

# Effects of predation and dispersal on *Mastomys natalensis* population dynamics in Tanzanian maize fields

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## Summary

1. We investigate the effects of different levels of predation pressure and rodent dispersal on the population dynamics of the African pest rodent *Mastomys natalensis* in maize fields in Tanzania.

2. Three levels of predation risk were used in an experimental set-up: natural level (control), excluding predators by nets and attracting avian predators by nest boxes and perch poles. Because dispersal of the rodents could mask the predation pressure treatment effects, control and predator exclusion treatments were repeated with enclosed rodent populations.

3. Population growth during the annual population rise period was faster in the absence of predators and peak population size was higher, but otherwise dynamics patterns were similar for populations where predators had access or were attracted, indicating that compensatory mechanisms operate when rodents are exposed to high levels of predation risk. Reducing dispersal of rodents removed the effect of predation on population growth and peak size, suggesting that local predators may play a role in driving rodent dispersal, but have otherwise little direct effect on population dynamics.

*Key-words:* Africa, birds of prey, dispersion, irregular population dynamics, pest rodents, predators

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## Introduction

The importance of predation in vertebrate prey population dynamics has been debated for many years, particularly in cyclic populations exhibiting regular density fluctuations in the northern temperate zones (see, e.g. reviews in Hanski *et al.* 2001; Klemola, Pettersen & Stenseth 2003). Predator enclosure experiments have shown considerable effects on populations of cyclic voles, lemmings and hares (Korpimäki *et al.* 2004). Tropical rodents possess a different population dynamics pattern often with large but irregular intra- and interannual fluctuations. Little attention has been directed to the role of predation in tropical rodent populations, but some evidence exists that predators may be important also for these populations. In South America, for example, capture–mark–recapture

modelling has indicated that predators are one of the key elements underlying the large, irregular population fluctuations in the leaf-eared mouse (Lima, Stenseth & Jaksic 2002), and also other studies on predation in small mammal populations from this continent have demonstrated a clear predator–prey interaction (e.g. Lagos *et al.* 1995; Meserve *et al.* 2003). In Africa, there is only indirect evidence for such effects. Handwerk (1998) reported on population fluctuations in rodents and birds of prey in Egypt, but predators and prey were monitored in areas distant from each other, making interpretation difficult. Leirs *et al.* (1997) showed that survival of nonreproducing *Mastomys natalensis* (Smith 1834) is an inverse density-dependent process, an effect that would be predicted if predation is an important mortality factor, although dispersal may also be responsible for this process. A pilot study in Tanzania demonstrated an increased survival of *M. natalensis* in areas excluding avian predators (Van Gulck *et al.* 1998), thus supporting the idea that predation is important for populations of this tropical rodent species.

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Rodents are considered a major pest in African agriculture and *M. natalensis* accounts for a large part of the pre- and postharvest damage in sub-Saharan Africa (Fiedler 1988; Makundi, Oguge & Mwanjabe 1999). The species is known to exhibit irregular eruptive population dynamics (see review in Leirs *et al.* 1996) but although extensive damage is experienced during such outbreak years, the mice do also cause considerable damage even at relatively low population densities (Fiedler 1988). Management of rodents in eastern Africa relies on the *ad hoc* use of chemical rodenticides (Makundi *et al.* 1999), and there is a need for economically and ecologically based, sustainable rodent management strategies (Singleton *et al.* 1999). Insight in the role of predation to population dynamics of *M. natalensis* will therefore not only be of scientific value but also be useful for considering the potential of biological control.

This paper, based on results from replicated experiments, documents for the first time the effects of different predation pressures and dispersal on the population dynamics of a tropical rodent species that is also an outbreaking species. We test the predictions that (1) higher predation pressure causes prey population growth to slow down, at least in some periods, leading to low rodent numbers, and (2) density-dependent dispersal drives rodents from high density areas (with low predation pressure) to low density areas (with high predation pressure).

The paper is part of a more extensive project evaluating the effects of different predation pressure levels on the dynamics, demography and reproduction in populations of *M. natalensis* as well as a study of the predator-prey relationship between *M. natalensis* and avian predators. Results of that work will be presented in separate publications.

## Materials and methods

### STUDY AREA AND CULTIVATION OF FIELDS

The study was conducted from March 1998 to August 2000 at the campus of the Sokoine University of Agriculture, Morogoro, Tanzania (06°51' S, 37°38' E). Morogoro has a bimodal rainfall pattern with a short wet season approximately from October to December and a long wet season from March to June with the dry season extending from the end of the long wet season to the beginning of the short wet season. In this area the population ecology of *M. natalensis* was already well documented (e.g. Leirs 1995; Christensen 1996; Leirs *et al.* 1996, 1997). In a 60 ha farm area consisting of a mosaic of cultivated and fallow land, we selected 12 study plots of 0.5 ha each. Preliminary trapping of rodents just prior to treatment application allowed selection of plots with approximately equal population sizes. Zones of fallow land or maize fields separated the study plots from each other; all plots were bordered on at least one side with fallow land or road verges, and the

distances between nearest placed neighbour plots ranged from 12 m to 450 m. Scattered kapok trees *Ceiba pentandra* (L.) or *Acacia* spp. were the most common trees in the area. The main grass species of the fallow land were *Panicum hanningtonii* (Staph), *Rottboellia cochinchinensis* (Lour.) Clayton, *Pennisetum polystachyon* (L.), *Cymbopogon* spp., *Andropogon* spp., *Hyparrhenia* spp. and *Themeda* spp. Fields were cultivated with the local maize variety 'Staha' once a year according to local recommended agronomic practices. Planting took place around mid-March using a standardized planting method and harvesting was done manually around the end of July/early August when the silks of cobs were dry. Prior to planting, fields were hand ploughed to least affect rodent burrows and old maize stubbles. During harvesting maize plants were bent and cobs removed leaving the stalks in the field.

### TREATMENTS

The experiment included three predation pressure treatments. Two of them could guarantee at least temporarily different levels of predation pressure: the natural situation (control) and predator exclusion (decreased predation pressure). The third one was a predator attraction treatment (increased predation pressure) but there was no a priori guarantee of its success.

Predator exclusion fields were covered with nets (mesh size 15.2 cm), which kept out owls and raptors. The nets were fixed to chicken wire fence (mesh size 3.5 cm) extending 20 cm below and 80 cm above ground. The fence allowed rodents to pass in and out but excluded most other predators, except snakes, from the fields. However, as initial attempts to trap snakes in the study area were unsuccessful, we assume that the snake population was low and its impact less important. Unfortunately there are, to our knowledge, no published data on the impact of snakes on African rodent populations that we can relate this assumption to.

In the predator attraction fields we increased the availability of perching and nesting sites for raptors and owls by placement of perch poles and nest boxes. The success of this method in increasing avian predator activity has been documented in various studies (e.g. Smal 1989; Wolff *et al.* 1999). Initially, we placed nine perch poles (3 m high with transverse sticks at the top for raptors to perch on) per predator attraction field and in November 1998 increased this to 49 perch poles per field, placed 10 m apart. Two barn owl nest boxes designed after Lenton (1978), Duckett & Karuppiah (1989) and Duckett (1991) were placed at two corners of each predator attraction field. The barn owl *Tyto alba affinis* (Blyth 1862) is common in the study area and is one of the main avian predators of *M. natalensis*, which also makes up the largest part of the owl's diet (Van Gulck *et al.* 1998). Numbers of barn owls readily increase by the provision of artificial nesting sites (Smal 1989).

Because dispersal of the rodents could mask the effects of the treatments, the control and predator

exclusion treatments were repeated in enclosures. Enclosures were fenced by metal sheet extending 20 cm below and 80 cm above ground. Although the fences impaired rodent dispersal, they were not completely dispersal proof. To ensure the passage of smaller ground predators (e.g. mongooses) in and out the control enclosures, square wooden platforms (35 × 35 cm) were placed on top of every third fence pole, serving as possible jumping points. Other ground predators such as feral and wild cats, genets and snakes certainly had no problems crossing the fences. The predator attraction treatment was not repeated in an enclosure.

All five treatment combinations were replicated twice except for the control treatment open to rodent dispersal, which was replicated four times. Thus in total we had 12 field plots split up into open predator attraction fields (PO), open control fields (CO), open predator exclusion fields (NO), control enclosures (CE) and predator exclusion enclosures (NE). In order to minimize interactions between predation treatments and as the available space was limited, we placed predator exclusion fields in between predator attraction and control fields. The distance between a predator attraction field and the nearest placed control field was between 80 m and 450 m. This distance does not rule out a possible interaction, but if perches and nest boxes attract avian predators, we expect that such locally present birds are more active in and around the attraction fields at least as long as they are not limited by food.

#### USE OF PERCH POLES BY AVIAN PREDATORS

Although our project did not provide direct quantitative data about predation pressure in the different treatments, we know that our netting treatment of course reduced predation compared with the control areas. In our perch pole/nest box treatment we collected pellets regurgitated from avian predators once a week from mid-April 1998 around the perch poles, thereby determining whether avian predators used the perch poles. All 98 perch poles were used as sample sites and the pellet collection was carried out in a standardized way using 1 min of searching per pole. Because avian predators had no perching possibilities inside the control fields it is reasonable to assume that frequent perch pole use increased the local predation pressure in the predator attraction treatment whether directly by increasing the number of rodents killed and/or indirectly by the mere presence of perching predators affecting the rodents' behaviour; Mohr *et al.* (2003) confirmed that rodents indeed changed their behaviour in those predator attraction fields.

#### RODENT POPULATION

A capture–mark–recapture rodent study was conducted from March 1998 to August 2000 using live traps (Sherman LFA Live traps, 7.5 × 9.0 × 23.0 cm, HB Sherman Traps Inc., Tallahassee, FL, USA) placed

in grids with trapping stations every 10 m. Thus each field plot contained 49 traps. Rodents were live-trapped for three consecutive nights every fourth week. Trapping sessions were organized simultaneously for all plots except for two open control plots that were always trapped 1 week later. Traps were baited with a mixture of peanut butter and chicken feed in late afternoon and checked in early morning. Captured rodents were marked at first capture by toe clipping. Species, sex, body weight, reproductive condition and trapping station were recorded at each capture before the animals were again released at the point of capture.

#### DATA HANDLING AND STATISTICAL ANALYSES

Closed-model population estimates for *M. natalensis* population size were calculated with the software program CAPTURE (White *et al.* 1982) using the jack-knife model for heterogeneous capture probability ( $M_h$ ). Peak density of rodents was assumed to be the highest population size estimate in a year and the time of the peak was recorded as the week number in the year. Population growth between each capture session was calculated for each replicate as  $\text{Log}(1 + (N_{t+1}/N_t))$ , where  $N_t$  is the population size at time  $t$ . Subsequently, the mean population growth for the population rise and decline period, respectively, was calculated for each replicate. Because the trappable number of animals reached zero during the seasonal population low period in all replicates, it was not possible to analyse the population growth during this period. Each year the population rise period in a treatment replicate was defined as the period from the occurrence of reproductively active females until peak density of the population had been reached. The decline period was defined as the period from peak density until the lowest population size had been reached before it increased again.

We investigated the effects of predation and rodent dispersal on *M. natalensis* population growth, and on the population peak size and peak timing. All data were analysed with mixed model regression (SAS 8.0, Littell *et al.* 1996) in two distinct models (P3 and P2D2). P3 was a one-factor model comparing the effect of predation between open control, predator exclusion and predator attraction fields (i.e. three predation pressure levels in open fields). Hence, predation was entered as fixed effect in the model. P2D2 was a two-factor model comparing the effects of predation and dispersal between open and enclosed control and predator exclusion fields (i.e. two predation pressure levels in open fields and in enclosures). In this model, predation, dispersal and the interaction predation × dispersal were entered as fixed effects. When the interaction term in the two-factor model analysis was nonsignificant, it was excluded from the model.

In both models, year was added as random effect to account for the annual variation in population fluctuations. Mixed model regressions were calculated using

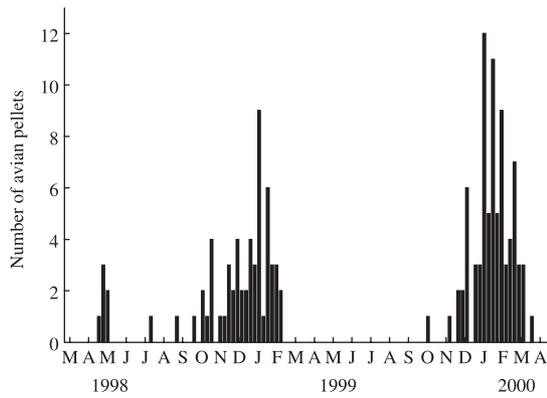


Fig. 1. Weekly number of avian predator pellets collected under perch poles.

the PROC MIXED module for analysis of *M. natalensis* population growth and decrease, and with the GLIMMIX macro for analysis of peak density and timing of peak (SAS 8.0, Littell *et al.* 1996). Population growth and decrease were tested with normal error and identity link, whereas peak density and timing of peak were tested with Poisson errors and log link. Degrees of freedom of the fixed effects *F*-test were adjusted for statistical dependence using Satterthwaite formulas. Variance components were estimated by the restricted maximum likelihood method (REML). Differences among treatment means were tested by least squares mean comparisons and further tested with the sequential Bonferroni correction procedure (Rice 1989), i.e. significant *P*-values that are still significant after sequential Bonferroni correction will be marked by an asterisk.

Results

AVIAN PELLETS

A highly variable number of avian pellets were collected around the perch poles in the predator attraction fields

(Fig. 1). The number of pellets fluctuated seasonally, increasing slowly from around September/October being highest in January and then low again from April. *M. natalensis* (the multimammate mouse) was by far the most abundant of the small mammal prey species found in the avian pellets. In 443 pellets, 384 small mammal skulls could be identified. Of those 323 (84.1%) were *M. natalensis*, 31 (8.1%) were the single-striped mouse *Lemniscomys rosalia* (Thomas 1904), six (1.6%) were the fringe-tailed gerbil *Tatera robusta* (Cretzschmar 1830), and 24 (6.3%) were shrews of the genus *Crocidura*.

RODENT POPULATION

Small mammal species captured included *M. natalensis*, *T. robusta*, *L. rosalia* and *Crocidura* sp. There were a total of 10 668 captures of 4565 individuals of which 94% were *M. natalensis* (4292 individuals, 10 104 captures). We therefore only present and discuss data on *M. natalensis*.

The fluctuation of estimated population sizes of *M. natalensis* in each of the treatments and controls is shown in Fig. 2. There was a large seasonal (intra-annual) population size variation in all plots regardless of treatment type. The trappable populations were very low during the dry season, although for a different length of time in the different study years (maximum period from approximately April–August). The populations increased at a fast rate during the short-rain season and peaked only a few months later (November–January) before they decreased again at a fast rate during the long-rain season (March–April).

There were no significant effects of predation or dispersal alone on the timing of the population peak, on the peak size or on the decrease rate during the population decline period (Table 1). There was, however, a near significant predation effect (P3 analysis) and a significant predation × dispersal interaction effect (P2D2 analysis) on the population growth during the rise period (Table 1). Populations in open predator exclusion fields

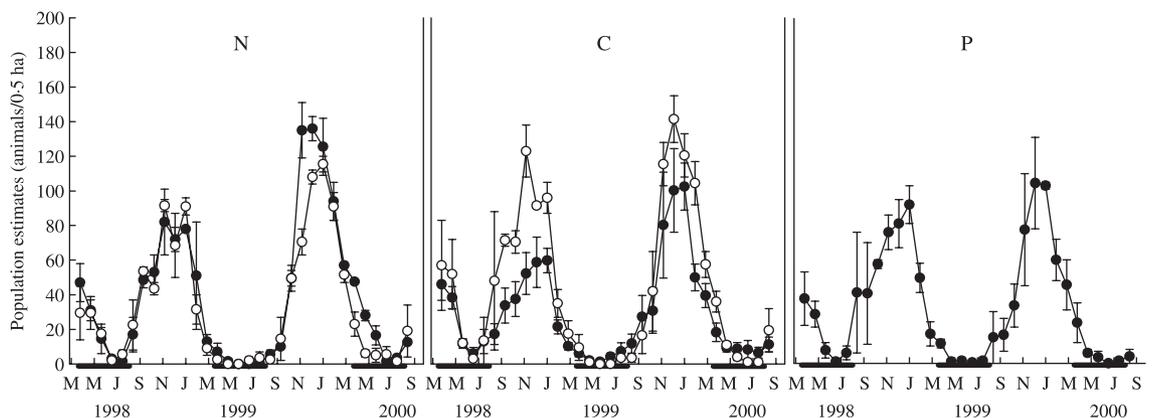
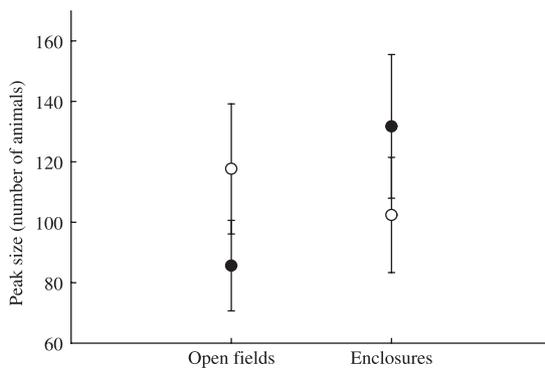


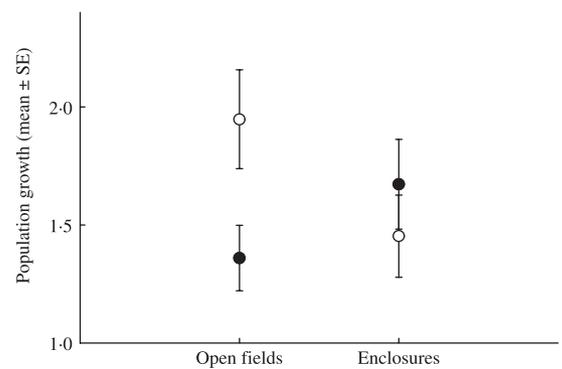
Fig. 2. *M. natalensis* population size fluctuations (mean of replicates ± SE) in open (●) and/or enclosed (○) predator exclusion (N), control (C) and predator attraction (P) fields. The maize maturation periods (—) are indicated along the x-axes.

**Table 1.** Results of mixed model regression analyses of *M. natalensis* population dynamics. *F*-values, degrees of freedom (Num d.f. and Den d.f., respectively, in brackets) and *P*-values (in italics) of *F*-tests from P3 models (one-factor comparison of predation pressure in three levels: control, predator exclusion and predator attraction) and P2D2 models (two-factor comparison of predation in two levels: control and predator exclusion; and dispersal in two levels: open fields and enclosures). Nonsignificant interaction terms between fixed effects in the two-factor models are excluded from the models. Significant *P*-values are underlined

	Predation	Dispersal	Predation × dispersal
Peak size			
P3	2.31 (2, 12) <i>0.142</i>		
P2D2	0.10 (1, 15) <i>0.756</i>	1.96 (1, 15) <i>0.182</i>	<u>7.48 (1, 15) <i>0.015</i></u>
Peak timing			
P3	1.24 (2, 12) <i>0.325</i>		
P2D2	0.06 (1, 17) <i>0.816</i>	0.62 (1, 17) <i>0.443</i>	
Population growth			
P3	3.59 (2, 12) <i>0.057</i>		
P2D2	1.51 (1, 15) <i>0.239</i>	0.28 (1, 15) <i>0.602</i>	<u>11.29 (1, 15) <i>0.014</i></u>
Population decrease			
P3	1.64 (2, 12) <i>0.236</i>		
P2D2	1.13 (1, 16) <i>0.303</i>	0.01 (1, 16) <i>0.925</i>	



**Fig. 3.** *M. natalensis* population peak size (mean of replicates ± SE) for populations in control (●) and predator exclusion (○) treatments (P2D2 analysis).



**Fig. 4.** *M. natalensis* population growth rate (mean of replicates ± SE) during the population rise period for populations in control (●) and predator exclusion (○) treatments (P2D2 analysis).

(NO) increased on average significantly faster (P3: 1.95 per capita growth rate between capture sessions; SE range 1.752–2.156; P2D2: Fig. 4) than populations in open control fields (CO) (P3: 1.36 per capita growth rate between capture sessions; SE range 1.248–1.476; P2D2: Fig. 4), while the difference with the populations in the open predator attraction fields had a lower probability (P3: 1.46 per capita growth rate between capture sessions; SE range 1.300–1.638) (\*significant after sequential Bonferroni correction: P3: CO vs. NO:  $t_{12} = -2.65$ ,  $P = 0.0199$ ; CO vs. PO:  $t_{12} = -0.51$ ,  $P = 0.6162$ ; NO vs. PO:  $t_{12} = 1.85$ ,  $P = 0.0869$ ). Furthermore, populations in open predator exclusion fields (NO) also increased faster than populations in predator exclusion enclosures (NE) (Fig. 4) (\*significant after sequential Bonferroni correction: P2D2: CE vs. CO:  $t_{15} = 1.71$ ,  $P = 0.1072$ ; CE vs. NE:  $t_{15} = 1.03$ ,  $P = 0.3216$ ; CO vs. NO:  $t_{15} = -3.06$ ,  $P = 0.0080$ \*; NE vs. NO:  $t_{15} = -2.19$ ,  $P = 0.0448$ ). There was also a significant predation × dispersal interaction effect on the peak size (Table 1). Peak size was higher in open predator exclusion fields (NO) and in control enclosures (CE) compared with open control fields (CO) (Fig. 3)

(\*significant after sequential Bonferroni correction: CE vs. CO:  $t_{15} = 3.18$ ,  $P = 0.0063$ \*; CE vs. NE:  $t_{15} = 1.63$ ,  $P = 0.1230$ ; CO vs. NO:  $t_{15} = -2.27$ ,  $P = 0.0384$ ; NE vs. NO:  $t_{15} = -0.88$ ,  $P = 0.3929$ ).

## Discussion

As in other studies (e.g. Leirs 1995 and references therein; Stenseth *et al.* 2003), also in our study *M. natalensis* population dynamics were characterized by pronounced seasonal fluctuations. In the northern hemisphere the shift from generalist to specialist predators from south to north Fennoscandia, has been linked with the shift from annual rodent population fluctuations to multiannual cyclic fluctuations (e.g. Hanski, Hansson & Henttonen 1991; Bjørnstad, Falck & Stenseth 1995). Generalist predators or nomadic avian specialist predators tend to stabilize and prevent multiannual cyclicality, due to their rapid response to fluctuating prey population dynamics, whereas specialist predators are implicated in generating multiannual cyclic population dynamics, due to their delayed density-dependent impact (Hanski *et al.* 1991; Klemola

*et al.* 2002; Korpimäki *et al.* 2002). Based on this knowledge, *M. natalensis* populations should largely be influenced by generalist and/or nomadic specialist predators. Model simulations with a reduction of generalist predators tend to increase the amplitude and period of cyclic vole population fluctuations (Korpimäki *et al.* 2002), and experimentally exclusion of predators in our study indeed increased the amplitude (i.e. growth rate and peak size) in the populations. Thus the effects of predators on *M. natalensis* populations provide excellent similarity with the stabilizing impact of predators to rodent population dynamics in the north. The timing of peak and rates of decrease, however, was not affected. This suggests that *M. natalensis* escaping predation in predator exclusion treatments are limited in growth by other factors than predation, very likely by food depletion. Shortage of food has the potential to limit the growth of rodent populations in a direct density-dependent manner, and, two-factorial manipulation experiments of predation level and food supply have shown that cyclic field vole populations escaping predators may be limited by lack of food during periods with food shortage (Huitu *et al.* 2003). The population growth of *M. natalensis* is probably not limited by food at the beginning of the rise period when there is a large amount of seeds available (Vibe-Petersen & Leirs unpublished). During especially the first part of the decline period, however, food is scarce (Hubert *et al.* 1981) and survival is low (Vibe-Petersen & Leirs unpublished). The highest seasonal presence of raptor pellets comes late in the season and avian predation pressure is thus higher during the population decline period than during the rise period. This agrees with our own observations of raptors and owls in the area, and suggests that the use of perch poles depended on the presence of avian predators determined by seasonal variations in their reproduction as well as in numbers of migratory birds (Brown, Urban & Newman 1982; Fry, Keith & Urban 1988). We propose that predation and food availability interact to affect rodent population dynamics. During the population rise period, food is abundant and predation (whether directly or through indirect effects) is the main factor in limiting population growth. During the population decline period, however, food is scarce and whatever the predation pressure is, it is food shortage, which governs population dynamics in the area. Thus, during the decline period, predation removes the 'doomed surplus' (Errington 1946) and although it contributes to mortality [survival of subadult *M. natalensis* in predator attraction fields, e.g. is indeed lowered during the population decline period (Solveig Vibe-Petersen, unpublished data)], its presence or absence will not affect the population dynamics.

*M. natalensis* population growth rate and peak size increased in the absence of predators only in open fields, whereas this pattern was not seen when rodents were enclosed. This effect of fencing was the opposite of what we expected. Originally, we anticipated that

social interactions would drive rodents from areas with high density to areas with low densities (Brandt 1992). Thus in open predator exclusion fields, rodent densities would increase due to high survival and individuals would then emigrate, we expected, to the surrounding areas with lower densities while fences would prevent this in the enclosures. Conversely, animals would immigrate from the surrounding habitats into predator attraction fields due to the reduction in rodent density by predators. According to our results, however, the predation effect disappears when the prey population is enclosed. A straightforward biological explanation is that ambient predation pressure is a stronger driving force than density for rodent dispersal: the rodents immigrate (or stay) in areas without predation and avoid (or leave) areas with predation. That effect disappears where fences impede dispersal. This hypothesis requires that the rodents accurately can recognize areas with lower predation pressure. Indeed, it has been shown that *M. natalensis* can assess the risk of both avian (Mohr *et al.* 2003) and mammalian (Petersen 2002) predators, and that they acted accordingly in our different treatments.

While exclusion of predators increased the population growth and peak size, perch poles and nest boxes did not show any obvious direct effect on the population fluctuations. There may be three explanations for this. A first reason could be that the perch poles and nest boxes simply were not successful in attracting and/or increasing the hunting efficacy of raptors. However, our collections of avian pellets around the perch poles, occasional observations of perching raptors and the breeding barn owl pair in one of the nest boxes, showed that the treatment was attractive for predators. A single barn owl couple obviously cannot change the predation pressure alone; but it may have an effect in the near surroundings of the nest box. Furthermore, video surveillance results of *M. natalensis*' foraging behaviour showed that *M. natalensis* perceived differences in the ambient predation pressure in our experimental fields (Mohr *et al.* 2003). Hence, we infer that local predation pressure in predator attraction fields was higher, at least periodically, whether directly by increasing the number of rodents killed and/or indirectly by the mere presence of perching predators affecting the rodents' behaviour. A second reason could be that because the home range of owls and raptors may exceed the size of the entire study area, the perch and nest box treatment would also affect populations in control fields. Yet, again, our direct video observations of the rodents' behaviour (Mohr *et al.* 2003) showed that the local differences in treatment were affecting the rodents' behaviour. So, even if an increase of raptor and owl numbers would affect a larger area, the treatments still concentrated the effects locally. A third reason for not seeing clear effects of the predator attraction treatment could be that predators actually do affect the rodent population, but (1) the rodent population is able to compensate for increased mortality (e.g. by changing reproductive

strategies or through density-dependent dispersal) and thereby maintains a population growth equal to populations under natural predation conditions (Boyce, Sinclair & White 1999), or (2) the rodents avoid predation by changing their individual behaviour and thereby increase their immediate survival chances (e.g. Desy, Batzli & Liu 1990). While our demographic analyses of *M. natalensis* detected no compensatory mechanism in the reproductive characteristics for populations in predator attraction fields, they did show compensation through survival as the survival probability increased in predator attraction fields during the population rise period (Solweig Vibe-Petersen, unpublished data). Hence, the use of perch poles seems effective in attracting avian predators and is probably likely to have most effect in areas limited by natural raptor and owl perching sites. Barn owl nest boxes may be useful to increase owl predation activity but any long-term effects on *M. natalensis* populations remain to be examined.

In conclusion, the only effect of experimentally manipulated predation levels on the rodent population was a faster population growth rate and a higher peak population size in the absence of predators. Otherwise, dynamics patterns were similar for populations where predators had access or were attracted, indicating that compensatory mechanisms operate when rodents are exposed to high levels of predation risk. Reducing dispersal of rodents removed the effect of predation on population growth and peak size, suggesting that local predators may play a role in driving rodent dispersal, but have otherwise little direct effect on population dynamics. Our results also indicate little hope for predator attraction as a biological control method to affect the densities of this rodent species.

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### References

- Bjørnstad, O.N., Falck, W. & Stenseth, N.C. (1995) A geographic gradient in small rodent density fluctuations: a statistical modelling approach. *Proceedings of the Royal Society of London B*, **262**, 127–133.
- Boyce, M.S., Sinclair, A.R.E. & White, G.C. (1999) Seasonal compensation of predation and harvesting. *Oikos*, **87**, 419–426.

- Brandt, C.A. (1992) Social factors in immigration and emigration. *Animal Dispersal, Small Mammals as a Model* (eds N.C. Stenseth & W.Z. Lidicker, Jr), pp. 96–141. Chapman & Hall, London.
- Brown, L.H., Urban, E.K. & Newman, K. (1982) *The Birds of Africa*, Vol. I. Academic Press, London.
- Christensen, J.T. (1996) Home range and abundance of *Mastomys natalensis* (Smith, 1834) in habitats affected by cultivation. *African Journal of Ecology*, **34**, 298–311.
- Desy, E.A., Batzli, G.O. & Liu, J. (1990) Effects of food and predation on behaviour of prairie voles: a field experiment. *Oikos*, **58**, 159–168.
- Duckett, J.E. (1991) Management of the barn owl (*Tyto alba javanica*) as a predator of rats in oil palm (*Elaeis guineensis*) plantations in Malaysia. *Birds of Prey Bulletin*, **4**, 11–23.
- Duckett, J.E. & Karuppiah, S. (1989) A guide to the planter in utilizing barn owls (*Tyto alba*) as an effective biological control of rats in mature oil palm plantations. *Proceedings of the PORIM International Palm Oil Development Conference, 5–9 September 1989*, pp. 357–372. Palm Oil Research Institute of Malaysia, Kuala Lumpur.
- Errington, P.L. (1946) Predation and vertebrate populations. *Quarterly Review of Biology*, **21**, 144–177.
- Fiedler, L.A. (1988) Rodent problems in Africa. *Rodent Pest Management* (ed. I. Prakash), pp. 35–65. CRC Press, Inc., Boca Raton, FL.
- Fry, H.C., Keith, S. & Urban, E.K. (1988) *The Birds of Africa*, Vol. III. Academic Press, London.
- Handwerk, J. (1998) Zur Ökologie von Prädatoren (Mammalia, Aves, Serpentes) und deren Wirkung auf die Populationen von *Mus musculus praetextus* Brants, 1827, und *Avicathis niloticus* Desmarest, 1822, im Niltal Ägyptens. PhD Thesis, der Rheinischen Friedrich-Wilhelms-Universität zu Bonn.
- Hanski, I., Hansson, L. & Henttonen, H. (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology*, **60**, 353–367.
- Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L. & Turchin, P. (2001) Small-rodent dynamics and predation. *Ecology*, **82**, 1505–1520.
- Hubert, B., Couturier, G., Poulet, A. & Adam, F. (1981) Les conséquences d'un supplément alimentaire sur la dynamique des populations de rongeurs au Sénégal. I. Le cas de *Mastomys erythroleucus* en zone Sahelo-Soudanienne. *Annual Review of Ecology and Systematics*, **35**, 73–95.
- Huitu, O., Koivula, M., Korpimäki, E., Klemola, T. & Norrdahl, K. (2003) Winter food supply limits growth of northern vole populations in the absence of predation. *Ecology*, **84**, 2108–2118.
- Klemola, T., Tanhuanpää, M., Korpimäki, E. & Ruohomäki, K. (2002) Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos*, **99**, 83–94.
- Klemola, T., Pettersen, T. & Stenseth, N. (2003) Trophic interactions in population cycles of voles and lemmings: a model-based synthesis. *Advances in Ecological Research*, **33**, 75–160.
- Korpimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. & Stenseth, N.C. (2002) Dynamics effects of predators on cyclic voles: field experimentation and model extrapolation. *Proceedings of the Royal Society of London B*, **269**, 991–997.
- Korpimäki, E., Brown, P.R., Jacob, J. & Pech, R.P. (2004) The puzzles of population cycles and outbreaks of small mammals solved? *Bioscience*, **54**, 1071–1079.
- Lagos, V.O., Contreras, L.C., Meserve, P.L., Gutiérrez, J.R. & Jaksic, F.M. (1995) Effects of predation risk on space use by small mammals: a field experiment with a Neotropical rodent. *Oikos*, **74**, 259–264.
- Leirs, H. (1995) *Population Ecology of Mastomys natalensis* (Smith, 1834); Implications for rodent control in Africa. PhD Thesis, University of Antwerp. *Agricultural Edition*,

35. Belgian Administration for Development Cooperation, Brussels.
- Leirs, H., Verhagen, R., Verheyen, W., Mwanjabe, P. & Mbise, T. (1996) Forecasting rodent outbreaks in Africa: an ecological basis for *Mastomys* control in Tanzania. *Journal of Applied Ecology*, **33**, 937–943.
- Leirs, H., Stenseth, N.C., Nichols, J.D., Hines, J.E., Verhagen, R. & Verheyen, W. (1997) Stochastic seasonality and non-linear density-dependent factors regulate population size in an African rodent. *Nature*, **389**, 176–180.
- Lenton, G.M. (1978) Owls on Fraser Estate, Johore. *Johore Planters' Association – Annual Report*, **1978**, 29–33.
- Lima, M., Stenseth, N.C. & Jaksic, F. (2002) Population dynamics of a South American rodent: seasonal structure interacting with climate, density dependence and predator effects. *Proceedings of the Royal Society Biology Sciences Series B*, **269**, 2578–2586.
- Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS System for Mixed Models*. SAS Institute Inc., Cary, NC.
- Makundi, R.H., Oguge, N.O. & Mwanjabe, P.S. (1999) Rodent pest management in east Africa – an ecological approach. *Ecologically-Based Rodent Management*. ACIAR Monograph 59. (eds G. Singleton, L. Hinds, H. Leirs & Z. Zhang), pp. 460–476. Brown Prior Anderson, Melbourne.
- Meserve, P.L., Kelt, D.A., Milstead, W.B. & Gutiérrez, J.R. (2003) Thirteen years of shifting top-down and bottom-up control. *Bioscience*, **53**, 633–646.
- Mohr, K., Vibe-Petersen, S., Jeppesen, L.L., Bildsøe, M. & Leirs, H. (2003) Foraging of multimammate mice (*Mastomys natalensis*) under different predation pressure: cover, patch-dependent decisions and density-dependent GUDs. *Oikos*, **100**, 459–468.
- Petersen, H.H. (2002) *Predation risk assessment in the African multimammate mouse Mastomys natalensis*. MSc Thesis, University of Copenhagen, Institute of Zoology.
- Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- Singleton, G.R., Leirs, H., Hinds, L.A. & Zhibin, Z. (1999) Ecologically-based management of rodent pests – re-evaluating our approach to an old problem. *Ecologically-based Rodent Management*. ACIAR Monograph 59 (eds G. Singleton, L. Hinds, H. Leirs & Z. Zhang), pp. 17–29. Brown Prior Anderson, Melbourne.
- Smal, C.M. (1989) Barn owls (*Tyto alba*) for the control of rats in agricultural crops in the tropics. *Proceedings Symposium Biological Control of Pests in Tropical Agricultural Ecosystems June 1988, Bogor, Indonesia, June 1st–3rd 1988*. SEAMEO-BIOTRO, Special Publication, **36**, 255–276.
- Stenseth, N.C., Leirs, H., Skonhøft, A., Davis, S.A., Pech, R.P., Andreassen, H.P., Singleton, G.R., Lima, M., Machang'u, R.M., Makundi, R.H., Zhang, Z., Brown, P.B., Shii, D. & Wan, X. (2003) Mice, rats and people: the bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment*, **1**, 367–375.
- Van Gulck, T., Stoks, R., Verhagen, R., Sabuni, C.A., Mwanjabe, P. & Leirs, H. (1998) Short-term effects of avian predation variation on population size and local survival of the multimammate rat, *Mastomys natalensis* (Rodentia, Muridae). *Mammalia*, **62**, 329–339.
- White, G.C., Anderson, D.R., Burnham, K.P. & Otis, D.L. (1982) *Capture-recapture and Removal Methods for Sampling Closed Populations* (ed. B. Leffler), p. 235. Los Alamos National Laboratory Report, Los Alamos, NM.
- Wolff, J.O., Fox, T., Skillen, R.R. & Wang, G. (1999) The effects of supplemental perch sites on avian predation and demography of vole populations. *Canadian Journal of Zoology*, **77**, 535–541.

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