and lacks meshed window. Cardboards were used to cover traps in order to moderate the effects of rain, sun, or cold; had to be changed frequently because they would often shelter ants or, were destroyed by termites. Trapping was conducted for six to eight consecutive days during every month. At first capture, each gerbil was given a numbered ear tag, evaluated for age-sex class; its location on the grid recorded; and then released at the point of capture. Minimum body weight for adults was 40 g. Animals weighing less than 40 g were considered to be juveniles (= young).

Alongside trapping, indices of population density were counted and recorded at roughly every five-meter distance. These included active warrens; spot lightening at dawn (when SR had slept in villages near the grids) and at dusk, as *G. gambianus* is nocturnal. Other indices counted were runways, gnawed shrubs, fresh grass cut (during the

rainy season), and fresh fecal pellets. The counting of these indices (only) was also completed in a separate segment of this study in 2015–2017 during the same months as in 1990–1992.

Population density estimates by capture-mark-recapture CMR

Analysis of capture-mark-recapture (CMR) data was made using the Fortran program CAPTURE (OTIS et al., 1978; WHITE et al., 1982) for the purpose of estimating population size and other related parameters. Survival rates were obtained using the program JOLLYAGE (POLLOCK et al., 1990) based on a modified Jolly-Seber open population model that allows for a specification of two age classes (POLLOCK, 1982; STOKES, 1984). Estimates for the first and last months or, last two months of a study period, are not available with JOLLYAGE.

Data distributions were checked for ANOVA requisites after which estimated population numbers were square-root transformed, while survivorship rates and capture probabilities were treated by arcsine transformation. Effects of season (rainy versus dry) on population size and survivorship were tested by the General Linear Model (GLM) procedure for ANOVA, while the effects of enhanced field moisture could not be tested since there were absolutely no gerbilline captures in the irrigated sites.

Population density estimates by indirect population indices

In the 1990–1992 segment of the study, population density indices which, as noted earlier, included limited spotlighting at dawn and dusk, active warren counts, cut-grass stem fragments, and fresh fecal pellets were subsequently calibrated to monthly population sizes by regression analysis. The indices recorded again during 2015–2017 served for indirect population estimates, made by matching their values to those of known population sizes in the regression. Monthly densities between 1990–1992 population estimator and 2015–2017 indirect indices methods were compared with non-parametric T-test.

Results

Population density of *G. gambianus* by CMR estimator, 1990–1992

Estimate of density was low, below 20 gerbils ha⁻¹ mid-rains in August, 1990, but rose to 55 gerbils ha⁻¹ the following month. The density reached 65 gerbils ha⁻¹ in October, and continued to rise steeply to highs of over 90 gerbils ha⁻¹ during December. Approximate 95% confidence interval ranged from 51 to 80 gerbils ha⁻¹ over the study months in 1990. On account of disruptions of trapping noted earlier, there was no data during February to July 1991; actually, March to June, since the software does

not offer parameter estimates for first and last months of a study period (Fig. 3).

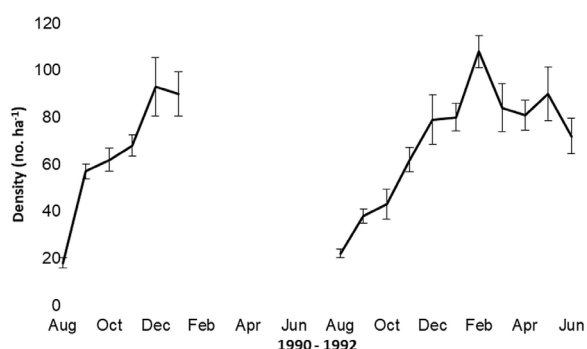


Fig. 3. Mean monthly composite population densities ha^{-1} (capture-mark-recapture, CMR method) of *G. gambianus* in natural fallow fields near Kano, Nigeria during June 1990–May 1992.

By August of 1991, the previous population trend (August 1990 to January 1991) was beginning to repeat, with very similar pattern between August 1991 to January 1992. Clearly, *G. gambianus* would enter the rainy season with modest to low numbers, and reach peak in the first half of the dry season (October–January). There was no pre-rain data in 1991 to compare to that of 1992, but the population went into the 1992 season with a healthy 70 gerbils ha^{-1} (SE 4.00; approximate 95% confidence interval 61–79 gerbils ha^{-1}) in June 1992 from an earlier 84 gerbils ha^{-1} in March 1992. However, the evidence of decline had set in by May, 1992 (Fig. 3).

Population density estimates of *G. gambianus* by indirect population indices, 2015–2017

By comparison, indirect estimates of population densities of 1990–1992 were generally higher than those of 2015–

2017 (Fig. 4). The demographic patterns for parts of the two periods (August 1990–January 1991 versus August 2015–January 2016) were very similar. The lows were in August (mid rains, as was the case in 1990) with only 11 gerbils ha^{-1} ; then a rise to slightly over 80 gerbils ha^{-1} in December of 2015, the peak for this two year second segment of the present study. The patterns in all of 1992 versus 2017 were not quite similar, with the 2017 density values showing decline during December to February, while those of 1992, in contrast, showed a rise (Fig. 4). By May–June the density was below 50 ha^{-1} , but declining though not as sharply as in 1992.

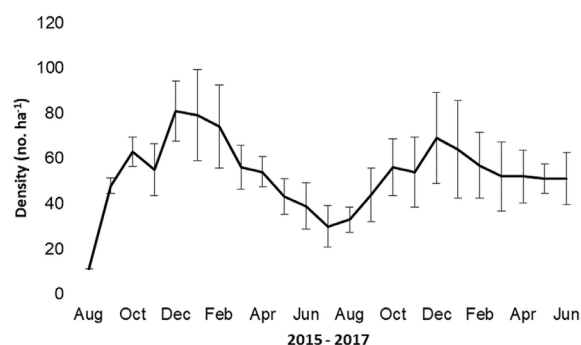


Fig. 4. Mean monthly composite population densities ha^{-1} (by indirect population density indices: fresh fecal pellets count and limited spotlighting) of *G. gambianus* in natural fallow fields near Kano, Nigeria during June 2015–May 2017.

Evaluation of indices of population

Of the seven indices of population density on which the indirect estimates of 2015–2017 population sizes were based, only two, namely, fresh fecal counts and spotlighting, appeared to have significant predictive value of population size. For example, fresh fecal index showed regression values: $S = 2.556$; $R\text{-sq}(\text{adj}) = 73.95\%$; (Equation: Fresh fecal counts = $4.88 + 0.1443$ density). One

Table 1. Multiple regression coefficients for population density indices (PDI) during August, 1990 –January, 1991; August, 1991–June, 1992

Predictors (Indices of population abundance)	N	Regression coefficient	SE coeff	T	P	VIF
Constant		46.83	14.24	3.29	0.00	8.7 ± 3.1
Sets of fecal pellets	522	2.17	0.87	2.78	0.02	5.95
Active warrens	396	0.15	0.91	0.17	0.87	2.69
Spotlighting	222	6.58	3.19	2.06	0.04	4.42
Cut grass stem	7,522	0.01	0.0006	-1.35	0.19	6.76
Runways	583	-1.35	1.00	0.14	0.89	7.58
Seed husk/debris	1,110	1.76	0.88	1.98	0.06	10.56
Gnawed shrub	250	-2.08	3.13	-0.661	0.51	2.39

Monthly population size estimates ranged from 19 gerbils ha^{-1} in August 1990 to 97 ha^{-1} in February, 1991.

N, sample size; Regression DF = 7; Total DF = 24; SE coeff, Standard error coefficient; T Statistics = Coefficient/Standard error; VIF, Variance inflation factor. Indices with P values, $P < 0.05$, made significant effect in predicting population size. VIF greater than 10 = strong collinearity, regarded as absence of contribution by the predictor.

other index, namely, number of clusters of seed husks and seed debris, had marginal ($T = 1.98$, $DF = 1$, $P = 0.06$) effect in predicting population size. There was a problem though, its corresponding Variance Inflation Factor (VIF) value (Table 1) exceeded 10, indicating very strong collinearity to other terms in the model. A value for VIF that exceeded 10, suggests absence of contribution (to prediction of population size) by the term, hence of little or no use. The performance of all the indices is shown in Table 1. The predictors were either moderately ($1 < VIF < 5$) to highly ($VIF > 5$) correlated, a case of mild multicollinearity, hence we did not check the effect of interactive predictors.

Analysis of population densities

As noted earlier, there were disruptions in trapping, hence lack of data between March to June 1991, and because JOLLYAGE does not provide estimates for first and last months, the gulf with missing density estimates widened further to six months. Now, since the 2015–2017 estimates were indirect (Fig. 4), using indices of population abundance, we extrapolated the densities on the basis of the calibrated estimator-indices from 1990–1992.

Statistical comparison of population densities of the two segments of the present study, i.e., 1990–1992 versus 2015–2017, indicated an overall monthly means of 67 gerbils ha^{-1} (SE, 6.1) and 56 ha^{-1} gerbils (SE, 4.9), respectively. This represented an estimate of the difference of 11 animals ha^{-1} ; 95% CI for difference (–5.16, 26.80);

and T-Test of difference = 0 (vs not = 0): T-Value = 1.38; P -Value = 0.177; $DF = 30$. Analysis of variance did not show significant effect of annual difference on populations densities within any of the two segments of the study (i.e., 1990–1992 or 2015–2017).

Seasonal effects on population estimates for *G. gambianus* could only be tested in the natural fields because it was entirely absent from the irrigated crop fields. The size of the populations during 1990–1992 study differed significantly among the seasons ($DF = 1$; $F = 7.41$; $P < 0.01$), being always higher in the dry season, after the end of the breeding season in December to February, as earlier noted. Thus, the gerbil increased in density starting about five weeks after the onset of the rains (Fig. 3). However, the seasons did not significantly affect ($DF = 1$; $F = 0.39$; $P = 0.543$) population densities during the 2015–2017 segment of the study.

Survival rates and recruitments

Mean survival rates during 1990–1992 for adult ($X = 0.790$) and young ($X = 0.677$) *G. gambianus* differed significantly among the seasons ($F = 4.86$, $DF = 1$, $P = 0.021$). Adult capture probability averaged 0.471 across the study period, and a mean of 23 recruits per month entered the population. Goodness-of-fit tests failed to reject the hypothesis of equal survival and capture probabilities for both young and adult *G. gambianus*. Overall survival rates across the 1990–1992 segment of the study were greater for adults 0.737 than for young, 0.625 with a significant difference ($F = 14.48$; $DF = 2$, $P < 0.001$). Also, seasonal

Table 2. Monthly survival rates, capture probabilities and recruitment of *G. gambianus* in old fallow fields near Kano, Nigeria during July 1990–June 1992

Month	Year	Adult survival rates (SE)	Young survival rates (SE)	Adult capture probability (SE)	New recruits
July	1990	0.72 (0.272)	*	–	–
August		0.79 (0.202)	0.55 (0.216)	0.40 (0.146)	9
September		0.82 (0.131)	0.58 (0.189)	0.31 (0.125)	11
October		0.84 (0.112)	0.67 (0.204)	0.51 (0.101)	16
November		0.95 (0.178)	0.83 (0.242)	0.56 (0.089)	29
December		0.86 (0.274)	0.65 (0.313)	0.35 (0.082)	30
January	1991	–	–	0.37 (0.113)	–
July		0.87 (0.151)	*	–	–
August		0.88 (0.171)	0.55 (0.191)	0.69 (0.177)	8
September		0.84 (0.157)	0.64 (0.184)	0.37 (0.117)	13
October		0.75 (0.129)	0.56 (0.173)	0.59 (0.109)	35
November		0.73 (0.118)	0.75 (0.137)	0.58 (0.102)	33
December		0.73 (0.102)	0.67 (0.165)	0.39 (0.075)	31
January	1992	0.85 (0.139)	0.84 (0.183)	0.71 (0.076)	38
February		0.63 (0.122)	0.69 (0.193)	0.41 (0.078)	20
March		0.63 (0.112)	0.82 (0.160)	0.41 (0.083)	19
April		0.72 (0.130)	*	0.63 (0.087)	20
May		0.76 (0.263)	*	0.42 (0.091)	3
June		–	–	0.34 (0.091)	–

Empty cells (–) indicate disruptions in sampling (see text also). *Absence of young gerbils during the month. SE refers to standard error.

differences in survival rates for each of the age classes were significant ($F = 10.56$, $DF = 3$, $P < 0.01$). Recruitment of new animals was low during August–September 1991 (8–11 animals per month) but higher in October and November 1991, late in the breeding season, with 20–30 animals per month; then declined to 3 animals in May 1992 at the onset of rains (Table 2). There were significant seasonal differences in mean survival rates (REGWF test, $DF = 1$, $P < 0.05$).

Survivorship and capture probabilities could not be estimated for the 2015–2017 segment of the study because density estimates were indirect (from indirect density estimator and not from a direct density estimator as in the 1990–1992 study).

Discussion

Population density estimate models for CMR data

Population size estimates by the age-dependent Jolly–Seber method, model A2 (OTIS et al., 1978; WHITE et al., 1982) was chosen over estimates obtained from the methodology CAPTURE for a number of reasons. The closure test in program CAPTURE indicated rejection of the closure hypothesis for most of the secondary sampling periods (daily trappings). Further, although the data for the majority of the months indicated strong evidence for heterogeneity of capture probabilities, the goodness of fit test did not select the Mh model as best option. Instead, in nearly all the primary periods (months), the procedure chose the M(tbh) or the M(tb) models. The M(tbh) lacks population estimators (OTIS et al., 1978; WHITE et al., 1982), while the M(tb) showed wide confidence intervals (and huge standard errors) reflecting unreliability of the model for this work. The resulting problem of failure to meet the assumption of closure means the results cannot be presented as valid estimates of the population size. For these reasons and the fact that capture probabilities obtained by the alternative JOLLYAGE (POLLOCK et al., 1990) procedure, were good, hence reduced estimate biases, population estimates by the Jolly–Seber method instead of the closed model CAPTURE were presented in the preceding results.

Population densities

Both distribution and population patterns of *G. gambianus* in northern Nigeria can be explained in terms of moisture application – rainfall, irrigation or, both. The monthly mean densities of gerbils by both CMR population estimator and indirect indices showed a seasonal pattern in densities with lows during the rains, and highs in the first half of the dry season. Such seasonal population cycle is not peculiar to *G. gambianus*, but rather consistent with many African rodent species (DELANY, 1986; NEAL, 1982; ODHIAMBO et al., 2005; RABIU and FISHER, 1987). Some species wean their first litter towards the end of rains, in times of harvest (RABIU and ROSE, 1997), the density of *G. gam-*

bianus also starts rising at the end of the rains in October (present study). This indicates an important population response to seasonal changes, with, perhaps, delayed natality until food supplies are firmed up. It is also possible that the heavy moisture, during mid-rains, about July–August, may have rendered the habitat unsuitable for breeding activities and recruitment. The restricted distribution of the common gerbil to well drained, sandy soil, and its obvious preference for drier savannah has been well documented (e.g., HAPPOLD, 1987; RABIU and ROSE, 1997; and ROSEVEAR, 1969). Our observations of its complete absence from irrigated and flooded localities is a strong affirmation of the influence of moisture on the ecology of *G. gambianus* even on a local, small spatial scale. Perhaps, being a tunnel dweller, predisposed to perpetual risk of getting plowed over or, flooded; and its tendency to drop to small densities, of fewer than 20 animals ha^{-1} during population lows, has probably made it difficult to sustain colonies inside cultivated farmlands. The lows we observed appear to echo data in BÂ et al. (2013), who note a near crash in the population of the species in Sudanian Guinea, West Africa, further west of our study country. It is in the light of the aforesaid points that we argue on the unlikely chance of *G. gambianus* becoming a potential pest. On the contrary, the concern is one of looming localized extinctions as dry season agriculture by irrigation continues to spread in northern Nigeria.

In the moister (than our present study area) Guinea and derived Savannah areas of Nigeria, relative numbers of *G. gambianus* to other rodents were very low (DEMEETER, 1981; EZEIFEKA et al., 1987). It appears *G. gambianus* has not yet completed its inroads into more vegetated and humid zones, further south, beyond its preferred drier Savannah and Sahel zones. As a burrow dweller (this study and others) and relatively slow breeder (NEAL, 1982), *G. gambianus* would find it difficult to maintain viable populations in fields that are regularly flooded with rain or irrigation water. JULLIARD et al. (1999) offer evidence of the negative effect of excessive rains on population of *M. natalensis*, a species that adopts to moist tropical climates considerably better than *G. gambianus*. By logic, it follows that *G. gambianus* would suffer greater negative impact of excessive moisture than *M. natalensis*, hence cannot help maintaining lower population levels. It is possible also that other rodent interspecies relations were in play, suggested by the heavy presence of *M. natalensis* in the irrigated fields that *G. gambianus* did not colonize. An indicted pest species, *M. natalensis* appears to be expanding into degraded habitats far better than other species, including *G. gambianus* (RABIU and ROSE, 1997). This would be an analogous situation to that of increasing population sizes of Striped field mouse, *Apodemus agrarius*, at the seeming expense of *Apodemus sylvaticus* and *Clethrionomys glareolus* in south-west Slovakia (TULIS et al., 2016).

The general dynamics of population sizes and distribution patterns documented here fits, partly, with the works of others, including GRANJON and DUPLANTIER (2009); NEAL (1982), and O'FARRELL et al. (2008), who

record the poor abundance of gerbilline rodents (compared to non-gerbilline ones) in most African habitats. For example, as noted, *G. gambianus* (ex *T. valida*) represents less than five percent of insectivores and rodents in Alatish National Park, northwestern Ethiopia. This was well below the relative numbers of other species, such as *A. niloticus* and *M. natalensis* (HABTAMU and BEKELE, 2008).

Performances of the population density indices

Many of the population indices failed to predict population sizes for *G. gambianus* in the field, leaving us with only two out of seven indices to work with. Active warren counts also failed, despite the low collinearity, evident in low VIF value (= 2.69) to other terms in the model. This was probably because other rodent species might have occupied burrow networks built by *G. gambianus*, a fact that has been documented (CHOATE, 1972; VESEY-FITZGERALD, 1963). In any case, this underscores one of the problems related to the deployment of indirect population indices for measuring population size, a difficulty that does not exist with direct population estimators, e.g., CMR or removal methods (MCKELVEY and PEARSON, 2001). Two indices, specifically cut grass stems and clusters of husks or debris of weed seeds, also failed to predict population density, notwithstanding that evidence of foraging might give some indication of population sizes; certainly not all individual gerbils might leave conspicuous traces of foraging, coupled with the fact that, being a tunnel dweller (HAPPOLD, 1987; This study), *G. gambianus* might feed from cache of grains inside the burrows, hence apparent index of foraging might be useful but may not always serve as strong population index that would help predict population density, as was probably the case in our present study.

Survival and recruitment

Onset of breeding (in the present study) which leads to natural recruitment late in the rains, is probably indicating the involvement of some trigger stimulant – photoperiod or, more likely (since day-light hours are practically uniform during June to August) insect-based foods that became abundant later in the rains but, was as yet, not abundant during the early rains. For many African rodent species, uncommonly heavy rains, or other forms of moisture enhancement can increase the food supplies, and possibly add to large population increases (MWANJABE and LEIRS, 1997; TAYLOR, 1968). Some recruitment beyond December, up to the next litter in August, might represent intrusion from neighboring fields into the relative security of our trapping sites, but the trapping success was rather poor, though did allow new animals to be trapped late in the dry season. Indeed, the adult probability of capture was rather low, under 0.40 and less than 0.60 for most of the study period, except January, 1991. In the populations of *T. valida* and *T. nigricauda* (= *Gerbilliscus* spp.) in eastern Africa, recruitment of young was markedly seasonal despite all year round breeding, a fact which seems to sug-

gest, according to (NEAL, 1982), heavy mortality. CHIDUMAYO (1980), who studied *T. leucogaster* (= *Gerbilliscus leucogaster*) a related species to *G. gambianus*, in Zambia, reports a 53% pre-weaning survival, and 66% or higher survival for juveniles and adults. The survival values for the adults are lower than in the present study.

Conclusion

In northern Nigeria the populations of *G. gambianus* showed obvious fluctuations between the end of rains high of about 90 gerbils ha⁻¹ (November–February) to fewer than 20 gerbils ha⁻¹ early to late rainy season (June–August). We saw evidence that laboriously easier assessment of population densities can be achieved for *G. gambianus* using specific indices of population density (in our case, fresh fecal count and limited spotlighting – perhaps augmented with camera) where previous data of population sizes from standard grid trapping or other direct estimator existed. This would allow calibration to match the indirect indices to population sizes. On many accounts, including the complete absence of *G. gambianus* from irrigated fields and water-logged sites during the rains, and its absence from thickly vegetated habitats; as well as, its apparent tendency towards population crash or sharp declines, especially in mid rains; coupled with slow breeding potential; the species may not likely present a serious pest issue in the crop fields of northern Nigeria. Should *G. gambianus* gain a new pest status in the region, we would suggest that control measures be deployed during June to August when the population density is at its lowest or sharply declining, and new recruitment at its lows.

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