Prey selection by barn owls in relation to small-mammal community and population structure in a Sahelian agro-ecosystem

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Abstract: Barn owl pellet content was studied on seven occasions over a 2-y period during which terrestrial small-mammal populations were assessed via a capture-mark-recapture (CMR) programme in a Sahelian agro-ecosystem of the Inner Delta of Niger River in Mali. Rodents (especially *Mastomys huberti* representing 78.5% of the total number of prey) were the major prey of the barn owl on all but one occasion, when bats were dominant. This exception coincided with the period of lowest abundance of *M. huberti* at the study site. Distribution of *M. huberti* prey into four age classes was assessed through analysis of tooth wear in remains from the seasonal pellet samples. Comparisons with age structure of the CMR population indicate that the barn owl tended to prey on smaller-than-average (thus younger) individuals, especially when these are rare in the population (non-reproductive period between June and October). The spectrum of prey consumed is compared with data previously reported in Sahelian Africa, showing for the first time in this region a major shift in prey choice by the barn owl when its preferred prey becomes rare. At the rodent population level, the apparent choice of younger *M. huberti* prey at some periods is interpreted in the light of our knowledge on population dynamics of the species in this habitat.

Key Words: bats, *Mastomys huberti,* Mali, murid rodents, Niger River delta, predation, prey choice

INTRODUCTION

The diet of the barn owl (*Tyto alba*) is mainly based on small mammals, mostly rodents (Brown *et al.* 1982). This characteristic has made the study of barn owl diet a useful tool for estimating small-mammal community composition at various temporal and spatial scales (Happold 1987, Love *et al.* 2000). The barn owl is generally considered an opportunistic predator which may prey on a large fraction of the species present in a community (Yom-Tov & Wool 1997). However, discrepancies are often observed between the spectrum of available prey and the actual diet of barn owls, as deduced from their pellet contents. These discrepancies can have an interspecific (some prey species are taken more than others), but also an intraspecific (some age/sex classes are consumed more than others) component. Prey size and behaviour have both been shown to play prominent roles in prey selection by the barn owl. In a certain range of body mass (usually less than 80–100 g; Ille 1991, Yom-Tov & Wool 1997), barn owls have been shown to choose either heavier (Castro & Jaksic 1995, Derting & Cranford 1989, Kotler *et al.* 1988) or lighter (Dickman *et al.* 1991 and references therein) than average individuals, depending on the prey species mean size. Activity rhythm is an evident factor determining the rate of predation: as a mainly nocturnal predator, the barn owl will predominantly take nocturnal prey (Jaksic & Yañez 1979). Prey microhabitat use (Dickman *et al.* 1991, Kotler *et al.* 1988, Ziv *et al.* 1995) and type of foraging activity (Castro & Jaksic 1995, Derting & Cranford 1989) also influence capture rate by the barn owl. Handling efforts needed by the barn owl, itself linked with prey behaviour, may also influence prey choice (Ille 1991). Last but not least, relative abundance of prey species within a given community may determine their proportion in the predator's diet (Hanney 1963, Love *et al.* 2000, Saint-Girons & Spitz 1966). In extreme cases of small-mammal population declines, the barn owl has been observed to
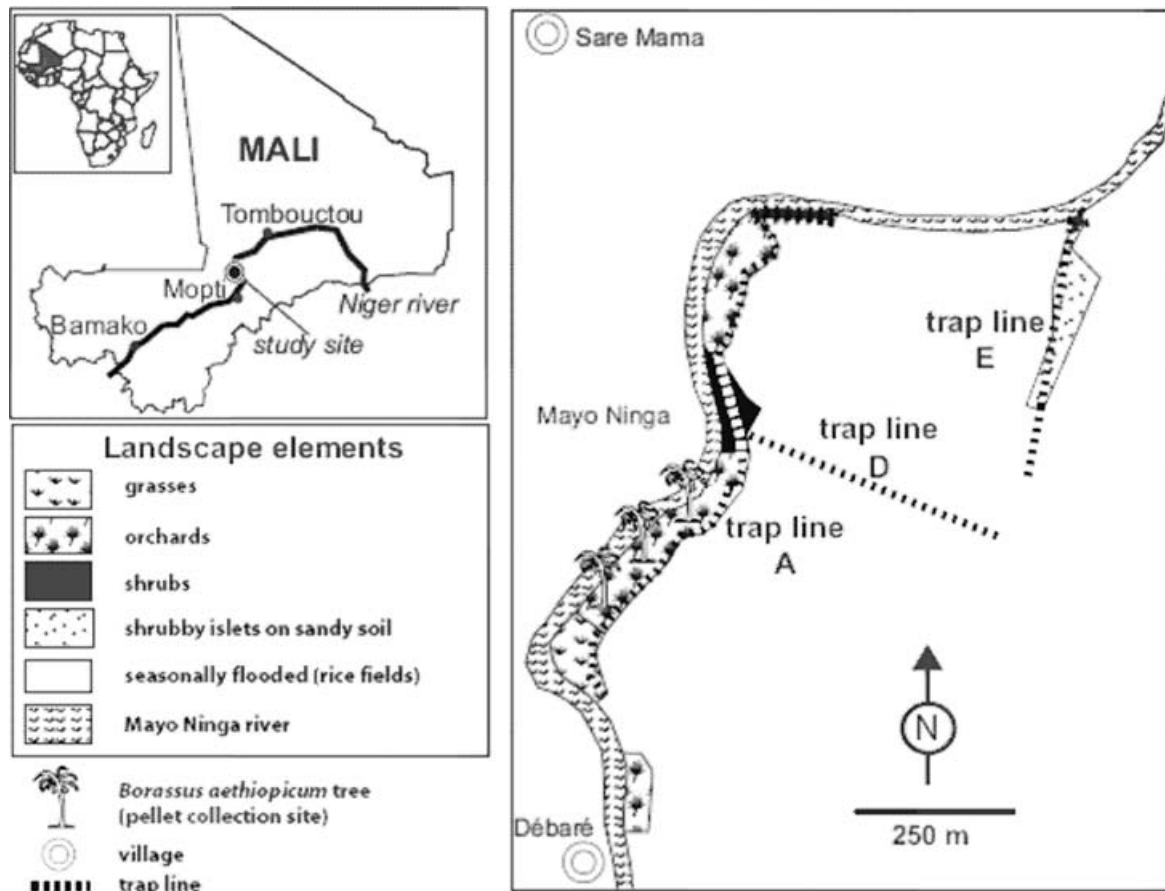
Figure 1. Map of the study area, showing the location of the area where pellets were collected (black vertical arrows) and trap lines of the CMR programme.

prey on birds (Drost & McCluskey 1992, Fritzell & Thorne 1984).

In Africa, rodents of the genus *Mastomys* are well-known for being both major pests of agricultural crops (Fiedler 1988, Leirs 1995) and potential reservoirs of a variety of human-transmitted diseases (Gratz 1997). Within the framework of ecologically based management of rodent pests (Singleton *et al.* 1999), predation is one of the methods that could be put forward. Predation has for long being hypothesized to be a key factor in the population dynamics of *Mastomys* species (Hubert & Adam 1985). At the same time, *Mastomys* has been shown to be a major prey item of barn owls in a number of studies conducted in Africa (Brown *et al.* 1982). Until recently, no specific studies on the effect of predation on *Mastomys* population dynamics were conducted. In the frame of a long-term programme conducted on *Mastomys natalensis* in Tanzania (Leirs *et al.* 1997), experimental protocols have been implemented to test for the influence of predation on various components of population structure of *M. natalensis* (Mohr *et al.* 2003, Van Gulck *et al.* 1998, Vibe-Petersen 2003, Vibe-Petersen *et al.* 2006). These studies have yielded contrasting results

concerning the impact of predation, especially by the barn owl, on *M. natalensis* population dynamics. Here, we used a field approach to evaluate predation by barn owls in an agricultural area of the Inner Delta of the Niger River (central Mali), mainly devoted to rice cultivation, and where rodents are known to cause crop damage in years of high abundance. Along with a capture-mark-release (CMR) programme aimed at a better understanding of rodent population dynamics in this area (Granjon *et al.* 2005), we collected barn owl pellets and analysed their content to: (1) assess seasonal fluctuations in the diet of the Barn Owl; (2) test for a potential selection by the barn owl of some age category of its preferred prey, *Mastomys huberti*, via the comparison of age structure variations observed in the pellet and in the CMR samples of this species.

STUDY SITE

The study site (04°02′06″W; 14°53′24″N; elevation: 266 m asl) is located 46 km north of Mopti, *c.* 1 km west of the main course of the Niger River (Figure 1). The

climate is typically Sahelian, with a single wet season between May and October, *c.* 80% of the rainfall being concentrated from July to September. The study area mainly consists of a vast basin bordered on its eastern side by the Niger River and on its northern and western sides by one of its small tributaries, the Mayo Ninga River (Figure 1). As the whole Inner Delta of the Niger River, the major part of this basin is flooded annually, especially between September and November when the peak of the flood occurs (Granjon *et al.* 2005). Most of the basin is cultivated for rice seasonally, with weeding fires occurring from January to May, ploughing in May–June, sowing around July and harvest in November–December (Maïga *et al.* 2002). Areas that remain above water at the flood peak mostly correspond to alluvial levees along the Mayo Ninga River, the highest parts of which are covered by orchards (Figure 1).

METHODS

Barn owl pellets were collected in one of these orchards on seven occasions: October 2000, March, June and October 2001, and March, June and October 2002. Most of the time they were found at the foot of palm trees (*Borassus aethiopicum*). At the same time live-trapping sessions were performed in the frame of a capture-mark-release (CMR) programme on various trap lines situated in the immediate vicinity of the area where barn owl pellets were collected (Figure 1). They provided data on abundance, age structure and spatial distribution of the rodent populations present, especially of *Mastomys huberti*, the main nocturnal species of the site (see Granjon *et al.* 2005 for details).

Treatment of barn owl pellets

The pellets were slightly dampened to facilitate extraction of prey remains. Vertebrate skull fragments were dried on Petri dishes and subsequently examined with a low-power stereo microscope for species identification. Rodents were identified using the IRD Bamako mammalogy laboratory collection and reference to Rosevear (1969). All *Mastomys* individuals recovered were assumed to belong to *M. huberti*. The presence of the sibling species *M. erythroleucus* and *M. natalensis* cannot be entirely ruled out, but *M. huberti* was the only species identified following chromosomal and molecular analyses on a number of individuals from this site (Granjon *et al.*, unpubl. data). Skull remains of bats were compared with a reference collection at the University of Ulm and identified following Hayman & Hill (1971) and Rosevear (1965). Species nomenclature follows Wilson & Reeder (2005).

The minimum number of prey individuals per pellet was determined from the highest number of either skull or mandible item present. For *Mastomys* individuals, tooth wear was assessed to estimate relative age according to four classes: 0 (juvenile), 1 (young adult), 2 (adult) and 3 (old adult), based on the categories proposed by Van der Straeten (1980) for another murine rodent genus, namely *Lemniscomys* (slightly modified by pooling his categories 2 and 3, and 4 and 5). The following four measurements were taken when possible, using digital calipers to the nearest 0.1 mm: partial skull length (PSL), i.e. from the tip of nasals to the posterior edge of parietals, the interparietal bone generally being broken; mandible length (MdL), without the incisor; upper molar row length (UMRL); lower molar row length (LMRL; see Rosevear 1969 for skull nomenclature). Tooth wear estimation as well as skull and dental measurements were taken from remains of intact pellets (i.e. those considered in Tables 1 and 2) as well as from remains found in damaged pellets.

Statistical treatment

The relationship between tooth wear and the measurements taken on *M. huberti* skulls was investigated using Spearman rank correlation tests. The aim was to choose the measurement that most appropriately reflects relative age variation and to subsequently use it for defining a number of length classes that would also represent age structure of the *M. huberti* prey samples, but in a

Table 1. Summary statistics of the contents of barn owl pellets. Number of pellets consist in those that yielded skull remains and (in parentheses) those that did not.

Session	Number of pellets	Number of prey items	Prey items per pellet	Number of individual rodents	Rodents as percentage of all prey items
October 2000	30 (1)	52	1.73	41	78.8
March 2001	115 (12)	184	1.60	177	96.2
June 2001	34 (5)	45	1.32	43	95.6
October 2001	31 (1)	45	1.45	7	15.6
March 2002	51 (7)	98	1.92	88	89.8
June 2002	44 (17)	63	1.43	57	90.5
October 2002	51 (2)	58	1.14	54	93.1
Total /Mean	356 (45)	545	1.53	467	85.7

Table 2. Numbers and percentage of the different categories of prey items found in barn owl pellets in different seasons.

		October 2000	March 2001	June 2001	October 2001	March 2002	June 2002	October 2002	Total
Rodentia									
Mastomys huberti	N	37	164	40	6	78	51	52	428
	%	71.2	89.1	88.9	13.3	79.6	81.0	89.7	78.5
Arvicanthis niloticus	N	4	9	2	0	2	2	0	19
	%	7.7	4.9	4.4	0.0	2.0	3.2	0.0	3.5
Mus (Nannomys) sp.	N	0	4	0	1	6	2	1	14
	%	0.0	2.2	0.0	2.2	6.1	3.2	1.7	2.6
Taterillus gracilis	N	0	0	0	0	1	1	1	3
	%	0.0	0.0	0.0	0.0	1.0	1.6	1.7	0.6
Desmodilliscus braueri	N	0	0	1	0	1	1	0	3
	%	0.0	0.0	2.2	0.0	1.0	1.6	0.0	0.6
Soricomorpha									
Crocidura viaria	N	9	5	0	1	7	6	2	30
	%	17.3	2.7	0.0	2.2	7.1	9.5	3.4	5.5
Chiroptera									
Mops condylurus	N	1	0	0	30	0	0	2	33
	%	1.9	0.0	0.0	66.7	0.0	0.0	3.4	6.1
Neoromicia rendalli	N	0	0	0	3	0	0	0	3
	%	0.0	0.0	0.0	6.7	0.0	0.0	0.0	0.6
Scotophilus viridis	N	0	0	0	1	0	0	0	1
	%	0.0	0.0	0.0	2.2	0.0	0.0	0.0	0.2
Taphozous mauritianus	N	0	0	0	1	0	0	0	1
	%	0.0	0.0	0.0	2.2	0.0	0.0	0.0	0.2
Birds	N	1	2	2	2	3	0	0	10
	%	1.9	1.1	4.4	4.4	3.1	0.0	0.0	1.8
Total		52	184	45	45	98	63	58	545

more detailed and continuous fashion. The distribution of the chosen measurement (i.e. MdL) was then compared, at each session, with the age structure of individuals trapped in the course of the CMR programme. The latter was inferred from the relationship between body mass (the only age-related variable that was available in the CMR samples) and MdL. This relationship was obtained from a sample of 142 specimens of *M. huberti* caught in 2004–2005 in the context of various field studies conducted in and around the Inner Delta of the Niger River. A regression was fitted between MdL and mass in this sample and subsequently used to transform 10-g classes of CMR-trapped individuals into the corresponding MdL classes. The relation between numbers of *M. huberti* individuals belonging to these MdL classes in the seasonal CMR samples and in the corresponding pellet samples was assessed using chi-square tests.

RESULTS

A total of 401 barn owl pellets was collected in the course of the study, ranging from 31 (October 2000) to 127 (March 2001) per session (Table 1). In 45 of them, no skull remains were found. Among the remaining 356 pellets, a minimum of 545 prey individuals were counted. The mean number of prey individuals per pellet ranged from 1.14 in October 2002 to 1.92 in March

2002 (global mean = 1.53; Table 1). Rodents always represented the vast majority of the prey (between 78.8% and 96.2% of occurrence), except in October 2001 when their percentage fell to 15.6% (Table 1). At that particular period, bats (especially *Mops condylurus*, the overall second-ranking prey with 6.1% of occurrence) became the most prevalent prey (Table 2). At all other occasions, *Mastomys huberti* was by far the dominant prey species. Among murine rodents, *Arvicanthis niloticus* and *Mus* (*Nannomys*) sp. were regularly found, but their overall frequencies were low (3.5 and 2.6% of occurrence, respectively). The gerbillines *Taterillus gracilis* and *Desmodilliscus braueri* were consumed only occasionally. The shrew *Crocidura viaria* was the third-ranking prey species, with 5.5% of overall occurrence (Table 2).

The relationship between the frequency of occurrence of *M. huberti* in pellets (data from Table 2) and their abundance in the field was better described by a logarithmic curve ($R^2 = 0.587$) than by a linear regression ($R^2 = 0.399$; Figure 2). Another possible representation of this relationship is proposed, corresponding to a sigmoid curve (Figure 2).

Tooth wear and skull measurement data on *M. huberti* prey items are summarized in Table 3. A quite consistent pattern emerged from tooth wear distributions in the four classes, with samples from October always showing a majority of individuals in category 2 (i.e. adults), whereas
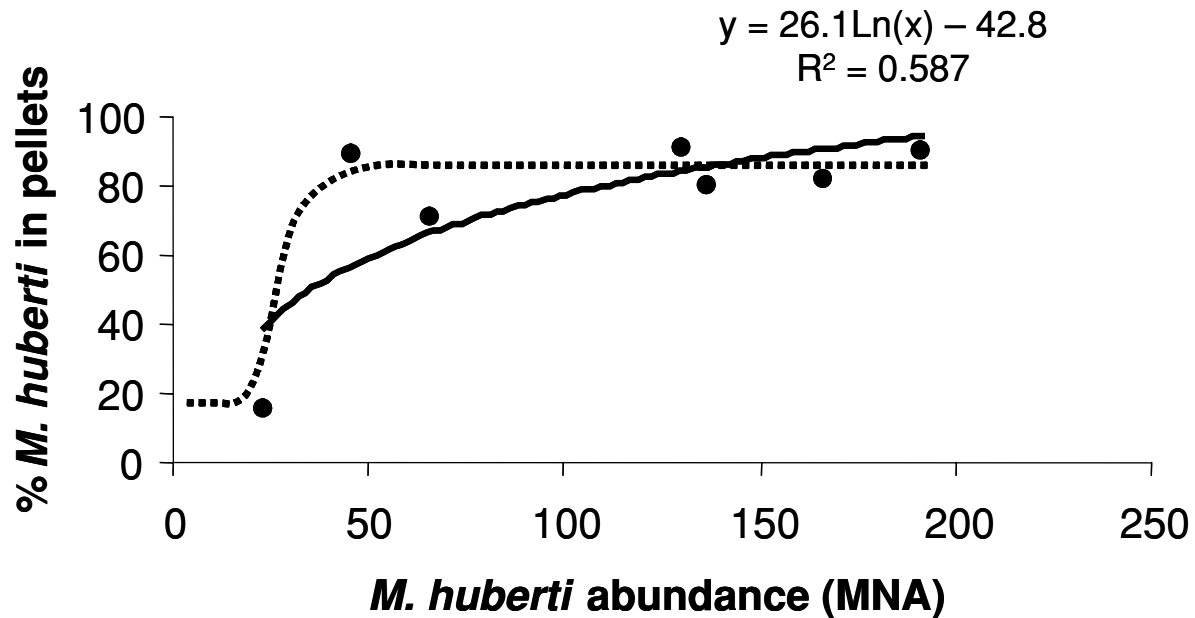
Figure 2. Relationship between the percentage of prey items made up of *Mastomys huberti* found in the pellets of barn owls (data from Table 2) and the abundance of the species as revealed by the trapping design shown in Figure 1 as minimum numbers of individuals alive (MNA), with equation and correlation coefficient of the logarithmic curve (continuous line) that describes this relationship. The dashed line represents another, hypothetical type of relationship, where predation rate on *M. huberti* would rise abruptly from low to high once the species abundance reaches a given threshold (see text).

samples from March were characterized by a dominance of young adults (category 1). The samples from June were variable, younger in 2001 than in 2002. This translates into mean values of skull measurements, large in October, and small in March. The same seasonal pattern was observed with MdL, and to a lesser extent with PSL. Upper and lower molar row lengths did not show any clear pattern of variation.

Values of the Spearman rank correlation coefficient (r_s) showed a poor correlation between tooth wear and molar row lengths (overall $r_s = 0.241$, $n = 250$, $P < 0.05$, and overall $r_s = 0.132$, $n = 252$, $P > 0.05$ for UMRL and LMRL, respectively). Conversely, statistically highly significant positive correlations were recorded between tooth wear and PSL ($0.01 < P < 0.001$ at 5 of 7 periods, overall $r_s = 0.632$, $n = 134$, $P < 0.001$) and between tooth wear and MdL ($0.01 < P < 0.001$ at 6 of 7 periods, overall $r_s = 0.700$, $n = 321$, $P < 0.001$). Only in October 2001 was the correlation between tooth wear and MdL not statistically significant, a period for which sample size was small ($n = 5$). Because of this high correlation, and also because mandible numbers were always much higher due to their better state of preservation in pellets, MdL was the variable chosen to represent age structure in the prey samples of *M. huberti* over the study periods.

The relation between body mass and MdL in the sample of 142 wild-caught *M. huberti* individuals was better fitted by a logarithmic regression: $MdL = 3.06 \ln(Mass) + 5.29$ ($R^2 = 0.819$; vs < 0.8 for linear or polynomial regres-

sions). This formula was subsequently used to generate MdL classes corresponding to body mass classes of 10-g intervals (in the range 0–90 g). The frequencies of seasonal samples of CMR-caught *M. huberti* individuals were then distributed into these nine MdL classes and these distributions were compared with those of pellet-recovered MdL, allocated to the same classes (Figure 3). The chi-square tests performed on the corresponding contingency tables were highly significant ($P < 0.005$ or $P < 0.001$) for five out of the six periods where the test could be run (numbers were too low in October 2001). In all cases, the distributions of pellet remains were skewed towards smaller values of MdL than trapped animals, suggesting the more frequent consumption of relatively small-sized individuals of *M. huberti* (thus on average probably younger) among those available.

DISCUSSION

In the region of Niono (*c.* 200 km west of our study site), the analysis of 1634 pellets (Wilson 1987) collected in the period 1980–1986, yielded results that show some similarities with ours in terms of the composition and frequency of prey species: *Mastomys erythroleucus* was by far the main prey species, representing 81.5% of all vertebrates, followed by *Arvicanthis niloticus* (7.6%) and *Mus* (*Nannomys*) sp. (then called *Leggada*; 5.1%), *Taterillus gracilis* (1.1%) and *Desmodilliscus braueri* (0.9%). Shrews

Table 3. Percentages of the four tooth wear classes, and basic statistics (mean ± SD and number) for tooth wear, partial skull length (PSL), mandible length (MdL), upper molar row length (UMRL) and lower molar row length (LMRL) in *Mastomys huberti* skulls of seasonal samples of barn owl pellets.

Session	Tooth wear 0	1	2	3	Mean of scores ± SD	N	PSL (mm) Mean ± SD	N	MdL (mm) Mean ± SD	N	UMRL (mm) Mean ± SD	N	LMRL (mm) Mean ± SD	N
October 2000	7.3	34.5	56.4	1.8	1.55 ± 0.63	55	19.6 ± 0.98	25	14.7 ± 1.19	46	4.44 ± 0.15	41	4.30 ± 0.17	42
March 2001	8.2	53.8	36.1	1.9	1.32 ± 0.65	158	19.5 ± 1.43	43	13.8 ± 2.04	127	4.51 ± 0.19	80	4.37 ± 0.20	80
June 2001	12.2	53.7	34.1	0	1.22 ± 0.65	41	18.9 ± 0.58	9	13.9 ± 1.44	30	4.49 ± 0.18	17	4.36 ± 0.14	26
October 2001	0	22.2	77.8	0	1.78 ± 0.44	9	19.9 ± 0.88	2	15.1 ± 1.18	5	4.51 ± 0.11	7	4.26 ± 0.14	4
March 2002	1.5	76.8	21.7	0	1.2 ± 0.44	69	18.7 ± 1.85	8	13.0 ± 1.69	49	4.48 ± 0.21	29	4.38 ± 0.10	27
June 2002	0	40.4	57.5	2.1	1.62 ± 0.53	47	19.0 ± 0.98	15	14.8 ± 1.55	32	4.56 ± 0.20	33	4.43 ± 0.13	32
October 2002	1.8	35.2	61.1	1.8	1.63 ± 0.56	54	19.5 ± 1.13	32	14.9 ± 1.41	48	4.47 ± 0.47	43	4.37 ± 0.14	47

(three species) represented 1.8%, and bats and birds only 1% of the total number of preys. We now know that *M. huberti* and *M. erythroleucus* coexist in the region of Niono (L. Granjon & K. Mouline, unpubl. data), hence the so-called *Mastomys erythroleucus* specimens of Wilson (1987) may well correspond to a mixture of both species. The figure was not very different in the recent study by Bâ *et al.* (2000) of the barn owl diet in the more northern Sahelian area of the Djoudj National Park in Senegal. Here, *Mastomys* spp. (most probably *M. huberti* and/or *M. erythroleucus*) represented 71.5% of the prey, followed by *A. niloticus* (20%) and some gerbilline species (including *Taterillus* sp. and *D. braueri*). Earlier, Yalden (1994) found an even stronger dominance of *Mastomys* (incorrectly called *M. natalensis*, see Bâ *et al.* 2000) in a smaller sample of barn owl pellets from the same site, with 86.1% of the total prey number. Conversely, the percentages of *Mastomys* specimens were low (less than 10%) in two locations from northern Nigeria where either *Crocidura nigeriae* or *Arvicanthis niloticus* were found as dominant species (Lekunze *et al.* 2001). All in all, however, *Mastomys* does appear as a dominant prey of the barn owl in Sahelian West Africa, which agrees well with its usual dominance in small-mammal communities (Happold 1987, Hubert 1977).

In the Inner Delta of the Niger River, *M. huberti* and *A. niloticus* represent the two dominant rodent species: from October 2000 to October 2002, they represented 49% (range = 27–67%) and 36% (range = 15–57%), respectively, of the total number of captures recorded in the whole area (Granjon *et al.* 2005). But while the former is nocturnal (Duplantier & Granjon 1990), *A. niloticus* is mostly diurnal (Blanchong & Smale 2000, Duplantier & Granjon 1990). Moreover, the average mass of *M. huberti* (*c.* 50 g for adults) is less that of *A. niloticus* (*c.* 110 g for adults). These characteristics make *M. huberti* an ideal prey for *Tyto alba*, as shown recently in northern Senegal by Bâ *et al.* (2000) and in southern Mauritania by Granjon *et al.* (2002). This was confirmed throughout our study, except in October 2001 when bats outnumbered *M. huberti* among the prey species consumed. This period corresponded to the lowest abundance of *M. huberti* during the whole study period (Granjon *et al.* 2005), which undoubtedly explains the shift in prey composition of barn owls. Similarly, Drost & McCluskey (1992) and Fritzell & Thorne (1984) showed that declines in small-mammal abundance induced a shift in the diet of barn owls towards birds. In our case, bats probably constituted a higher proportion because of their abundance in the study site. The most frequently consumed bat species, *Mops condylurus*, is an anthropic species that originally roosted in rock crevices or cracked trees, but which is also frequently found in houses or huts where it dwells under roofs (J. Fahr, pers. comm.). Whether this peak in *M. condylurus* consumption corresponded to an increase
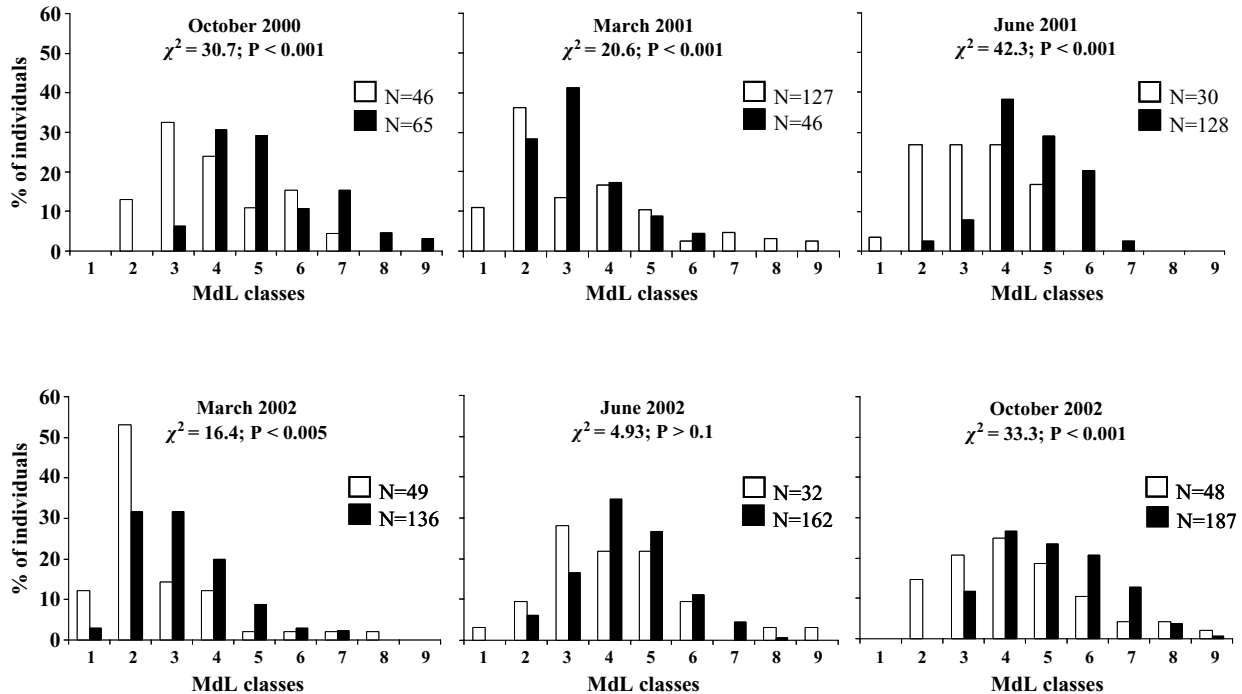
Figure 3. Distribution (%) of *Mastomys huberti* mandible lengths observed in the seasonal samples of pellets (white bars) and estimated in the corresponding samples of individuals trapped during the CMR programme (black bars, see text for details). Classes 1 to 9 correspond to classes of 10 g body mass (0–90 g), which translate into the following MdL values (in mm): <12.35; 12.35–14.47; 14.48–15.70; 15.71–16.59; 16.60–17.28; 17.29–17.84; 17.85–18.3; 18.31–18.72; >18.72. Chi-square tests were performed on corresponding numbers. Data from October 2001 not shown (numbers too low).

in the species abundance at this particular period could not be ascertained. It seemed apparently locally less abundant than *Scotophilus leucogaster*, identified from a few individuals among hundreds which were seen roosting under the dried leaves of the same palms where the barn owls perched for regurgitating their pellets. This may indicate an active selection of *M. condylurus* by the barn owls among the bat species present at the site. The composition of bat species found in the pellets also suggests that the barn owls captured bats in open space as these species are known to forage mostly in open space rather than near or within vegetation (J. Fahr, pers. comm). This could mean that the owls shifted from a ground-oriented towards an air-oriented hunting mode, thereby emphasizing the shift in prey composition.

In Tanzania, a linear correlation was found between the number of pellets collected and rodent overall abundance at the same periods (Van Gulck *et al.* 1998). In our study, the logarithmic relationship found between the frequency of occurrence of *M. huberti* in pellets and their abundance in the field, suggests a positive correlation between these two variables at low to medium *M. huberti* densities, with a rapid saturation of *M. huberti* percentage in pellets relative to population abundances at high densities. Another explanatory hypothesis is that of a threshold effect, with an abrupt change in the prey composition of

barn owls once the abundance of its usually consumed prey drops below a certain level (Figure 2). Data are lacking for intermediate values of *M. huberti* abundances but whatever the pattern, the observed shift may have been facilitated by the fact that this low in the number of small mammals occurred at the maximum of the flood of the Niger River. At that time, small mammals are confined to relatively small patches of dry land corresponding to orchards and shrubs (Granjon *et al.* 2005), where they could be relatively well protected from barn owl predation. Concerning rare prey species, *Mus* (*Nannomys*) sp. and *D. braueri* were found in owl pellets whereas they never entered a live trap (Granjon *et al.* 2005), a fact that has already been mentioned in various instances (Granjon *et al.* 2002, Poulet 1984). *Crocidura viaria* was found in similar frequencies in traps and in pellets, whereas *Taterillus gracilis* was found in pellets at rather lower frequencies than in traps (Granjon *et al.* 2005). The preferred habitats of *T. gracilis* (sandy areas) were located quite far (*c*. 800 m) from the perching sites of the barn owls, and one may hypothesize that the main hunting range of the owl hardly reached these areas.

The relationship between age structure in samples of a given prey species in barn owl pellet remains and in population samples of the same species trapped in the field has been explored by different authors

(Castro & Jaksic 1995, Dickman *et al.* 1991, Hanney 1963, Sinclair *et al.* 1990). Tooth wear is generally considered as a good estimator of age, but it could be misleading when one wants to compare samples from different time periods when food and other environmental conditions influencing it may differ. Various skull and tooth characters have been used in rodents to try to assess age variation more precisely than with molar wear, especially in studies dealing with predation: cranial dimensions (Blem *et al.* 1993 in *Microtus* spp; Castro & Jaksic 1995 in *Phyllotis darwini*), tooth measurement (Zalewski 1996 in *Clethrionomys glareolus*), or qualitative craniodental characters (de Oliveira *et al.* 1998 in *Bolomys lasiurus*). Lidicker & MacLean (1969) also showed that a series of cranial (including mandible) and body measurements enabled to estimate the age of *Microtus californicus* individuals more accurately than previously observed, based on tooth wear, in *Mus musculus*. In Malawi, Hanney (1963) used palatilar length from *M. natalensis* skulls as (1) this measurement proved to correlate well with head and body length in a sample of autopsied individuals, and (2) the palate is often intact in skulls from pellets, so that large sample sizes can be achieved. Here, we preferred to retain mandible length as the best age-related measurement (as in Sinclair *et al.* 1990). Indeed, murid mandibles are often relatively well preserved in pellets (Bruderer & Denys 1999). Moreover, it is larger than the palatine bone, and, in practice, was easier to measure with accuracy. Finally, MdL proved to correlate very well with tooth wear, both in seasonal and overall analyses. Using additional skull measurement may have improved slightly the precision of these estimations, but to the detriment of sample sizes as mandibles were by far better preserved than skulls.

The procedure here applied to extrapolate MdL-classes from body masses of the CMR-trapped *M. huberti* individuals may have introduced some bias, linked to the fact that this MdL-body mass relationship was built from a sample of *M. huberti* belonging to another population rather than the target one. Nevertheless, it has to be underlined that the relationship between MdL and mass was established from a fair sample of individuals, which were caught in the same kind of environmental conditions as the ones prevailing at the study site in the Inner Delta of the Niger River (i.e. mostly rice-growing areas), and not very far from it (i.e. mostly the Canal du Sahel area, less than 200 km west of our study site). The high coefficient of correlation found between these two variables makes the building of MdL classes from body mass distribution of CMR-caught individuals a sufficiently robust procedure to further compare MdL distributions in this live-trapped population and the pellet samples.

Another potential bias associated with comparisons between age structure in pellet samples and in live-trapped population samples lies in the fact that the former result from the accumulation of materials over a certain period while the second represent a snapshot at a given moment. In our case, pellet samples could theoretically contain prey hunted during the previous three to four months. However, the good state of preservation of most of the intact pellets collected suggests that they were relatively recent. The damaged (and thus possibly older) pellets used for increasing the skull samples on which tooth wear estimation as well as skull and dental measurements were based always represented a minority (less than 5% except in October 2000: 43%). Thus, one can reasonably think that the age-structure pattern deduced from skulls recovered from pellets provides a good estimate of the age structure of the prey population in the few weeks preceding each collection of pellet samples.

Overall, variation in the age structure of the *M. huberti* prey samples matches results obtained in the course of the CMR programme: mostly young individuals in March, following the main period of reproduction during the first part of the dry season; a mixed population in June (end of the dry season), with the proportion of young individuals varying according to the length of the reproductive period; and mainly old individuals in October at the end of the wet season and flood peak of the Niger River, when reproduction has stopped and large areas are flooded (Granjon *et al.* 2005). However, the clear differences in MdL distributions observed most of the time between pellet and CMR samples (see Figure 3) strongly suggest a preferential consumption of young *M. huberti* by the barn owl. This trend is especially conspicuous for periods when the proportion of young is rather low in the population, which is usually the case in October (Granjon *et al.* 2005). At that period, reproduction has ceased and the spatial extent of available habitat for rodents is declining due to the flood of the Niger River. The younger individuals would then occupy less-favourable habitats in which they are more vulnerable to predation from the air. This scenario has been shown by Dickman *et al.* (1991) in an island population of *Mus domesticus* preyed upon by the barn owl. On an interspecific level, the higher predation risk incurred by smaller species of gerbils confined to more open habitats via competition with larger species has also been shown in various cases (Granjon *et al.* 2002, Kotler *et al.* 1988, Ziv *et al.* 1995). Ille (1991) has also demonstrated that barn owls would choose the smaller prey more frequently when confronted with a choice between increasingly larger prey items. This is the case in the October population of *M. huberti* in the Inner delta of the Niger River, when the average body mass may reach 60 g (Granjon *et al.* 2005). A trapping bias where younger animals would be less likely to be captured than older ones could be an alternative explanation for the different age structure in pellets and traps. This is unlikely however, as very young individuals (of less than 15 g) have been trapped at a frequency coherent with the demographic

cycle of the species, either in the 2000–2003 period (see Figure 6 in Granjon *et al.* 2005), or in the 2003–2004 period when other sites were monitored in this area using a similar protocol (Granjon *et al.* unpubl. data).

Here we showed that: (1) *Mastomys huberti* was by far the dominant prey species of the barn owl, except when its abundance falls below a rather low threshold and (2) the barn owl showed a possible trend towards the consumption of smaller (thus younger) than average individuals of *M. huberti*. This nearly constant predation pressure may have other, more indirect, negative effects on *M. huberti* dynamics, as suggested or demonstrated in various other cases (Dickman *et al.* 1991, Mohr *et al.* 2003, Vibe-Petersen 2003). The maintenance of barn owls in this area where terrestrial predators of rodents have been widely extirpated should be encouraged.

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