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Does bird predation enhance the impact of Green Muscle® (*Metarhizium acridum*) used for grasshopper control?*

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Abstract

A study at Khelcom, Central Senegal, from September 2008 till June 2009 tested two different dose rates (25 and 50 g conidia/ha) of the mycoinsecticide Green Muscle® (*Metarhizium acridum*) and an untreated control, against grasshoppers in a field trial on nine 400-ha plots in three blocks. The study area was a deforested sylvo-pastoral reserve, 12.5% cultivated, whereas the remainder was fallow or grassland in succession. Grasshopper densities were calculated by executing transect and quadrat counts on plots. The grasshopper community structure was assessed by systematic sweep-net sampling on plots. From these data grasshopper biomass on plots was calculated for each sampling date. Bird numbers were counted on the same transects by the Distance Sampling technique and their densities calculated from Effective Strip Widths (ESW). Energetic requirements of individual bird species were calculated from digestibility-corrected Field Metabolic Rates (FMRs) and for acridivorous species their daily intake of grasshoppers was calculated. Grasshopper densities were very high, with up to 90 ind./m² in September and 30-35 ind./m² in October. Numbers and biomass decreased on treated plots as grasshoppers became infected, and remained significantly different from control plots for three months (until January). The relative importance of grasshopper consumption by birds increased between October (high grasshopper densities) and December (medium densities) from an initial 0.06 (±0.03) %/day to a ceiling of 1.6 (±0.9) % per day. Total grasshopper removal during the dry season was 70 %, whereas during the rainy season this was < 1%. Birds specifically captured large and medium-bodied grasshoppers, but rarely small-bodied species, whose numbers initially increased. These findings were corroborated by field observations and by analysis of regurgitated pellet contents of Montagu's Harriers, *i.e.*, small-bodied grasshoppers were only 1.4 - 2.6% of all grasshoppers taken, whereas they constituted 61 - 68% of random samples from the field. Densities of acridivorous Palaearctic migratory birds, in particular White Stork, *Ciconia ciconia*, Montagu's Harrier, *Circus pygargus* and Lesser Kestrel, *Falco naumanni*, were very high and unprecedented elsewhere. Their numbers largely exceeded the 1% criterion for international importance.

Key words

deforestation, entomopathogen, mycopesticide, commensalism, grasshopper consumption, transect counts, bird densities, *Circus pygargus*, *Falco naumanni*, *Oedaleus senegalensis*, *Ornithacris cavaioisi*, *Acorypha clara*

Introduction

Locust and grasshopper control in the Sahel still heavily relies on chemical insecticides. During the 2003-05 Desert Locust, *Schistocerca*

gregaria, upsurge in western and northern Africa, over 13 million liters of organophosphate and pyrethroid compounds were used, but no biopesticides (Brader *et al.* 2006). This is surprising because the entomopathogenic fungus *Metarhizium acridum*, formerly *M. anisopliae* var. *acridum* (Bischoff *et al.* 2009) (Green Muscle®, further GM) has been commercially available for operational use since 1999 (Lomer 1999) and has been assessed for use against Desert Locust at a dose rate of 50 g conidia (spores)/ha (PRG 2004). Its use in locust control has meanwhile been recommended by the FAO (Magor 2007, FAO 2009) and it obtained full registration from the "Comité Sahélien des Pesticides" (CSP-CILSS) in nine Sahelian countries in January 2010.

Despite the recommendations and registration, there is still very little operational use of GM in Africa because users a) consider the time lag before the onset of mortality as a constraint, b) find its price prohibitive at the recommended dose rate, c) consider the temperature dependency as a drawback and d) consider current oil-based formulations (OF) as too rapidly deteriorating under prevalent field conditions (*e.g.*, van der Valk 2007).

Meanwhile, it has been shown that the dose rate of GM in grasshopper control can be reduced to 25 g conidia/ha (Mullié & Guëye 2009) without compromising efficacy, making it directly competitive with chemical insecticides. Following these results, the Senegalese Crop Protection Directorate used GM successfully in 2009 in *ca* 50% of its treatments against the Senegalese Grasshopper *Oedaleus senegalensis* at a dose rate of 25 g/ha (Khalifa Ndour, DPV Dakar, pers. comm.). New formulations with longer shelf-lives have also been tested and found to perform very well against Desert Locust under operational conditions (Ould Mohamed 2009).

Natural predation of locusts and grasshoppers by vertebrates can be so important that (chemical) control by man becomes redundant (Mullié 2009). Nevertheless, predation is rarely if ever considered in the decision-making processes applied to locust and grasshopper control.

The effect of entomopathogens on the predator-prey relationship is completely different from that of chemical insecticides. In a study design very much comparable with ours described hereafter, but by using the organophosphorous compounds fenitrothion and chlorpyrifos at two different dose rates, Mullié & Keith (1993a) found that apart from direct mortality of 2-7% of the avian community due to anticholinesterase poisoning, bird numbers on transects decreased significantly by as much as 50% following treatments and colonies of Buffalo Weavers, *Bubalornis albirostris*, were deserted. This was caused by the impact of the organophosphates on nontarget arthropods such that insectivores faced an immediate depletion of their food resources (Mullié & Keith 1991, 1993a, 1993b).

Biopesticides do not kill immediately, as the pathogens need time to develop after insects become infected (Langewald *et al.* 1999). Because mycopesticides are very selective, no impact on nontarget species occurs (Lomer 1999, Peveling *et al.* 1999, Mullié & Guèye 2009) and birds neither leave sprayed areas, nor do they become intoxicated. Instead, there are indications that their numbers may temporarily increase (Mullié 2007). The insects become sluggish, and an easy prey for birds, when basking to induce behavioral fever, *i.e.*, by altered thermoregulatory behavior raising body temperature in reaction to infection by a pathogen (Blanford *et al.* 1998). There is indeed field evidence of synergy between the impact of entomopathogens and predation (Cheke *et al.* 2006a, 2006b; Mullié 2007), but this has never been tested experimentally.

The current article addresses the question of whether birds do indeed enhance the impact of *M. acridum* and if so, to what extent and under which conditions. Medium sized plots (400 ha) were sprayed with GM in a field trial and grasshopper and bird densities monitored over an 8-mo period posttreatment. Grasshopper consumption by birds over time was calculated for each of the treatments, based on energetic requirements and compared to available grasshopper biomass. Grasshopper removal rates were assessed to compare treatments.

Methods

Study area.—The study took place from September 2008 until June 2009 at Khelcom, also known under the name of Mbégué, central Senegal (lat 14°28' - 14°43' N, long 15°22' - 15°36'W).

Between 1991 and 2004, 55,400 ha (as measured by GPS) out of the 73,000 ha Mbégué Sylvopastoral Reserve was gradually deforested to allow for groundnut production. However, in 2008 the total cultivated area was only 12.5%, of which about 60% consisted of groundnut and the rest of millet and some smaller surface areas that were grown with crops such as maize, tapioca and sesame. Typically, a field cultivated with groundnut would be sown with millet during the following rainy season one year later, and thereafter left fallow for one or more years. As a consequence, Khelcom is now a mosaic of cropland, fallow and never-cultivated but deforested land, in various stages of succession, mainly with the shrub *Guiera senegalensis* ('Nger' in Wolof) and regrowth of *Combretum glutinosum* ('Rat').

Of special mention is the liana *Leptadenia hastata* ('Thiakhat'). This evergreen plant, forming large green patches in an otherwise barren environment, harbors reproducing Pyrgomorphidae throughout the dry season, and is also exploited by other grasshopper species, most notably *Cryptocatantops haemorrhoidalis*, *Metatymecus gracilipes*, *Diabolocatantops axillaris* and *Heteracris annulosa*. Hence stands of *L. hastata* are often favored by acridivorous birds during the dry season.

Except for 15 so-called Daras (small settlements each housing up to several hundred children who receive religious training and labor in the surrounding fields), there are no other permanent dwellings in the area. There are, however, dozens of temporary camps inhabited by seminomadic herders.

Wildfires occur annually at Khelcom between November and the end of the dry season. In Fig. 1, a map of Khelcom is given showing the layout of our experimental plots and of the areas being burnt.

Floristic composition.—The floristic composition of the study plots was assessed from the diagonals which also served as transects for counts of grasshoppers and birds (Fig. 1). In the middle of each

subtransect of 100 m the herbs present on a 10×10-m quadrat were identified with Berhaut (1967), Terry (1993) and Sankara (2008), and their coverage (%), height (cm) and the percentage of bare soil noted. Trees and shrubs present were identified with von Maydell (1990) and counted on a 100 × 100-m bloc and their height and number noted.

Meteorology.—Data on rainfall, wind, temperature and relative humidity were obtained from the National Meteorological Station at Touba Khelcom (lat 14°34'N, long 15°30'W; Mr Moussa Sy, National Meteorological Service, Khelcom, pers. comm.) situated in the middle of our study area, Fig. 1. Ambient temperatures (T, °C) and relative humidity (RH, %) values were also recorded with Hobo® Pro Series (Onset Computer Corporation, USA, 1998) weather recorders, placed on the ground in the center of each of our plots. The latter observations were believed to provide the best meteorological information of the grasshopper environment and thus for the action of the entomopathogen.

Plots and treatments.—Nine plots of 2 by 2 km, 400 ha per plot, in three blocks of three plots each were delimited. Each block, coded P, Q and R, received three replicate treatments of 0 g (control; P3, Q3, R1), 25 g (P1, Q1, R3) and 50 g (P2, Q2, R2) conidia of *M. acridum* (strain IMI 330189) per hectare. Plots were at least one kilometer apart to avoid contamination during treatments (Fig. 1).

GM was available in two OF formulations, respectively with 2.5 and 1.25 × 10¹³ conidia/l and was mixed in a 1:10 ratio with diesel fuel prior to treatment. Samples of the formulations before mixing were analyzed for viability and concentration of conidia. After calibration plots were treated with four Micronair™ AU 8115 rotary atomizers (Micron Sprayers Ltd, UK) mounted on four four-wheel drive pick-up vehicles, operating simultaneously at a speed of 10 km/h, with a track spacing of 50 m, dose rate of 1 l/ha and a flow rate of 833 ml/min. Treatments took place between 9 and 11 October 2008 from 8 till 11 AM and again from 4 till 7 PM. To prevent clogging of the spray system by conidia, filters and hoses of all Micronairs were cleaned repeatedly after several passes.

Deposition of droplets was measured in the center of each of the spray plots by placing oil-sensitive papers over a length of 600 m perpendicular to the spray paths and facing the wind at 15-m intervals, 60 cm above ground level.

Grasshopper availability.—Two monitoring periods were distinguished. A period of intensive monitoring was applied from 4 d before until 18 d after treatment, at three-day intervals, during the month of October 2008. Extensive monitoring (once a month) was applied from November 2008 until May 2009, with the exception of April, when no observations were made. In September, three more series of counts, respectively at 20, 18 and 14 d pretreatment, were made in nine other plots in the same study area, which were to be sprayed aerially. We will also refer to some of the data obtained from these plots.

All observations were done on transects. One of the 2800-m long diagonals of each plot, usually SE-NW, in a few cases NE-SW (Fig. 1), was divided in three transects of 700 m, starting at 250 m from the corner of the plot, with a 100-m buffer between successive transects and again 250 m at the end of the third transect. Each transect was divided in seven subtransects of 100 m to facilitate observations and to differentiate observations spatially. Observations on subsequent transects within the same plot were considered as being independent.

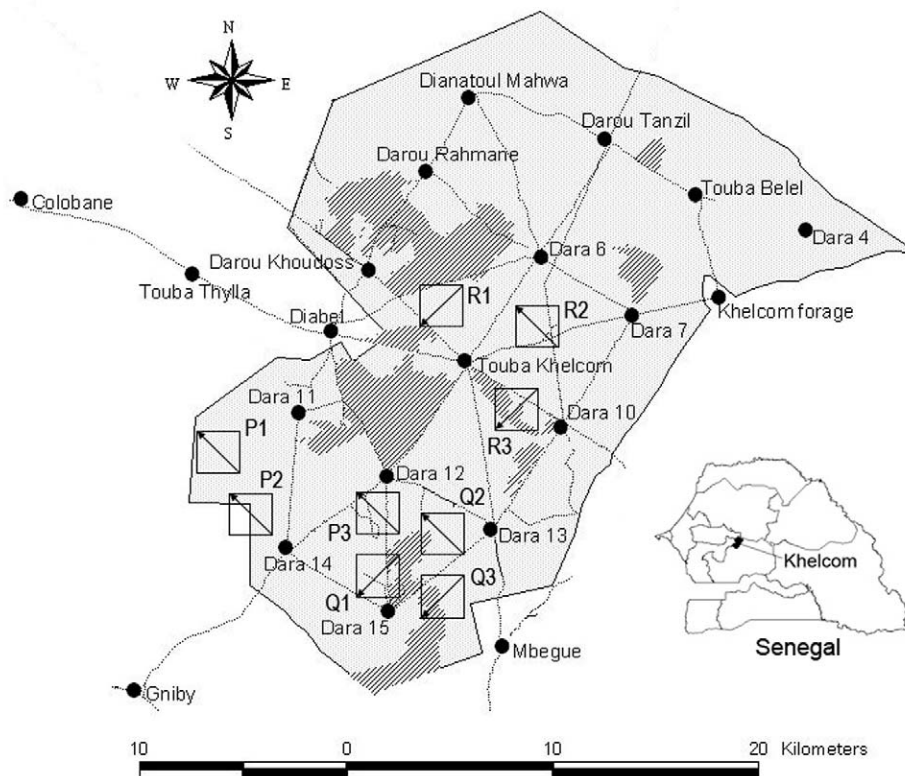


Fig. 1. Map of the Khelcom study area. Squares are study plots with diagonals indicating transects and flashes (arrows) indicating the direction of the counts. Codes of plots sharing the same letter (P, Q and R) are in the same block. Hatchings are areas that were burnt during the study.

Density.—During the intensive monitoring period, two observers walked on either side of the transects, starting at about one to two hours after sunrise. On each subtransect of 100 m, and spaced at 20-m intervals, five open quadrats of 1 m² were selected *at random* and total number of grasshoppers (nymphs plus imago) counted. For each subtransect of 700 m this produced 35 observations or 105 observations for each plot. The densities for the two observers were averaged for each paired quadrat and these figures used in calculations.

During the extensive monitoring, counts were done by a single observer. As it was anticipated that grasshopper densities and proportion of nymphs would drop during the dry season, making the use of quadrat counts inappropriate, during the last count of the intensive monitoring period, both quadrat and full-transect counts (Cressman 2001) were executed successively on the same transects. All grasshoppers seen within 50 cm on either side of the walked track were counted and totals for each subtransect of 100 m were noted. Average numbers per m² (\bar{x}) were subsequently regressed against average numbers counted by the quadrat method (\bar{y}) on the same subtransect. To make counts during both periods comparable, the regression equation ($y = 1.0905x$; $r^2 = 0.9388$) was used to convert densities counted by transect counts into densities calculated by the quadrat method during the period of intensive monitoring.

Community structure.—As the transect counts did not produce information on individual species, after each count insects were captured with sweep nets. Over the entire diagonal, between the 250-m limits from each corner, on three repetitions each of 150 m, grasshoppers were captured in a way as representative as possible: to assure representation of the various habitats available on the plot and to assure the capture of "difficult" stages, such as first instars (less mobile, difficult to capture when on the ground) and such as adults of the larger grasshoppers, the latter particularly difficult

when temperatures were elevated and imago were highly mobile. To reduce variability among samples and dates and to standardize sampling, the capture continued until at least 500 individuals per plot were trapped during each sampling. To prevent interaction with counts, grasshoppers were captured on an imaginary line which was *ca* 100 m away from and parallel to the transects.

Grasshopper imago were identified with Lecoq (1979, 1988, 2008) Mestre (1988) Launois & Launois-Luong (1989) and Launois-Luong & Lecoq (1989). If necessary they were compared to specimens in the reference collection of the Crop Protection Directorate. Nymphs were identified with Popov (1989).

Biomass.—A subsample of the grasshoppers captured for establishing community structure, to which were added individuals captured between September and December 2009 during a follow-up study on the same plots, was used to take both fresh and dry body masses to calculate grasshopper biomass.

Bird numbers.—The same transects and subtransects used for grasshopper counts (see under grasshopper availability) were used for bird counts. As birds were most active in the first hours of daylight and grasshoppers only after they had increased their body temperatures, the onset of bird counts on transects preceded those of grasshoppers, usually starting within the first hour after sunrise. The only exception was when heavy rains prevented an early start. We believe this did not influence the quality and comparability of the counts, as all three observers had the same delays and birds usually exhibited a peak of activity immediately following rains.

As the observers had only basic experience in field ornithology and in estimating distances, the senior author organized a three-day intensive practical training course in the field prior to the onset of the study. Individual performances, both on visual identification and by sound, were tested at the end of the training to assure that

the most important and/or most common species could be properly identified. In the course of the monitoring period these training sessions were repeated several times to account for species having newly arrived, e.g., Palaearctic-African migrants. For visual identification of birds Brown *et al.* (1982), Urban *et al.* (1986, 1997), Fry *et al.* (1988, 2000), Keith *et al.* (1992) and Borrow & Demey (2001) were used. For identification of bird song the CD collections of Chappuis (2000) and Barlow *et al.* (2002) were used.

To standardize counts temporally (monitoring per plot) and spatially (comparison with other plots), each subtransect of 100 m was counted in 5 min. (cf. Mullié & Keith 1993a), or 35 min per transect. All birds that could be seen with the naked eye or heard at unlimited distance on either side of the transect, were noted on field forms. Binoculars (8×40, 10×40) were used to identify species that otherwise were too distant to be properly identified, or to distinguish between similar species. It was decided not to apply a maximum observation distance *a priori*, because otherwise the sample of raptors and storks might become too small. However, during analysis (see under statistics) observation width was sometimes limited *a posteriori*.

For each observation, i.e., a single bird or a group of two or more individuals close together, the number and the distance perpendicular to the transect was noted, according to the methodology of distance sampling (Buckland *et al.* 1993). Nonidentified species were noted with a description. In many cases these species could later be identified. The Distance software (Thomas *et al.* 2006) allows for a calculation of true densities, as it accounts for the probability of detection: small or secretive species will only be observed at rather short distances, whereas flocks, large species or species with a conspicuous behavior tend to be noticed at larger distances.

Grasshopper consumption by birds.—Based on existing knowledge of the food and feeding behavior of the bird species present on our transects (cf. Morel & Morel 1978, Mullié & Keith 1993a, Mullié 2009), as well as on the basis of visual observations during the study, on gizzard contents of birds found dead, e.g., as road victims in our study area, and on the contents of regurgitated pellets (see also next paragraph) collected in roosts of communal species such as White Stork, Montagu's Harrier and Lesser Kestrel, *Falco naumanni*, observed species were classified as acridivorous or nonacridivorous.

As the total observation period, from September till June, included both a part of the rainy season and the major part of the dry season, some species were present in only a part of this period. Certain species such as the Village Weaver, nested and fed their young with insect prey. During the dry season they became granivorous. The Village Weaver is considered as one of the principal predators in Senegal of the Senegalese grasshopper *Oedaleus senegalensis* during the rainy season (Axelsen *et al.* 2009). Other common species, such as the Singing Bushlark, *Mirafra cantillans*, and the White-billed Buffalo Weaver, are acridivorous during the rainy season, feeding themselves and their young with grasshoppers (Mullié & Keith 1993), but become granivorous during the dry season (pers. obs. WCM). Other species may change the proportion of grasshopper prey in their diet throughout the season. As yet, we do not have sufficient information to estimate accurately for each species which proportion of its diet consists of grasshoppers throughout the year.

To be on the conservative side, we assume here that the diet of any species considered to be acridivorous does not consist by more than 50 % of grasshopper prey, even if we know for certain species (Montagu's Harrier, Lesser Kestrel; Mullié 2009) or suspect for others (White Stork, Abyssinian Roller, *Coracias abyssinica*, Woodchat

Shrike, *Lanius senator*) (this study) that the proportion by weight of grasshoppers in their diet may be as high as 80-90%. Furthermore we follow Axelsen *et al.* (2009) that any *breeding* granivorous species only feeds on grasshoppers during the rainy season and from November onwards only feeds on grains.

Individual field metabolic rates (FMRs) of birds were calculated by using an allometric analysis of log-log transformed data of fresh body mass (Mb) in g and FMR in kJ/day of 229 vertebrate species ($p < 0.007$, $F_{1,227} = 547$; $FMR = 2.25Mb^{0.808}$) (Nagy 2005). A database was developed in Excel (Microsoft Inc.) containing for each record, along with bird species name, number observed and distance, information on bird body mass, FMR, FMR corrected for food digestibility, effective strip width (ESW; see under statistics), origin (Palaearctic or Afro-tropical) and detection probability (Table 1). From these data, bird densities/km² and their grasshopper consumption were calculated.

To estimate the percentage of grasshopper biomass taken daily by the acridivorous bird community, the calculated daily consumption (kg DM/km²) was divided by the calculated daily total biomass of grasshoppers present + daily consumption (kg DM/km²) and multiplied by 100.

Food remains in regurgitated pellets.—Only data on pellet contents from Montagu's Harriers became available during the study; data from other species will be published elsewhere. All Montagu's Harriers feeding in Khelcom used up to 4 communal roosts within the area. During the extensive monitoring period regurgitated pellets were randomly collected in the roosts (ca 100 pellets per roost and per visit), individually wrapped in plastic foil and labelled for future analysis and identification of the prey remains. As the main orthopteran remains in pellets are mandibles, a key had to be developed to identify individual species (Franck Noel, in prep.), taking into account the wear of the mandibles (cf. Chapman 1964, Zouhourian-Saghiri *et al.* 1983, Gangwere & Spiller 1995, Smith & Capinera 2005). Prey remains per pellet were counted (using maxima of left or right mandibles, tibiae, femurs, and other identifiable parts) and biomass of grasshoppers calculated from data in Appendix 1.

Statistics: grasshopper densities.—Count data were log transformed before analysis. Because data were not independent in time, a BACI (Before-After-Control-Impact) design was applied (Stewart-Oaten *et al.* 1986). In this design, the effect parameter $[\text{Log}(n+1)_{\text{treated}} - \text{Log}(n+1)_{\text{control}}]_{\text{before}}$ was tested against $[\text{Log}(n+1)_{\text{treated}} - \text{Log}(n+1)_{\text{control}}]_{\text{after}}$. It was thus implicitly assumed that the log difference of 'to be treated' and control plots was constant in time before treatments and that any change in this ratio, after spraying of GM, was caused by a treatment effect.

Statistics: bird densities.—The results from the transect counts were analyzed with the software Distance 5.0, release 2 (Thomas *et al.* 2006). For each individual species (for common species) or group of species (for less common species) Effective Strip Width (ESW) was calculated, a measure that depends on the probability of detecting a bird. To obtain a larger sample size, the less-common species were grouped into three categories: from 1 (low) to 3 (high) probability of detection. These categories corresponded approximately with detection distances of 0-100 m (1), 0-200 m (2) and 0->400 m (3). For about half the number of bird species, a Hazard Rate model was used to calculate ESW, for the others a Half-normal with Cosine Expansion model. The chosen observation interval was manual in half of the cases and automatic in the others, whereas truncation of

observation distance was applied in most cases to allow for a better fit of the chosen model. Details are given in Table 1.

To transform count data into densities, the following formula was applied: Density (ind./km²) = number counted / (2 × 2.1 × ESW). In this formula the factor 2 corrects for the two sides of the transect counted and the factor 2.1 is the total length in km of the

three subtransects per plot. As an example we can take 9 Singing Bush-larks counted on a plot, which would give a density of $9/(2 \times 2.1 \times 0.0326) = 65.73$ ind./km². Calculated densities were neither corrected for breeding females nor for nestlings, as was done by Axelsen *et al.* (2009).

Table 1. Information on body mass, (corrected) field metabolic rates (FMR), origin, detection probabilities, effective strip width (ESW) and model parameters used in calculations of species considered as acridivorous during at least a part of the study period.

Scientific name	n	Body Mass	FMR	corr. FMR	origin	Detect.	ESW (m)			details of model applied		
							95% conf.			type	interval	truncation (m)
							avg.	min.	max.			
<i>Bubalornis albirostris</i>	405	75.4	199.4	269.4	A	ind.	61	55	69	HR	manual	1000
<i>Bubulcus ibis</i>	144	335	550.5	743.9	A	ind.	316	274	364	HN	manual	2000
<i>Bucorvus abyssinicus</i>	1	4000	2979.8	4026.8	A	3	243	227	261	HR	manual	1175
<i>Centropus senegalensis</i>	14	170	346.8	468.7	A	2	71	68	75	HN	manual	375
<i>Chelictinia riocourii</i>		110	257.9	348.5	A	1	243	227	261	HR	manual	1174
<i>Ciconia ciconia</i>	28	3473	2706.5	3657.4	P	3	243	227	261	HR	manual	1175
<i>Circus aeruginosus</i>	763	627.5	844.0	1140.6	P	ind.	236	222	252	HN	automatic	-
<i>Circus pygargus</i>		315.5	528.5	714.1	P	ind.	236	222	252			-
<i>Cisticola juncidis</i>	662	7.7	42.2	57.0	A	ind.	20	19	22	HN	manual	140
<i>Cisticola sp.</i>		7.7	42.2	57.0	A	ind.	20	19	22			
<i>Coracias abyssinica</i>	542	114	264.2	357.0	A	ind.	102	93	112	HR	automatic	-
<i>Cursorius temminckii</i>	3	68.5	186.8	252.4	A	2	71	68	75	HN	manual	375
<i>Elanus caeruleus</i>	3	240	438.6	592.8	A	3	243	227	261	HR	manual	1175
<i>Eupodotus savilei</i>	78	615	832.6	1125.1	A	2	71	68	75	HN	manual	375
<i>Falco naumanni</i>	422	152.5	322.1	435.3	P	ind.	233	214	255	HN	manual	2000
<i>Halcyon senegalensis</i>	56	56.9	164.6	222.4	A	ind.	59	40	87	HR	automatic	-
<i>Lamprotornis caudatus</i>	74	121	275.1	371.8	A	ind.	80	64	99	HN	manual	600
<i>Lamprotornis chalybaeus</i>	19	100	241.7	326.6	A	2	71	68	75	HN	manual	375
<i>Lanius meridionalis</i>	2	65.5	181.2	244.8	A	2	71	68	75	HN	manual	375
<i>Lanius senator</i>	269	31.9	111.0	150.0	P	ind.	106	91	123	HR	manual	200
<i>Leptoptilos crumeniferus</i>	2	6325	4071.1	5501.5	A	3	243	227	261	HR	manual	1175
<i>Macronyx croceus</i>		47.6	145.8	197.0	A	1	36	34	37	HR	manual	105
<i>Merops albicollis</i>	143	24.2	92.0	124.3	A	ind.	43	38	49	HR	automatic	200
<i>Milvus migrans</i>	11	704	912.8	1233.5	P	3	243	227	261	HR	manual	1175
<i>Mirafra cantillans</i>	655	18.7	77.1	104.3	A	ind.	33	31	34	HN	automatic	-
<i>Motacilla flava</i>	5	17.6	74.0	100.0	P	1	36	34	37	HR	manual	105
<i>Myrmecocichla aethiops</i>	7	56.6	164.0	221.6	A	2	71	68	75	HN	manual	375
<i>Neotis denhami</i>	1	4120	3040.4	4108.7	A	3	243	227	261	HR	manual	1175
<i>Oenanthe oenanthe</i>	111	23.2	89.3	120.7	P	ind.	54	47	62	HN	automatic	125
<i>Oenanthe sp.</i>		23.2	89.3	120.7	P	ind.	54	47	62			
<i>Passer griseus</i>	243	28.1	101.8	137.6	A	ind.	35	30	40	HR	automatic	-
<i>Ploceus cucullatus</i>		37.5	123.9	167.4	A	ind.	38	34	42			
<i>Ploceus sp.</i>	420	37.5	123.9	167.4	A	ind.	38	34	42	HR	manual	250
<i>Ploceus velatus</i>		24.2	92.0	124.3	A	ind.	38	34	42			
<i>Prinia subflava</i>	54	9	46.9	63.4	A	1	36	34	37	HR	manual	105
<i>Spreo pulcher</i>	34	64.2	178.7	241.5	A	ind.	61	47	79	HN	manual	170
<i>Tchagra senegala</i>	88	53.9	158.6	214.4	A	ind.	53	38	74	HR	automatic	-
<i>Tockus erythrorhynchus</i>	65	146	312.7	422.6	A	ind.	87	68	112	HR	automatic	-
<i>Tockus nasutus</i>	106	208	397.9	537.7	A	ind.	36	23	57	HR	manual	800
<i>Turnix sylvatica</i>	4	23.2	89.3	120.7	A	1	36	34	37	HR	manual	105
<i>Upupa epops</i>	16	51.9	154.6	208.9	P	2	71	68	75	HN	manual	375
<i>Vanellus tectus</i>	417	112.5	261.8	353.8	A	ind.	67	59	75	HR	automatic	-

n: number of observations (not necessarily number of birds; some species occur in groups). Body mass: fresh body mass (g) (*cf.* Dunning 1993). FMR: FMR in kJ/day = $10.5 \times \text{body mass (g)}^{0.681}$ (according to Nagy 2005). corr FMR: FMR corrected for digestibility [= (FMR/74) × 100] (According to Petersen *et al.* 2008). origin: A = Afrotropical, P = Palearctic. detect. Detect[ability]: ind. = individual. ESW could be calculated. 1 = species with low detectability; 2 = species with medium detectability; 3 = species with high detectability (see text for details). ESW: Effective Strip Width (Buckland *et al.* 1993, Thomas *et al.* 2006), see under Statistics. Energy content grasshopper 22 kJ/g DW (Petersen *et al.* 2008); % water in grasshopper 71.6 (Petersen *et al.* 2008). Type: HR = Hazard Rate model, HN = Half Normal with Cosine Expansion model.

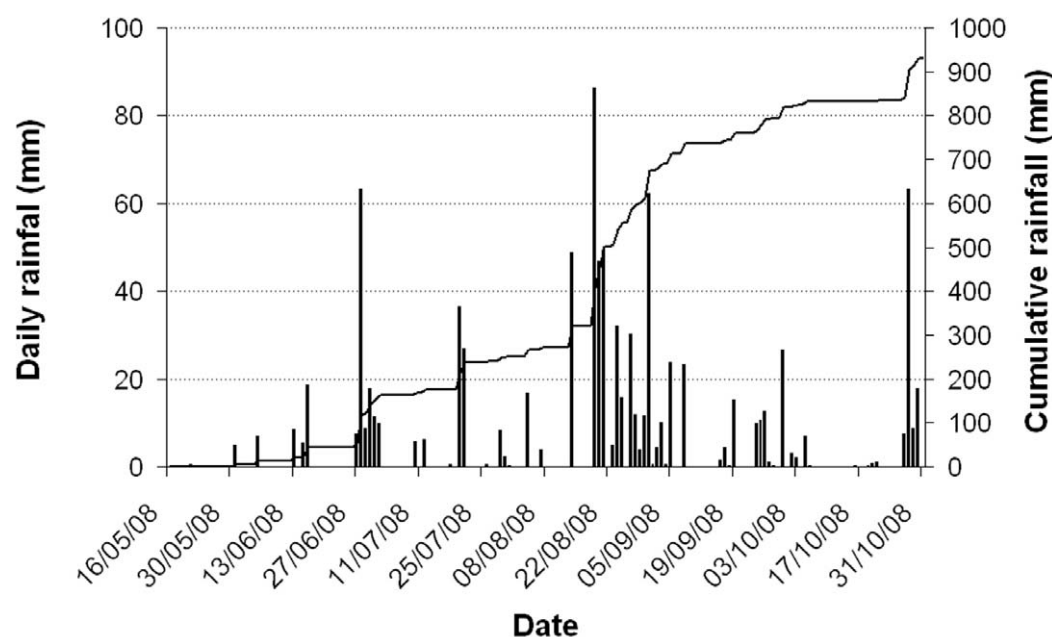


Fig. 2. Daily and cumulative rainfall (mm) during the 2008 rainy season at Touba Khelcom.

Treatment effects were analyzed by Repeated Measures ANOVA (SPSS, v.13.0; SPSS Inc., Chicago, Illinois, USA). Missing values on day -1 for plots R1 and R2 were obtained by interpolation of count data on days -4 and +3.

Results

Detailed information on the quality and efficacy of the treatments, droplet deposition, germination and persistence of conidia of *M. acridum* and of meteorological conditions during treatments is given elsewhere (Mullié & Guèye 2009) and will be summarized here. Germination of spores just prior to the first treatments was 93.6 (± 1.8) % ($n=14$) in the 500 g/l formulation and 92.4 (± 2.5) % ($n=17$) in the 250 g/l formulation (SenBiotech *in litt.*). Droplet distribution was regular and similar on all treated plots, with an average of 13 droplets/cm². Efficacy of treatments, corrected accord-

ing to Henderson-Tilton (1955) for grasshopper counts on control plots, was 83.8-87.1%. Median Lethal Times (MLT) were 8.24 (95% CL 5.97-10.07) and 8.19 (95% CL 6.58-9.74) days and LT_{80} values were 15.85 (95% CL 11.99-28.00) and 13.06 (95% CL 10.93-17.11) days respectively for 25 and 50 g/ha, with no differences between the two dose rates. The maximum effect of GM was between 6 and 12 d posttreatment. Mortality of >90% due to *Metarhizium* infection (confirmed by sporulation) of untreated grasshoppers placed in persistence cages on treated plots for 72 h, showed that *M. acridum* activity persisted for at least 18 d post treatment.

Meteorological conditions.—Daily and cumulative rainfall during the 2008 rainy season are given in Fig. 2. Minimum and maximum daily temperatures at ground level during October are given in Fig. 3. The 2008 rainy season at Khelcom was characterized by extremely wet conditions and a cumulative rainfall of 935 mm,

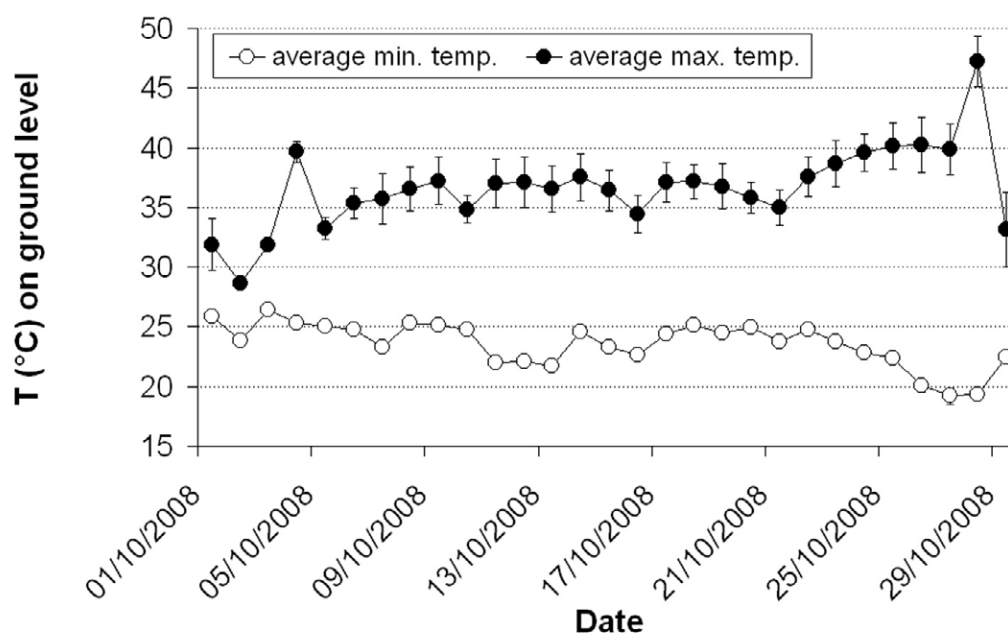


Fig. 3. Average daily minimum and maximum temperatures ($n=7$) at ground level in study plots at Khelcom in October 2008.

which is well above normal and approximately twice the annual amount of the past 20 y in the same area. No rains were recorded during treatments and the following period of intensive monitoring. The interval of minimum and maximum daily temperatures during treatments and thereafter was favorable for a rapid development of *M. acridum*, as the optimum ambient temperature range for the pathogen development is between 24 and 38°C (C. Kooyman, FAES Dakar, pers. comm.).

Floristic composition.—Average shrub density in our plots was 17.9 shrubs/ha and consisted of *G. senegalensis*, *C. glutinosum*, *Balanites aegyptica*, *Calotropis procera*, *Cassia occidentalis* and *Bauhinia rufescens*. Tree density was 1.3 trees/ha, the commonest tree being *C. glutinosum*. Locally stands of Baobabs, *Adansonia digitata*, had been saved to provide shade for man and livestock. More rarely *Tamarindus indica*, *Piliostigma reticulatum*, *Mitragyna inermis* (in temporary flooded depressions), *Acacia (Faidherbia) albida* or *Sterculia setigera* were still present. The few remaining trees are heavily exploited for firewood and browse.

The herbaceous layer was mainly composed of Gramineae, such as *Andropogon* sp., *Cenchrus biflorus* ('Cram cram'), *Ctenium elegans*, *Eragrostis tremula*, *E. tenella* and *Digitaria* sp. Adventives such as *Mitracarpus villosus* and *Spermacoce (Borreria) radiata* dominated on sites which had been cultivated in recent years.

Wildfires.—In November 6046 ha of Khelcom was burnt, whereas throughout the dry season, but in particular during April-May, an additional 1307 ha fell prey to wildfires, making a total of 13.4 % of Khelcom being burnt during the study. Some of our plots were partially affected by the fires. Based on our monitoring, this concerned 5.3% of the transects in November, 13.2% from December till March and 18.0% in May.

Grasshopper densities.—Immediately prior to treatments, average densities of grasshoppers (all stages confounded) were between 30 and 35 ind./m² in all plots (Fig. 4). At the end of second decade of September (not shown in Fig. 4), three weeks prior to treatments, average densities of 90 ind./m² were even recorded. Densities remained at pretreatment levels in the control plots until 15 d post-treatment, after which date they gradually decreased due to natural

factors related to the end of the rainy season.

Starting from day 6 after treatment, grasshopper densities in both the 25 and 50 g/ha treated plots decreased rapidly as a result of exposure to *M. acridum* conidia, which was confirmed by sporulation of *M. acridum* on caged individuals.

Grasshopper numbers remained low in treated plots and were statistically different from densities in control plots until 74 d after treatment. Only from 109 d posttreatment onwards (January), densities on all plots were no longer different from each other (Fig. 4).

Grasshopper community structure.—In total, 79,480 grasshoppers were captured and identified. The grasshopper community consisted of at least 32 species. In addition, 5 taxa could only be identified to the genus level and at least one or more species remained unidentified. The latter category was only 0.3 % of the total number captured. For 31 species and seven stages (adult and 6 larval stages) fresh body mass (WW, n=1731) and dry body mass (DW, n=908) were taken (Appendix 1). For species and stages for which only fresh body masses were available, these were multiplied by 0.3 to obtain DW values (based on Appendix 1; n=908, ratio DW/WW=0.295). For two rarely captured species lacking field information on body mass (*Aiolopus simulatrix* and *Homoxyrhopes punctipennis*), a regression analysis was obtained from body length vs DW of the captured specimens and the regression equation applied to body-length data from the literature (Mestre 1988), to calculate corresponding DW (imagos only).

On the basis of numbers captured, the Senegalese grasshopper *Oedaleus senegalensis* (producing diapausing eggs at the end of the rainy season) dominated during the rainy season (58-66%), and was absent from February onwards. Species with diapausing adults or continuous reproduction were present during the entire period (Fig. 5). Numerically the most important species were *Acorypha clara*, *Acrotylus blondeli*, *Ornithacris cavroisi*, *Pyrgomorpha cognata* complex and *P. vignaudi*. These species, together with *O. senegalensis*, comprised 75-85 % of grasshopper numbers in the community at any moment.

On the basis of body mass, the situation is slightly different. *O. senegalensis* dominated during the rainy season (47%), followed by *O. cavroisi* (14%), *Acorypha glaucopsis* (9%) and *A. clara* (7%). These

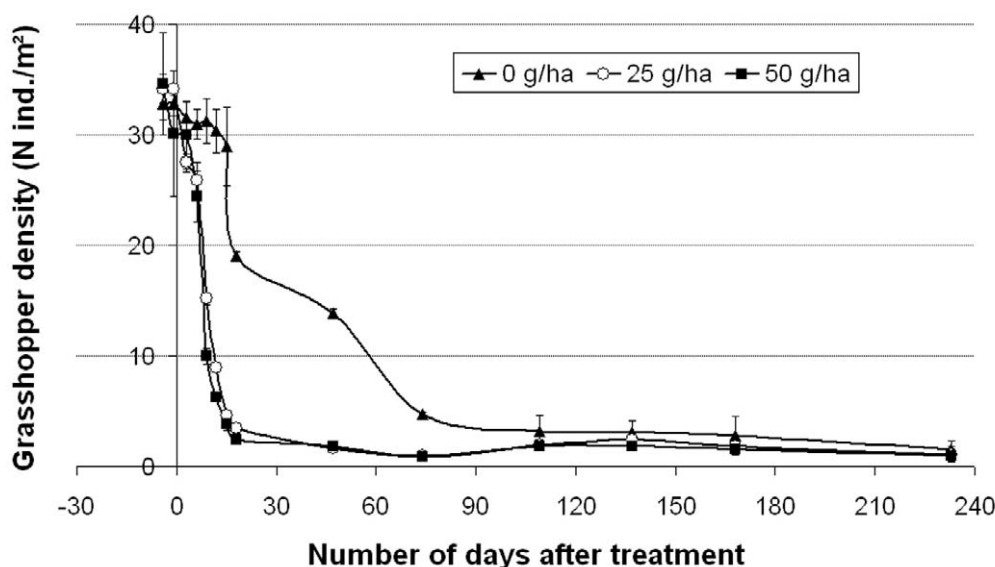


Fig. 4. Average density of grasshoppers (ind./m²) per treatment in time. Bars indicate Standard Errors.

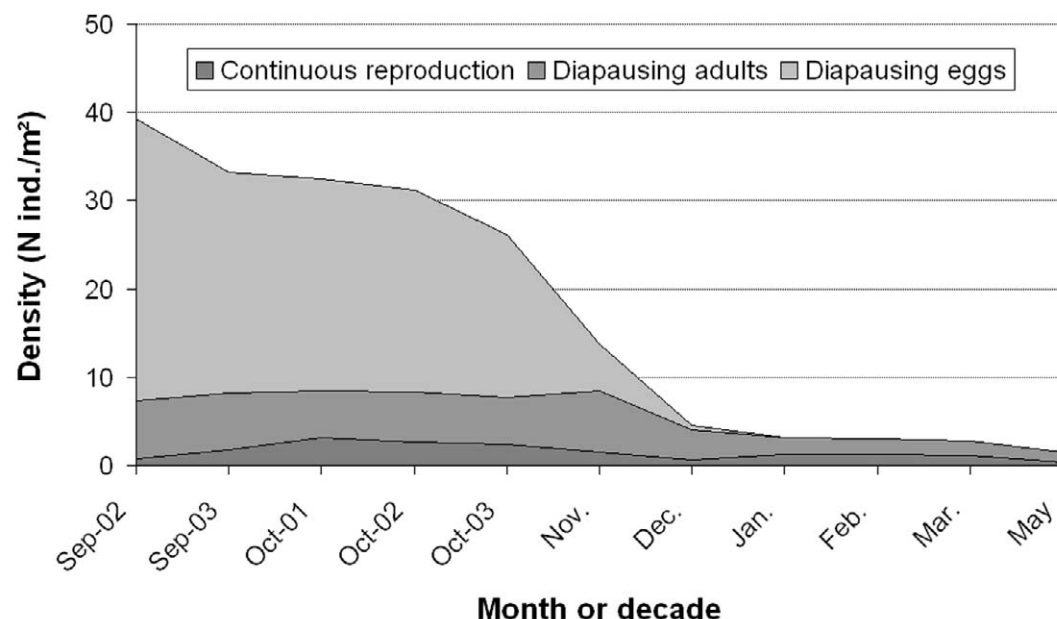


Fig. 5. Densities (ind./m²) overtime of the grasshopper community according to life history strategy.

four species represented 77% of the grasshopper community. During the dry season, from December onwards, *O. cavroisi* (53%) *A. clara* (23%) and *Diaolocantantops axillaris* (6%), represented 82% of the grasshopper community by biomass. From December onwards Catantopinae (*D. axillaris*, *Harpezocatantops stylifer*, *Catantops stramineus*, *Cryptocatantops haemorhoidalis*) and Pyrgomorphidae replaced species laying diapausing eggs (*O. senegalensis*, *A. glaucopsis*). In Fig. 6, the grasshopper biomass in time in kg DW/km² is given.

Birds.—During transect counts, 83 bird species were identified. Of these, 42 were classified as acridivorous, at least during a part of the time (Table 1). In Table 1, details are also given on the various parameters used for calculating densities. Tables with detailed count results per plot and per species can be found in Mullié & Guèye (2009) and are summarized in Appendix 2.

The bird community consisted of a mix of Palearctic-African (all migratory) and afro-tropical (both migratory and resident) species. Consequently, during the course of the study some species arrived,

while others left our study area.

Commensalistic feeding associations were common and contributed to an efficient removal of grasshoppers from plots. Species implicated were White-billed Buffalo Weaver, White-throated Bee-eater *Merops albicollis*, White Stork, Lesser Kestrel, Cattle Egret *Bubulcus ibis* (Fig. 7) and Abyssinian Roller.

The results from the repeated measures ANOVA applied to acridivorous bird species on transects, showed a significant time effect ($F=8.582$, $df=4.562$ (Huynh-Feldt correction), $p<0.001$) but independent of treatment (N.S.): bird numbers gradually increased over time on all plots, with no differences between treatments (Mullié & Guèye 2009).

Although bird numbers were not influenced by treatments, absolute grasshopper consumption by birds increased on all plots, whereas daily removal rates increased on treated plots only. From day -4 until day 6, treated and control plots were not different. Starting from day 9 until day 18, daily removal of the available grasshopper biomass on treated plots increased tenfold from 0.04-

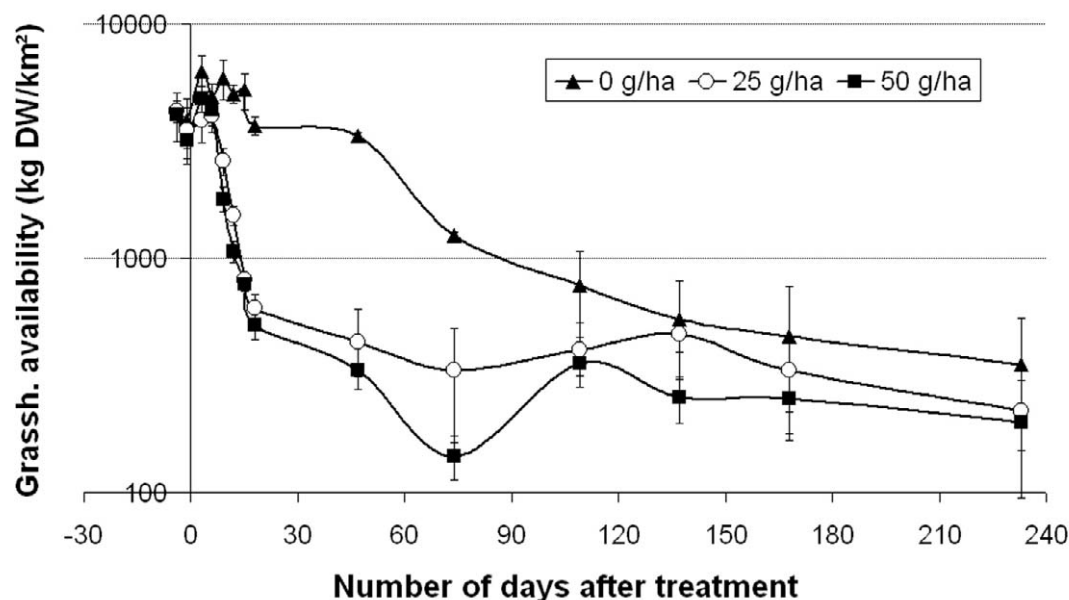


Fig. 6. Average grasshopper biomass (kg DW/km²) over time per the three treatments. Bars indicate Standard Errors.

0.08% to 0.48%, whereas grasshopper consumption on control plots remained at a low 0.03–0.04% daily removal in the same period (Fig. 8).

The increase of grasshopper removal was due to a combination of two factors. Firstly, and most importantly, GM treatments caused a strong reduction of grasshopper densities, while densities of acridivorous birds did not significantly change. Secondly, although acridivorous bird densities remained in the same order of magnitude, the species composition changed due to migration, with generally heavier migrant species such as Montagu's and Marsh Harriers (*C. aeruginosus*) arriving and smaller species such as White-throated Bee-eaters and Woodland Kingfishers (*Halcyon senegalensis*) leaving (Appendix 2).

From 18 till 74 d posttreatment, treated and control plots remained significantly different. In this period both removal rates and consumption continue to increase, as more and heavier bird species arrived, White Storks in particular. From January (day 109) onwards, grasshopper removal rates level off at 1.58 (± 0.25)% daily removal and are no longer different between treatments.

To verify the validity of our approach, we also calculated grasshopper removal from monthly decreases in densities on control plots from December onwards (interval between dashed lines in Fig. 8). Control plots were taken to avoid confounding factors such as a prolonged mortality due to persistence of viable *M. acridum* conidia. The results are very much in agreement with the calculations based on energetic requirements, although the grasshopper removal rate is slightly lower at 1.07 (± 0.63)%.

As the community structure data did not provide any evidence for major grasshopper immigration to or emigration from the plots from December onwards, it was assumed that population declines on plots in this period were mainly resulting from predation. The daily population decline, as calculated by regression analysis on $\log n \text{ ind./m}^2 \text{ (y)}$ in time (x): ($y = -0.0882x + 0.7427$, $r^2 = 0.9304$; ANOVA: $df = 524$, $F = 7.097$, $p = 0.008$; Fig. 9) showed that the rate of decrease of grasshopper densities between December and May was constant. In December, average densities had fallen to below 5 ind./m².

The composition of the bird community changed considerably during the course of the study. During the rainy season it consisted of about 90% acridivores, dropping to ca 10% in May (Fig. 10). However, this change was not caused by decreasing densities of acridivorous birds ((ANOVA; $df = 9$, $F = 1.671$, N.S.), but by a very strong increase of granivorous species during the dry season, most notably Golden Sparrows (ANOVA; $df = 9$, $F = 48.456$, $p < 0.001$).

Pellet contents.—Based on numbers of prey items recovered from Montagu's Harrier pellets in the period January to March, grasshoppers constitute 87.4–91.0% of the diet, whereas on the basis of biomass, they constitute 51.0–61.0% (Mullié & Koks unpub. data). In Table 2, recovered grasshopper species are given from high to low body mass. The harriers do not take grasshoppers proportionally to their occurrence ($\chi^2 (13, n = 1623) = 3701.04$, $p < 0.0001$). Common species (i.e., > ca 5% of the community) with a body mass > 0.73g are taken significantly more often than smaller species. The latter represent only 1.4–2.6% of all grasshoppers being taken by the harriers, whereas they represent 61–68% of the grasshopper community in the field. The three preferred prey species in order of importance are *Acorypha clara* (57–65%), *Ornithacris cavroisi* (23–26%) and *Diabolocatanops axillaris* (9–15%).



Fig. 7. Cattle Egret with *Acorypha clara* as prey. Cattle Egrets, *Bubulcus ibis*, often in commensalistic feeding associations with Lesser Kestrels, *Falco naumanni*, exploited medium-sized grasshoppers in green patches of the liana *Leptadenia hastata*.

Discussion

The 2008 rainy season at Khelcom was characterized by exceptionally abundant rainfall (935 mm) and very high grasshopper densities (up to 90 ind./m² in September, 30–35 in October) showing a low mobility. This low mobility can be explained by the presence of a well-developed herbaceous layer, due to abundant rainfall and by the absence of favorable winds at the right moment for the second generation of the Senegalese Grasshopper to migrate north (J. Bak, National Environmental Research Institute, DMU, Denmark, pers. comm.). This resulted in two subsequent generations of *O. senegalensis* reproducing at Khelcom, leading to very high densities. The treatments with GM were executed against a population of *O. senegalensis* of which adults predominantly belonged to the second generation, and nymphs to the third generation.

The composition of the grasshopper community, consisting of 32+ species, was dominated numerically by the Senegalese grasshopper (58–66%) before treatments and during the intensive monitoring period at the end of the rainy season, but in terms of both numbers and biomass, species with diapausing adults such as *O. cavroisi* and

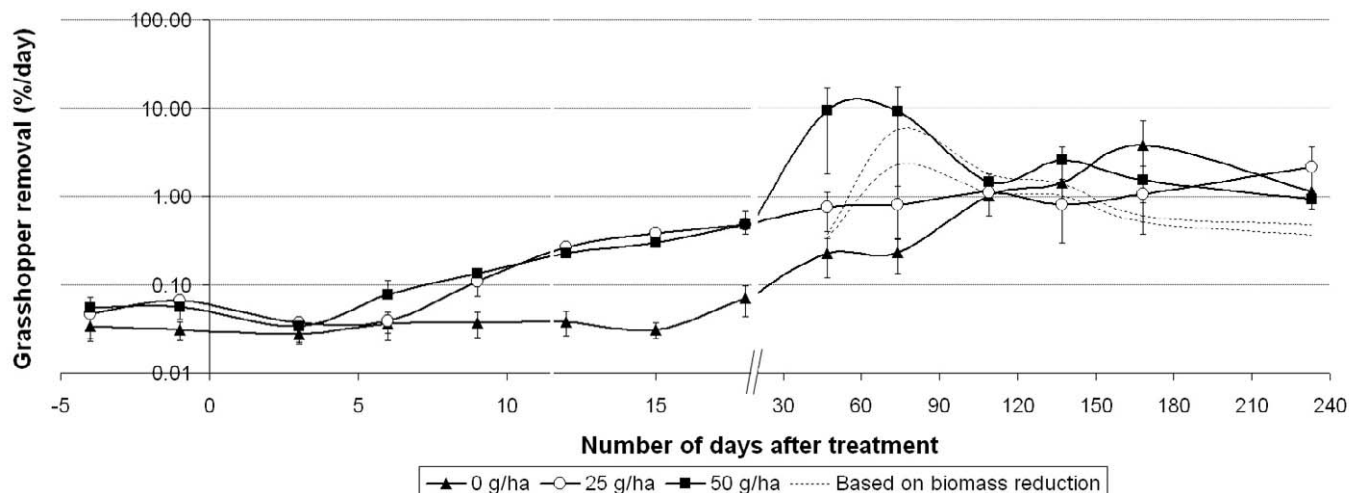


Fig. 8. Average percentage of the grasshopper community (by weight) removed per day per treatment by acridivorous birds. Bars indicate Standard Errors. The dashed lines indicate minimum and maximum biomass reduction, based on the difference in availability on successive monitoring dates. The time scale changes in the middle of the x-axis. See text for further explanation.

A. clara, were common throughout the entire study period (Fig. 5). Their continuous presence is likely the main reason that they form an important part of the diets of many acridivorous birds (Mullié 2009). Nymphs were the dominant life-form until mid-October. Starting from December onwards, only nymphs of continuously reproducing species were present.

In recent years Khelcom has become an important reproduction area for an array of grasshopper species, some of which are important pests to rain-fed agriculture. Until 1991, Khelcom was part of the 73,000-ha protected Mbégoué Sylvopastoral Reserve, of which 55,400 ha were gradually cleared until 2004 to make way for groundnut production. Grasshopper problems were unknown from the area before 1991 (data from Crop Protection Directorate). The resulting mosaic of cropped areas (not exceeding 12.5% of the surface area during the study), fallow and cleared land and partially regenerating former forest, has become an ideal habitat for grasshopper development. This in turn has attracted acridivorous bird

species, such as Montagu's Harrier, characteristic for areas rather low in the succession cycle. Numbers of Montagu's Harriers that use Khelcom either for foraging or as a night roost are maximally 5000-6000 individuals (Mullié & Guèye 2009). These numbers are unprecedented elsewhere and are among the highest recorded anywhere in the world (Clarke 1996). They constitute about 16% of the population of about 37,000 individuals estimated to migrate via Spain to the African mainland (B. Koks, SWGK, The Netherlands, pers. comm.) and 2% of the entire world population estimated at 300,000 individuals (C. Trierweiler, Groningen University, The Netherlands, in litt.).

Some of the other acridivorous species reach very high densities, rarely found in such concentrations elsewhere in the Sahel, e.g., White Stork (3,500 ind.; 1.75% of the flyway population) and Lesser Kestrel (5,000; 10%) (Mullié & Guèye 2009). All these species exceed the 1% criterion for areas of international ornithological importance (Ramsar Convention-COP9 2005; www.ramsar.org/key_criteria)

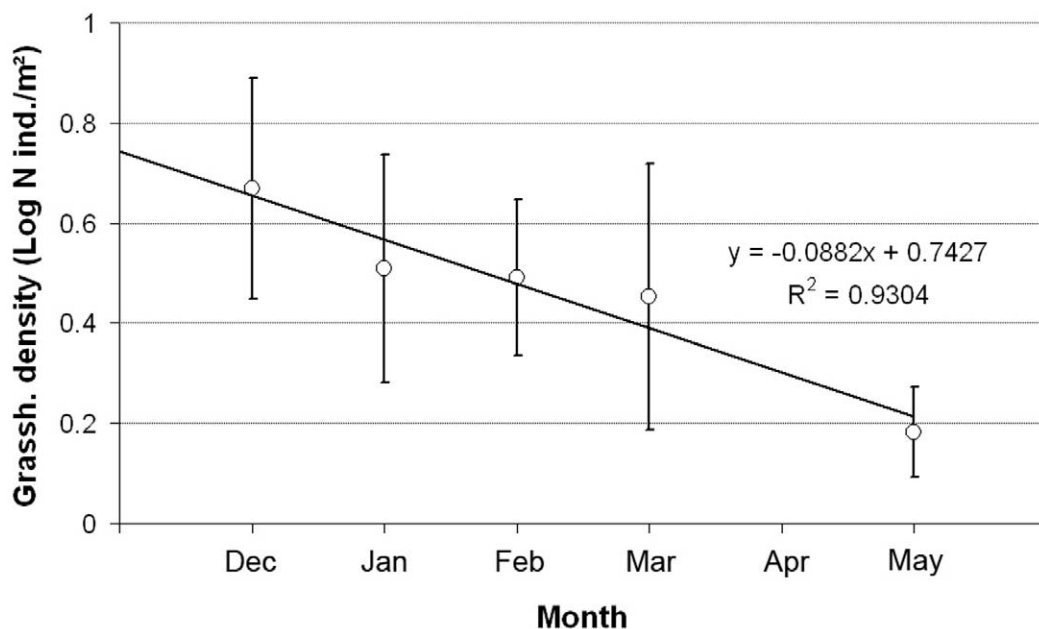


Fig. 9. Decrease in grasshopper densities (Log n ind./m²) on control plots between December and May. Bars indicate Standard Errors.

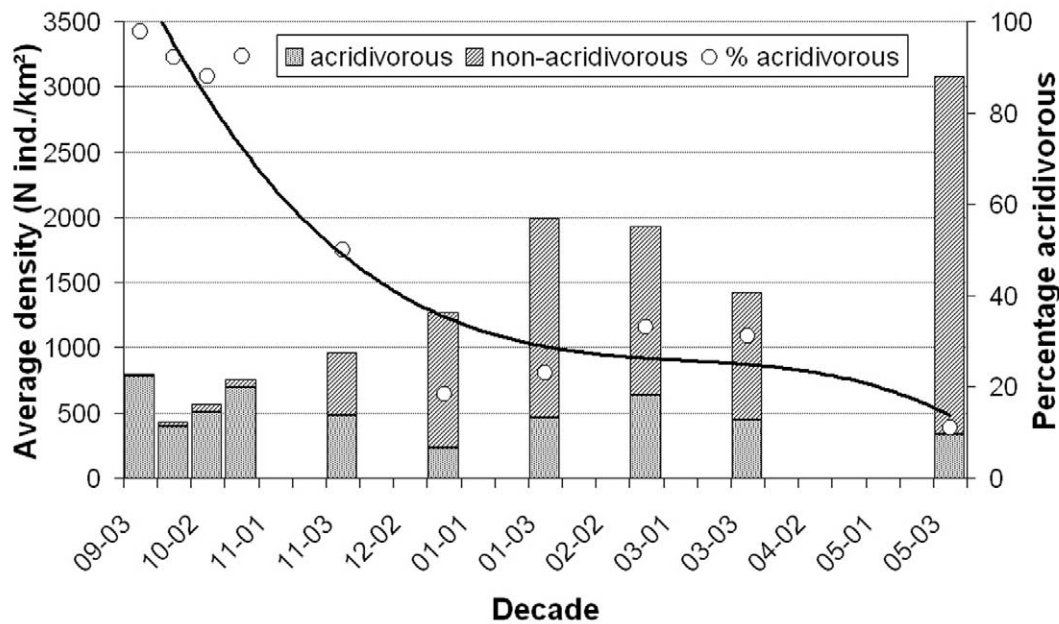


Fig. 10. Average bird densities (ind./km²) in time according to diet.

and are protected under the Bonn Convention of which Senegal is signatory (CMS-COP9 2008).

The consistent data of the temporal composition of the structure of the community supports the hypothesis that grasshopper movements during the entire study period were rather limited and that continuously decreasing densities between December and May were largely caused by predation. They logarithmically decreased (all species combined) from 4.66 ind./m² in December to 1.51 ind./m² in May, or a reduction of 67.2%. A constant decrease of grasshoppers due to predation started at densities below *ca* 5 ind./m², which can be considered as a medium density. Total grasshopper biomass was reduced from 1,256 kg DW/km² in December to 352 kg DW/km² in May, a reduction of 71.9%. Some local displacements, might have occurred as dead grasshoppers, in particular *Diabolocantops axillaris*, showing sporulation of *M. acridum*, were found up to 12 km from the nearest treated plots in October and November (Mullié & Guëye 2009), and also the small increase of densities on treated plots between December and January may have been the result of either local redistribution of grasshoppers or of small-scale immigration.

An important finding of this study is that GM did not have an impact on bird numbers and densities; these changed significantly over time, but were unrelated to treatments. [Treatments of grasshoppers with the organophosphates (OPs) chlorpyrifos and fenitrothion in Senegal were shown to have large and significant negative effects on bird displacements, apart from direct mortality and reproduction effects (Mullié & Keith 1993).]

While numbers of acridivorous bird species did not change, their biomass did when heavier migrant species arrived. This increased grasshopper removal rates on all plots, but more steeply on treated plots, because grasshopper densities had already been affected by GM. It is only at 3.5 mo posttreatment that grasshopper removal rates level off and are no longer different from controls. Hence by increasing the duration of the GM impact (Fig. 8), bird predation enhanced its action.

When taking body size into account, we observed that large (*O. cavroisi*) and medium-bodied (*A. clara*) species significantly declined, whereas small-bodied species (Pyrgomorphidae) first increased adult population levels, to decline only during the last count. Grasshopper remains from Montagu's Harrier pellets show the same tendency:

small bodied grasshoppers (<0.73 g) represented <2.6% of the prey by body mass, while they represented 61-68% of the grasshopper community in the field. Montagu's Harriers preyed preferentially on *A. clara*, *O. cavroisi* and other medium bodied species such as *D. axillaris*. [Lesser Kestrels also prey preferentially on *O. cavroisi* (Mullié 2009).]

Our data also confirm earlier findings of Branson (2005b) who reported that birds reduced the proportion of medium-bodied grasshoppers, while small-bodied grasshoppers increased in abundance. Belovsky & Slade (1993) found a predation-mediated reduction of large-bodied grasshoppers, whereas changes in abundance of medium and small-bodied species that they observed could not be explained by predation.

There was a large difference between grasshopper removal during the rainy season and during the dry season. Because most grasshoppers reproduced between September and November, predation by birds could not be calculated in the same way as during the dry season. Therefore, cumulative daily predation rates were integrated over time (September – November) to obtain an estimate of the total predation during this period. As vegetation development started at the onset of the first significant rains (*i.e.*, > *ca* 20 mm), which was in mid-June (Fig. 2) and grasshopper reproduction soon afterwards, our data do not cover the entire reproductive period and the importance of predation may have been underestimated. Nevertheless, predation did not remove more than 1% from the community, which can be considered as insignificant. This is in contrast with modelling results presented by Axelsen *et al.* (2009) that birds reduce *O. senegalensis* populations in Senegal and Niger during the rainy season by 20-25%. It should be mentioned that bird densities in their study have been corrected for breeding females and for nestlings as well as for reduced reproductive output of the grasshopper population, but this alone does not explain the large difference.

Data from North American studies are much more variable. Predation rates of 30-50% have been reported at low and medium grasshopper densities (Joern 1986, 1992; Fowler *et al.* 1991; Bock *et al.* 1992). However, in some cases no measurable effect of predation was present (Joern 2000). Our data are corroborated by those of Branson (2005) who states that bird predation becomes less

Table 2. Species composition of grasshoppers captured in the field by sweep-net sampling and found as prey remains in regurgitated pellets of Montagu's Harriers, collected in night roosts, at Khelcom between January and March 2009.

Scientific Name	Wet Weight (g)	January		February		March	
		field	M. Harrier	field	M. Harrier	field	M. Harrier
		n=2655	n=1628	n=3037	n=971	n=3232	n=1632
<i>Acanthacris ruficornis citrina</i>	3.5	-	-	-	-	0.09	0.06
<i>Hieroglyphus daganensis</i>	3.41	-	-	-	0.1	-	-
<i>Ornithacris cavroisi</i>	2.66	15.07	25.55	10.41	25.75	9.13	22.61
<i>Truxalis johnstoni</i>	1.57	0.26	-	-	-	-	-
<i>Truxalis</i> sp.	1.57	-	0.06	-	-	-	0.18
<i>Acridoderes strenuus</i>	1.07	-	-	-	0.1	-	0.31
<i>Acrida bicolor</i>	0.91	0.45	-	-	-	-	-
<i>Acrida</i> sp.	0.91	0.26	-	-	-	-	-
<i>Acorypha clara</i>	0.9	18.57	61.18	14.55	57.16	15.16	65.32
<i>Heteracris annulosa</i>	0.77	-	-	-	-	2.2	-
<i>Diabolocatantops axillaris</i>	0.73	4.6	11.55	7.08	15.45	5.85	8.88
<i>Metaxymecus gracilipes</i>	0.64	0.45	-	0.82	-	-	-
<i>Acorypha picta</i>	0.57	5.46	1.66	7.41	1.34	6.13	2.27
<i>Oedaleus senegalensis</i>	0.53	0.23	-	-	-	-	-
<i>Catantops stramineus</i>	0.5	1.13	-	0.86	-	1.58	-
<i>Harpezocatantops styliifer</i>	0.3	0.56	-	1.98	-	3.96	-
<i>Chrotogonus senegalensis</i>	0.29	1.51	-	2.54	-	0.46	-
<i>Cryptocatantops haemorrhoidalis</i>	0.23	0.11	-	3.79	0.1	3.47	0.31
<i>Pyrgomorpha vigneaudii</i>	0.19	19.47	-	17.42	-	20.2	0.06
<i>Zacompsa festa</i>	0.18	-	-	-	-	-	-
<i>Pyrgomorpha cognata complex</i>	0.09	19.66	-	21.24	-	21.6	-
<i>Acrotylus blondeli</i>	0.07	11.19	-	11.43	-	10.18	-
Unidentified species		1.02	-	0.49	-	-	-
Total		100	100	100	100	100	100

important at high grasshopper densities, which was also the case during the rainy season in our study. However, when grasshopper densities decreased to medium levels (ca 5 ind./m²), bird predation became very important.

The removal of grasshoppers by birds was calculated under some broad assumptions about diet composition (maximum 50% of the diet of acridivorous species supposed to be composed of grasshoppers) and temporal aspects of predation (granivorous species which were known to feed on acridids during their breeding season were supposed not to do so from December onwards). As compared to calculations derived from grasshopper densities in successive months, calculations from bird consumption produced very similar results, supporting the idea that under conditions of less stable grasshopper populations, bird consumption of grasshoppers can be approximated by a few rough assumptions about predation rates, if the densities of acridivorous species have been assessed. The peak in consumption in November and December (days 47-74) in Fig. 8 is due to the presence of large concentrations of White Storks on some of the plots treated with 50 g conidia/ha, which has a strong influence on calculated biomass removal. The shape of the curves of grasshopper removal calculated from monthly biomass reduction (dashed lines in Fig. 8) strongly suggests that White Storks had also been present on control plots, but were not seen during the monthly count.

Commensalism may be an advantageous strategy for feeding on orthopterans in particular, in dense vegetation and at high grasshopper densities. In addition to our observations, Cheke *et al.* (2006a, b) observed Lanners, *Falco biarmicus*, exploiting Desert Locust by following men and camels in dense *Schouwia thebaica* vegetation in Northern Niger and stooping on locusts being flushed. Jensen *et al.* (2008) very frequently observed Lanners exploiting grasshoppers

(probably *O. senegalensis*) flushed by Abdim's Storks, *Ciconia abdimii*, in SE Niger. In Waza National Park (Extreme North of Cameroon), Ralph Buij (*in litt.*) observed Yellow-billed Kites, *Milvus parasitus*, doing the same when people flushed grasshoppers in high grass. He also observed Northern Carmine Bee-eaters, *Merops nubicus*, with goats (they also travel on goatbacks) and Arabian Bustards, *Ardeotis arabas*, and Piapiacs, *Ptilostomus afer*, with small livestock, and Abyssinian Rollers with Abdim's Storks at the start of the rains. Only once two adult Montagu's Harriers were observed flying amongst a herd of over 200 cattle catching flushed grasshoppers (Ralph Buij, *in litt.*).

Deforestation for expansion of groundnut production destroyed the formerly protected forest at Khelcom, reputedly with a high biodiversity (Schoonmaker-Freudenberger 1991). In turn it also created a habitat low in the succession cycle and rich in orthopterans and their predators. Some of them, such as the Montagu's Harrier, are so abundant that their numbers are unprecedented anywhere else in the world. The semi-arid Sahelian agricultural habitat is currently under a severe human pressure (Zwarts *et al.* 2009) and avian predators in the Sahel have faced a decline of over 90% in the last 30 years (Thiollay 2006a, b). Biopesticides and predators can play a vital role in controlling grasshoppers considered to be a pest to agriculture without compromising agro-ecosystem functioning. Therefore their complementary role should be exploited instead of neglected.

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Appendix 1. Fresh (WW) and dry body mass (DW) of grasshoppers captured on plots and used for calculations of grasshopper biomass.

Species	imago				L1				L2			
	n	WW	n	DW	n	WW	n	DW	n	WW	n	DW
<i>Atractomorpha acutipennis</i>	2	0.184	-	-	-	-	-	-	-	-	-	-
<i>Acrida bicolor</i>	32	0.912	20	0.307	1	0.005	1	0.001	8	0.042	2	0.006
<i>Acrotylus blondeli</i>	8	0.072	5	0.041	-	-	-	-	-	-	-	-
<i>Acorypha clara</i>	176	0.889	172	0.386	34	0.022	19	0.008	65	0.062	31	0.018
<i>Acorypha glaucopsis</i>	59	1.518	25	0.270	4	0.036	4	0.011	11	0.123	8	0.020
<i>Acorypha picta</i>	25	0.568	-	-	-	-	-	-	-	-	-	-
<i>Acanthacris ruficornis citrina</i>	-	-	-	-	-	-	-	-	2	0.707	-	-
<i>Acridoderes strenuus</i>	9	1.120	2	0.245	-	-	-	-	-	-	-	-
<i>Acrida sulphuripennis</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cataloipus cymbiferus</i>	5	4.356	-	-	-	-	-	-	-	-	-	-
<i>Cataloipus fuscocoeruleipes</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cryptocatantops haemorrhoidalis</i>	50	0.214	32	0.085	-	-	-	-	-	-	-	-
<i>Chrotogonus senegalensis</i>	16	0.289	9	0.112	-	-	-	-	4	0.041	2	0.008
<i>Catantops stramineus</i>	8	0.505	-	-	-	-	-	-	-	-	-	-
<i>Diabolocatantops axillaris</i>	54	0.729	10	0.288	-	-	-	-	-	-	-	-
<i>Duronia chloronota</i>	2	0.155	2	0.050	-	-	-	-	-	-	-	-
<i>Heteracris annulosa</i>	20	0.773	18	0.352	-	-	-	-	-	-	-	-
<i>Hieroglyphus daganensis</i>	3	3.407	1	1.429	-	-	-	-	2	0.084	2	0.025
<i>Harpezoatantops styliifer</i>	7	0.226	7	0.114	-	-	-	-	-	-	-	-
<i>Humbe tenuicornis</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Kraussella amabile</i>	46	0.426	7	0.068	-	-	-	-	7	0.060	1	0.030
<i>Kraussaria angulifera</i>	16	3.073	1	0.638	-	-	-	-	2	0.587	-	-
<i>Morphacris fasciata</i>	1	0.153	1	0.052	-	-	-	-	-	-	-	-
<i>Metaxymecus gracilipes</i>	2	0.422	-	-	-	-	-	-	-	-	-	-
<i>Ornithacris cavroisi</i>	175	2.661	163	1.177	25	0.029	16	0.010	40	0.071	25	0.025
<i>Oedaleus nigeriensis</i>	5	0.598	5	0.230	-	-	-	-	-	-	-	-
<i>Oedaleus senegalensis</i>	153	0.534	25	0.128	44	0.018	20	0.006	51	0.055	30	0.015
<i>Pyrgomorpha cognata complex</i>	26	0.088	26	0.041	2	0.007	2	0.002	2	0.016	2	0.005
<i>Pyrgomorpha vigneaudii</i>	12	0.195	2	0.047	2	0.006	2	0.002	2	0.010	2	0.003
<i>Truxalis longicornis</i>	2	1.568	-	-	-	-	-	-	-	-	-	-
<i>Truxalis sp.</i>	1	0.317	1	0.094	-	-	-	-	-	-	-	-
<i>Zacompso festa</i>	9	0.181	2	0.034	-	-	-	-	-	-	-	-
n total WW	924				112				196			
n total DW			536				64				105	

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L3				L4				L5				L6				n WW
n	WW	n	DW	n	WW	n	DW	n	WW	n	DW	n	WW	n	DW	Total
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
2	0.092	2	0.027	8	0.343	1	0.038	5	0.808	2	0.283	-	-	-	-	56
-	-	-	-	1	0.034	1	0.010	-	-	-	-	-	-	-	-	9
40	0.193	18	0.038	32	0.383	7	0.072	15	0.638	3	0.181	-	-	-	-	362
9	0.265	5	0.076	15	0.722	4	0.170	6	1.064	6	0.339	-	-	-	-	104
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25
-	-	-	-	8	1.509	-	-	1	1.161	-	-	-	-	-	-	11
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9
-	-	-	-	-	-	-	-	1	0.631	1	0.170	-	-	-	-	1
5	0.078	2	0.045	1	0.046	-	-	1	0.505	1	0.148	-	-	-	-	12
-	-	-	-	2	0.473	2	0.158	1	0.236	1	0.068	-	-	-	-	3
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	50
7	0.067	4	0.024	9	0.127	7	0.037	6	0.099	6	0.035	-	-	-	-	42
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	54
2	0.105	2	0.035	2	0.159	2	0.048	1	0.205	1	0.063	-	-	-	-	7
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20
1	0.108	1	0.030	7	1.316	-	-	-	-	-	-	-	-	-	-	13
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
2	0.123	1	0.050	1	0.120	1	0.040	-	-	-	-	-	-	-	-	3
27	0.121	9	0.055	14	0.148	5	0.079	3	0.315	3	0.100	-	-	-	-	97
2	0.938	-	-	4	1.430	-	-	2	1.711	-	-	-	-	-	-	26
-	-	-	-	-	-	-	-	1	0.207	1	0.069	-	-	-	-	2
1	0.334	-	-	11	0.490	-	-	2	0.478	-	-	-	-	-	-	16
47	0.228	26	0.064	35	0.501	16	0.136	23	1.304	12	0.237	10	1.487	4	0.314	355
3	0.078	3	0.021	-	-	-	-	-	-	-	-	-	-	-	-	8
53	0.134	18	0.050	39	0.223	10	0.086	21	0.389	6	0.141	-	-	-	-	361
2	0.028	2	0.008	2	0.040	2	0.010	1	0.044	1	0.010	-	-	-	-	35
1	0.020	1	0.005	-	-	-	-	-	-	-	-	-	-	-	-	17
-	-	-	-	1	1.188	-	-	-	-	-	-	-	-	-	-	3
1	0.071	1	0.024	-	-	-	-	-	-	-	-	-	-	-	-	2
2	0.062	2	0.017	-	-	-	-	-	-	-	-	-	-	-	-	11
207				192				90				10				1731
		97				58				44				4		908

Appendix 2. Number of birds observed per species and per count from 18 d before until 233 d after treatment. Acridivorous and non-acridivorous species are given separately.

Scientific Name	Number of days after treatment																Total
	-18	-14	-4	-1	3	6	9	12	15	18	47	74	109	137	167	233	
nonacridivorous																	
<i>Anthus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	6	2	-	8
<i>Apus affinis</i>	-	-		-	-	-	-	-	-	-	-	12	11	10	-	-	33
<i>Apus apus</i>	1	-	15	1	-	-	-	-	-	-	-	-	-	-	-	-	17
<i>Aquila rapax</i>	-	-	-	-		-	-	-	-	-	1	-	-	-	-	-	1
<i>Ardea cinerea</i>	-	4	-	-	-	-	1	-	2	4	3	-	1	-	-	-	15
<i>Asio flammeus</i>	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	4
<i>Bubalornis albirostris</i>	-	-	-	-	-	-	-	-	-	-	288	116	489	81	212	56	1242
<i>Buphagus africanus</i>	-	-	-	-	-	3	7	9	12	12	10	13	17	3	7	17	110
<i>Calandrella brachydactyla</i>	-	-		-	-	-	-	-	-	-	-	-	-	10		2	12
<i>Camaroptera brachyura</i>	-	1	-	1	-	-	-	-	-	-	-	-	-	-	1	1	4
<i>Cercotrichas podobe</i>	-	-	-	-	-	-	-	-	-	-	1	-	-	-		8	9
<i>Ciconia nigra</i>	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	2
<i>Cinnyris pulchellus</i>	1	1	-	-	-	-	-	1	-	-	-	14	-	2	-	8	19
<i>Circaetus beaudouini</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Circaetus cinereus</i>	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
<i>Circaetus gallicus</i>	-	-	-	-	-	3	7	7	8	13	14	4	14	1	1	1	73
<i>Corvus albus</i>	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	4	7
<i>Crinifer piscator</i>	-	-	-	-	-	-	-	-	-	-	-	-	-		1	2	3
<i>Delichon urbica</i>	-	-		-	7	2	12	3	3	-	-	-	-	10	6	2	45
<i>Eremopterix leucotis</i>	-	-	-	-	-	4	6	3	10	20	62	62	81	208	245	251	952
<i>Eremopterix nigriceps</i>	-	-	-	-	-	-	-	-	-	-	-	-	18	26	48	-	92
<i>Euodice cantans</i>	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	2
<i>Euplectes franciscanus</i>	-	-	9	-	1	-	6	2	2	-	-	-	-	-	-	-	20
<i>Falco ardosiaceus</i>	-	-	-	-	3	1	-	-	-	1	-	-	-	-	-	-	5
<i>Falco chicquera</i>	2	-	3	-	-	-	1	-	-	-	-	-	-	-	-	-	6
<i>Falco</i> sp.	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	2	4
<i>Ficedula hypoleuca</i>	-	-	3	3	3	1	-	-	1	-	-	-	-	-	-	-	11
<i>Gyps africanus</i>	-	1	-	-	10	-	-	2	2	8	6	-	5	8	-	-	42
<i>Gyps rueppellii</i>	-	-	-	-	-	9	4	9	7	-	-	-	10	-	-	-	39
<i>Gyps</i> sp.	-	-	-	-	-	-	-	-	-	-	28	22	20	24	25	21	140
<i>Hirundo rustica</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-	12
<i>Hirundo senegalensis</i>	-	2	17	4	4	2	3	2	3	10	-	-	5	-	2	4	58
<i>Hoplopterus spinosus</i>	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	4
<i>Lagonosticta senegala</i>	-	-	1	-	-	-	-	-	-	-	-	150	128	176	6	-	461
<i>Laniarius barbarus</i>	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
<i>Macronyx croceus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	4
<i>Mirafra cantillans</i>	-	-	-	-	-	-	-	-	-	-	59	39	199	157	233	268	955
<i>Necrosyrtes monachus</i>	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
<i>Oena capensis</i>	-	-	-	-	1	-	1	4	1	-	4	7	7	8	6	10	49
<i>Otus leucotis</i>	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
<i>Passer griseus</i>	-	-	-	-	-	-	-	-	-	-	42	67	8	1	3	1	122
<i>Passer luteus</i>	-	-	-	-	-	-	-	-	-	-	244	1210	1958	1677	1032	5128	11249
<i>Ploceus cucullatus</i>	-	-	-	-	-	-	-	-	-	-	97	144	26	-	-	-	267
<i>Polyboroides typus</i>	-	-	-	-	-	1	-	-	-	1	1	-	-	-	-	-	3
<i>Psittacula krameri</i>	-	4	-	1	-	4	20	18	19	23	27	26	14	8	26	3	193
<i>Pterocles</i> sp.	-	-	-	2	1	2	7	6	6	5	29	-	-	-	-	-	58
<i>Riparia riparia</i>	-	-	-	-	125	7	10	-	7	-	-	-	21	-	-	-	170
<i>Serinus leucopygius</i>	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
<i>Spiloptila clamans</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
<i>Sporopipes frontalis</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Streptopelia decipiens</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
<i>Streptopelia senegalensis</i>	9	17	23	8	16	29	40	49	64	68	37	52	27	33	28	66	566
<i>Streptopelia</i> sp.	-	-	-	-	-	-	-	-	-	2	-	-	2	-	-	-	4
<i>Streptopelia vinacea</i>	8	7	9	7	6	5	11	10	15	15	28	25	20	12	5	13	196
<i>Sylvia</i> sp.	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	2

Scientific Name	Number of days after treatment																Total
	-18	-14	-4	-1	3	6	9	12	15	18	47	74	109	137	167	233	
<i>Torgos tracheliotus</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
<i>Uraeginthus bengalus</i>	-	-	1	-	-	2	1	4	1	2	1	-	-	-	-	-	12
<i>Urocolius macrourus</i>	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	6
<i>Vanellus senegallus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
<i>Vidua orientalis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2
unidentified species	1	-	-	-	-	-	-	-	-	-	22	5	4	-	-	1	33
Total	22	47	81	27	177	80	137	132	165	191	1008	1972	3089	2464	1907	5871	17362
Acridivorous																	
<i>Bubalornis albirostris</i>	457	703	214	149	94	127	101	121	204	156	-	-	-	-	-	-	2326
<i>Bubulcus ibis</i>	-	-	-	-	1	-	3	-	-	15	10	53	1872	418	165	839	3376
<i>Bucorvus abyssinicus</i>	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	2
<i>Centropus senegalensis</i>	-	-	-	-	-	1	4	-	2	-	1	9	-	-	2	-	19
<i>Chelictinia riocourii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3
<i>Ciconia ciconia</i>	1	-	-	-	-	-	-	-	-	-	1634	400	-	-	-	-	2035
<i>Circus aeruginosus</i>	6	11	29	11	19	24	22	31	41	37	18	8	3	2	6	-	268
<i>Circus pygargus</i>	11	24	37	19	18	28	33	42	34	36	87	46	124	139	48	16	742
<i>Cisticola juncidis</i>	35	26	52	40	77	101	155	169	200	168	46	22	14	2	-	-	1107
<i>Cisticola</i> sp.	-	-	-	1	7	3	2	3	-	1	-	-	-	5	23	25	70
<i>Coracias abyssinica</i>	2	8	4	14	15	24	49	57	46	49	46	118	148	157	93	75	905
<i>Cursorius temminckii</i>	-	-	-	-	-	-	-	-	-	2	-	-	2	2	4	5	15
<i>Elanus caeruleus</i>	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	5
<i>Eupodotus savilei</i>	3	5	10	9	4	9	9	10	5	6	8	-	1	-	6	-	85
<i>Falco naumanni</i>	11	10	7	3	4	2	3	5	-	3	1122	123	592	198	95	6	2184
<i>Halcyon senegalensis</i>	12	12	13	3	2	2	13	11	3	-	5	-	-	-	1	1	78
<i>Lamprotornis caudatus</i>	6	8	6	2	10	4	13	16	7	18	28	23	17	5	6	-	169
<i>Lamprotornis chalybaeus</i>	-	-	-	-	-	-	-	-	-	-	5	1	65	53	128	62	314
<i>Lanius meridionalis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	4	2	-	6
<i>Lanius senator</i>	-	1	1	1	-	19	30	30	27	19	28	35	54	51	45	12	353
<i>Leptoptilos crumeniferus</i>	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	2
<i>Macronyx croceus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	3
<i>Merops albicollis</i>	47	160	78	39	79	18	25	-	-	-	-	-	-	-	-	62	508
<i>Milvus migrans</i>	-	-	-	-	-	-	-	-	-	-	17	-	-	1	-	-	18
<i>Mirafra cantillans</i>	28	44	55	40	24	68	118	232	136	104	-	-	-	-	-	-	849
<i>Motacilla flava</i>	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	10
<i>Myrmecocichla aethiops</i>	-	-	-	-	-	-	-	-	-	-	-	10	1	-	-	83	94
<i>Neotis denhami</i>	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	2
<i>Oenanthe oenanthe</i>	-	-	-	-	-	-	3	-	2	8	27	17	39	49	16	5	166
<i>Oenanthe</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2
<i>Passer griseus</i>	23	36	40	33	14	12	76	49	49	105	-	-	-	-	-	-	437
<i>Ploceus cucullatus</i>	118	373	89	26	112	43	105	3	-	88	-	-	-	-	3	-	960
<i>Ploceus</i> sp.	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	2
<i>Ploceus velatus</i>	60	52	53	46	85	82	68	89	180	81	-	-	-	-	-	-	796
<i>Prinia</i> sp.	-	1	2	-	3	22	10	12	6	7	-	-	-	-	-	-	63
<i>Prinia subflava</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	4
<i>Spreo pulcher</i>	-	-	-	-	-	2	-	-	-	3	4	8	9	750	459	29	1264
<i>Tchagra senegala</i>	2	-	5	5	7	10	6	19	16	19	-	-	-	-	-	-	89
<i>Tockus erythrorhynchus</i>	4	8	6	3	2	-	7	-	1	1	22	18	15	27	22	9	145
<i>Tockus nasutus</i>	-	-	1	-	2	49	33	82	21	58	21	12	17	49	17	30	392
<i>Turnix sylvatica</i>	-	-	-	-	-	-	-	-	-	-	-	5	1	-	-	-	6
<i>Upupa epops</i>	1	-	-	-	-	-	-	-	3	-	1	3	4	5	2	1	20
<i>Vanellus tectus</i>	41	51	43	30	64	73	49	63	50	52	95	142	192	203	165	186	1499
Total	868	1533	745	474	643	726	941	1044	1033	1036	3231	1053	3182	2120	1311	1453	21393