Major decline of bat abundance and diversity during the last 50 years in southern Belgium.

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ABSTRACT. In order to identify long-term population trends in bats in southern Belgium, we compared results of winter bat banding between 1939 and 1952 to winter bat counts between 1995 and 2008 in 58 hibernacula.

The results show a strong decrease in the populations of *Rhinolophus ferrumequinum*, *R. hipposideros, Barbastella barbastellus, Myotis dasycneme* and *M. myotis*. In contrast *M. daubentoni* and *M. mystacinus/brandtii/alcathoe* show a numeric increase between these time periods.

The bat diversity within these hibernacula has decreased by half over the last fifty years.

KEY WORDS : Chiroptera, long-term trend, Belgium

INTRODUCTION

Whilst it is generally accepted that bat populations in Western Europe have declined markedly, the detailed figures on each species' decline over several decades are seldom available. An accurate historical record is, however, indispensable to enable the circumscription of any changes that may have come about, and then to allow conservation goals to be set in their wake (FAIRON, 1967; DAAN & GLAS, 1980; RANSOME, 1989; LESIÑSKI et al., 2005).

Although local studies have been conducted on some sites in Wallonia (FAIRON, 1977; HUBART, 1993; FAIRON, 1999; FAIRON, 2001) or some species have undergone more in-depth investigation at the regional scale (FAIRON et al., 1982; FAIRON 1997; FAIRON & BUSCH, 2003), only a single recent publication (LAMOTTE, 2007) has compiled old and recent data for the Walloon Region. Based on a comparison of distributional ranges and species richness on a 10 by 10km grid across the region's entire territory, it is suggested that most of the species' ranges have shrunk. Yet this geographical approach does not account for numerical differences in sizes of populations (JOSEPH & POSSINGHAM, 2008).

The aim of this paper is to document changes that have occurred in bat populations hibernating in fifty-eight underground roosts in the Walloon Region by comparing banding data from the period 1939-1952 with data obtained recently from censuses conducted between 1995 and 2008.

MATERIALS AND METHODS

The study published by FRECHKOP (1955) is a major source of historical information about the composition of bat populations that hibernate in Belgium's underground cavities. It describes the banding of bats (n=6,809 individuals) at 229 sites in Belgium, of which 195 are located in the Walloon Region. One of the authors (J.V.) banded a quarter of these bats.

Among these 195 sites of the Walloon Region, we did not include sites that satisfied one of the following five criteria:

- sites whose names and locations were not sufficiently precise or explicit in order to avoid ambiguity and confusion between sites.
- vast roosts where it was practically impossible to band the entire bat population (examples are Montagne-Saint-Pierre, Orp-Jauche, and Folx-les-Caves).
- roosts that were not underground sites.
- roosts that have been destroyed between the two survey periods.
- roosts for which insufficient recent census data were available, despite supplemental surveying done for the purpose of this comparison.

In light of these constraints, we were finally able to compare data for 58 roosts (Table 1). Some major current hibernation roosts for bats in the Walloon Region were not specifically indicated in the old counts. These were the underground quarries of La Malogne in Mons, Le Grand Banc at Comblain-au-Pont, La Montagne Saint-Pierre at Visé, and a few slate quarries in the Upper and Middle Ardennes.

Most of the roosts that we chose (48/58 sites) are natural karst formations. They are distributed, by natural

region, as follows (Fig. 1): 43 in Condroz and Calestienne; 9 in Famenne; 4 north of the rivers Sambre and Meuse; and one each in Ardennes and Lorraine.

The old data extracted from FRECHKOP's (1955) study consisted of the number of individuals of each species that were banded or recaptured in a roost during a winter. Even though a major banding effort was made, a very powerful light was used, and all the tricks for capturing highly inaccessible individuals were employed (VER-SCHUREN, 2001), the possibility that the technique for exploring such cavities has improved over the decades cannot be ruled out (GILSON & MOËS, 1982; FAIRON, 1999). Despite under-estimation being plausible, we assumed that the number of individuals banded was considered to be the total number of observed individuals. Only later were the populations' waning numbers, then the impact of banding, and finally the need to protect these mammals (FAIRON, 1981; VERSCHUREN, 2001) ascertained.

Banding in each roost was generally conducted in multiple years. As species composition and numbers of each species varied considerably between years, we decided to use the maximum number of individuals that were banded for each species annually in each roost between 1939 and 1952. If banded and recaptured individuals were present simultaneously, both numbers were added to yield the total value used.

Recent data came from the observers network of Natagora's Plecotus Working Group and the Walloon Region's Nature and Forests Department's personnel. No individual was handled during these recent winter censuses. As for the older data, roosts where counts were conducted over several winters were described by the maximum number of individuals counted during any one of the annual censuses between 1995 and 2008. Although this way of regrouping the maxima might be seen as distorting reality, it was the only way to make a comparison that was as objective as possible.

The statistical analyses of trends concerning taxa, species richness and diversity were carried out using the Wilcoxon signed rank test. Kruskal-Wallis test was also used to test trends among ecological regions and cavity type. The other statistical analyses were performed by ANOVA-2.

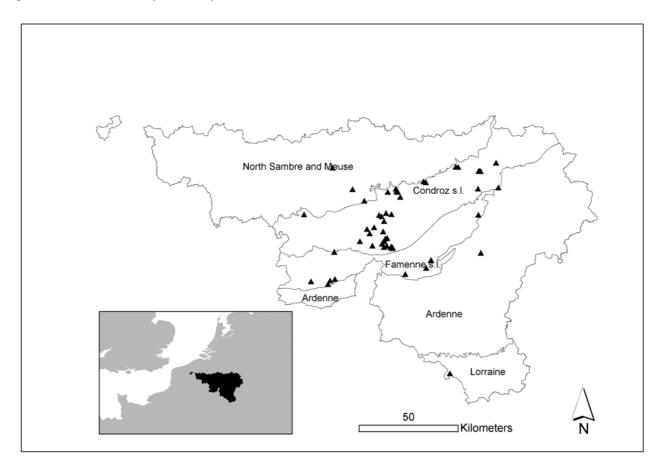


Fig. 1. - Distribution map of underground roosts inventoried in the Walloon Region.

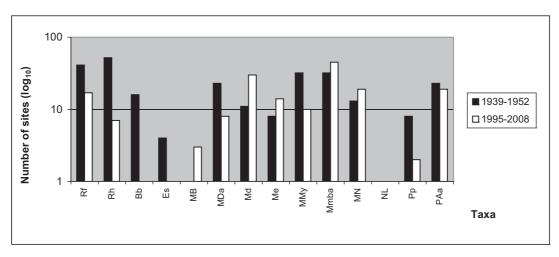


Fig. 2. – Number of roosts occupied by each taxon in 1939-1952 and 1995-2008. Taxa acronyms are explained in Table 3.

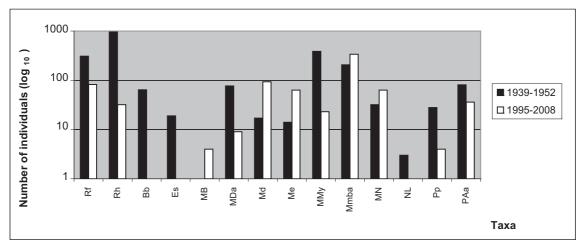


Fig. 3. – Maximum number of individuals of each taxon counted in the 58 roosts in 1939-1952 and 1995-2008. Taxa acronyms are explained in Table 3.

TABLE 1

List of the 58 underground roosts inventoried in the Walloon Region. Geographical coordinates are given in the 1972 Belgian Lambert system.

Name in Frechkop (1955)	Present name	X	Y	Ecoregion	n Cavity type	
Laroche en Ardenne - souterrain	Mine de Plomb à Laroche en Ardenne	236460	97910	Ardenne	artificiel	
Brumagne - tunnel	Tunnel de Brumagne à Maizeret	193840	128870	Condroz s.l.	artificiel	
Falaën - ruines du Château de Montaigle	Ruines du Château de Montaigle à Anhée	180310	107620	Condroz s.l.	artificiel	
Flavion - trou des Nutons	Trou des Nutons à Flavion	175350	103629	Condroz s.l.	artificiel	
Landelies - abbaye d'Aulne	Souterrains de l'Abbaye d'Aulne	147262	117181	Condroz s.l.	artificiel	
Philippeville - souterrain	Souterrains de Philippeville	162430	98410	Condroz s.l.	artificiel	
Warnant-Salet - souterrain	Carrière souterraine des Poules à Warnant- Salet	182623	110688	Condroz s.l.	artificiel	
Anseremme - grotte de Colébi	Grotte Margaux à Anseremme	187520	100720	Condroz s.l.	karstique	
Anseremme - grotte Moniat	Trou du Vivier à Anseremme	187779	103660	Condroz s.l.	karstique	
Ben-Ahin - trou de la Truite	Trou de la Truite à Ben-Ahin (Huy)	207500	133950	Condroz s.l.	karstique	
Ben-Ahin - trou du Renard	Trou du Renard à Bas-Oha (Wanze)	208660	133429	Condroz s.l.	karstique	
Ben-Ahin - trou Manto	Trou Manto à Ben-Ahin (Huy)	208690	133389	Condroz s.l.	karstique	

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Name in Frechkop (1955)	Present name	Х	Y	Ecoregion	Cavity type
Bouvignes - Trou Madame	Trou Madame à Dinant	187110	108580	Condroz s.l.	karstique
Burnot-lez-Profondeville - Trou du Curé	Trou du Curé à Burnot-lez-Profondeville	185130	116940	Condroz s.l.	karstique
Chaleux - chantoir des Sources	Galerie des Sources à Hulsonniaux (Houyet)	191380	100730	Condroz s.l.	karstique
Chaleux - trou de la Naulette	Trou de la Naulette à Hulsonniaux (Houyet)	190950	100650	Condroz s.l.	karstique
Comblain-au-Pont - grotte	Grotte de l'Abîme à Comblain-au-Pont	235009	130250	Condroz s.l.	karstique
Dinant - grotte de	Grotte la Merveilleuse à Dinant	188180	104940	Condroz s.l.	karstique
Dinant - grotte jardin Casino	Grotte du Casino à Dinant	189160	105220	Condroz s.l.	karstique
Engihoul - grotte des végétations	Grotte aux Végétations à Yvoz-Ramet (Flémalle)	225050	141250	Condroz s.l.	karstique
Engihoul - grotte Lyell	Grotte Lyell à Ehein (Engis)	223740	141309	Condroz s.l.	karstique
Furfooz - grotte de la Gatte d'Or	Grotte de la Gatte d'Or à Furfooz (Dinant)	191880	100260	Condroz s.l.	karstique
Furfooz - puits des Vaux	Puits des Vaulx à Furfooz (Dinant)	191669	100440	Condroz s.l.	karstique
Furfooz - trou de la Machoire	Trou de la Machoire à Furfooz (Dinant)	191910	100310	Condroz s.l.	karstique
Furfooz - trou des Nutons	Trou des Nutons à Furfooz (Dinant)	191930	100420	Condroz s.l.	karstique
Furfooz - trou Louis	Trou Louis à Chaleux-Furfooz (Houyet)	191130	100800	Condroz s.l.	karstique
Furfooz - trou qui fume	Trou qui fume à Furfooz (Dinant)	191900	100440	Condroz s.l.	karstique
Godinne - grotte Chauvaux	Grotte inférieure de Chauvaux à Mont- Godinne (Yvoir)	186320	116279	Condroz s.l.	karstique
Goyet - grottes de	Grottes préhistoriques de Goyet à Mozet (Gesves)	195779	126089	Condroz s.l.	karstique
Hastière-Lavaux - grotte du pont d'Arcole	Grotte du Pont d'Arcole à Hastière	181750	101389	Condroz s.l.	karstique
Lives - souterrain	Trou de l'Eau à Lives (Namur)	189490	128540	Condroz s.l.	karstique
Lustin - trou d'Haquin	Trou d'Haquin à Maillen (Assesse)	188570	117860	Condroz s.l.	karstique
Pont-à-Lesse - trou de la Tour à Samson	Grotte Roger à Thon-Samson (Andenne)	194509	128580	Condroz s.l.	karstique
Pont-à-Lesse - Trou Magritte	Trou Magritte à Dinant	188940	101330	Condroz s.l.	karstique
Remouchamps - grotte	Grotte de Remouchamps à Sougné- Remouchamps (Aywaille)	245339	130789	Condroz s.l.	karstique
Sosoye - trou des Nutons	Trou des Nutons à Sosoye	178990	109810	Condroz s.l.	karstique
Tilff - grotte Brialmont	Grotte Brialmont à Tilff (Esneux)	236339	139080	Condroz s.l.	karstique
Tilff - grotte Dumonceau	Grotte de Monceau à Esneux	235380	139229	Condroz s.l.	karstique
Tilff - grotte Ste-Anne	Grotte Saint-Anne à Tilff (Esneux)	235840	139100	Condroz s.l.	karstique
Trooz - grotte	Grottes préhistoriques de Fond-de-Forêt à Forêt (Trooz)	244180	143310	Condroz s.l.	karstique
Waulsort - grotte de Freyr	Grotte de Freyr	186559	102349	Condroz s.l.	karstique
Waulsort - trou des Moines	Trou des Moines à Waulsort	186800	102430	Condroz s.l.	karstique
Yvoir - orphelinat	Grotte Toulemonde à Yvoir	187619	113809	Condroz s.l.	karstique
Yvoz-Mailen - trou Balza	Trou Balza à Maillen (Assesse)	191309	117319	Condroz s.l.	karstique
Bomal - Hohière, grotte	Grotte de Hohière à Heyd (Durbuy)	235229	117019	Famenne s.l.	karstique
Couvin - abîme	Trou de l'Abîme à Couvin	159305	82100	Famenne s.l.	karstique
Han s-Lesse - grottes	Grotte de Han à Han-sur-Lesse (Rochefort)	208860	90269	Famenne s.l.	karstique
Honnay - grotte de Revogne	Grotte de Revogne à Honnay (Beauraing)	198350	87230	Famenne s.l.	karstique
Lompret - grotte	Grotte de Lompret	150750	83500	Famenne s.l.	karstique
Nismes - grotte	Grotte du Pont d'Avignon à Nismes (Viro- inval)	162735	84714	Famenne s.l.	karstique
Petigny - grotte de l'Adugeoir	Grotte de l'Adugeoir / grotte de Neptune à Couvin	160339	83879	Famenne s.l.	karstique
Rochefort - grotte de	Grotte touristique de Rochefort à Roche- fort	211259	94169	Famenne s.l.	karstique
Rochefort - trou Maulin	Grotte du Nou-Maulin à Rochefort	211300	94300	Famenne s.l.	karstique
Orval - ruines de l'Abbaye	Souterrains de l'Abbaye d'Orval	220851	36972	Lorraine	artificiel

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Name in Frechkop (1955)	Present name	Х	Y	Ecoregion	Cavity type
Marche-les-Dames - mines de fer	Galerie de Férauge à Marche-les-Dames	193520	130190	Nord sillon Sambre et Meuse	artificiel
Villers-la-Ville - abbaye	Ruines de l'abbaye à Villers-la-Ville	161520	140850	Nord sillon Sambre et Meuse	artificiel
Floreffe - grottes de	Grotte touristique de Floreffe	177602	124062	Nord sillon Sambre et Meuse	karstique
Spy - grotte de	Grotte de Spy	171699	129969	Nord sillon Sambre et Meuse	karstique

TABLE 2						
Comparison of old and recent counts						

	Old survey	Recent survey
Survey periods	1939-1955	1995-2008
Objective	ringing	census
Number of census	192	266
Average number of census per cavity	3.3 +/- 2.2	5.3 +/- 4.5
Number of individuals	2190	748
Number of taxa	13	12
Average species richness per cavity	4.5 +/- 2.8	3.0 +/- 2.4
Average species diversity per cavity	1.4 +/- 1.2	0.7 +/- 0.9

RESULTS

Whereas in the earlier period the 58 roosts were covered by a total of 192 censuses, the recent observations came from 266 censuses (Table 2). On average, each roost was visited 3.3 times during the earlier period compared with 5.3 times during the recent period.

The older data were composed of 2,190 banded or recaptured individuals belonging to thirteen different taxa. The recent data concerned 748 individuals belonging to twelve different taxa. One species, Bechstein's bat (*Myotis bechsteini*), was observed during the recent period only, whereas two species – *Barbastella barbastellus* and *Nyctalus leisleri* – were no longer encountered recently (Table 2). Moreover, not a single bat was found in eight of the fifty-eight roosts visited recently.

The 58 roosts that were selected cover around 11% of the hibernating bats counted annually in the Walloon Region in recent years (n=about 6,600 for 2005, SPW-DGARNE database).

The mean species richness by roost was 4.5 species during the first census period and dropped to 3.0 for the recent period (F=9.59, p<0.01; Wilcoxon signed rank test, p<0.001). Moreover, the species diversity index (as defined by Shannon-Weaver) fell from 1.4 to 0.70 (F=12.71, p<0.01; Wilcoxon signed rank test, p<0.001).

The two periods were compared by testing numbers for each taxon (Table 3) by a the Wilcoxon signed rank test, as well as species richness and diversity site by site. A bivariate non-parametric Kruskal-Wallis test was used to test potential breakdown by ecological region and type of cavity (natural versus man-made).

Changes in numbers of sites occupied and numbers of individual encountered by species before 1953 and after 1994 are shown in Figs 2 & 3. Whereas 309 *R. ferrume-quinum* were banded in these roosts before 1953, only 82 specimens were observed recently.

R. hipposideros used to be the most abundant species hibernating in the underground cavities, with nearly a thousand individuals and accounting for more than 43% of the banded bats. In the recent survey, only 32 individuals were counted, which is about 3.4% of the previous number of individuals.

B. barbastellus showed an even more severe decline: a total of 64 individuals were formerly counted in the roosts studied, whereas not a single individual was found recently in these roosts.

The population of *M. dascyneme*, a migratory species that is present in Wallonia almost exclusively during the hibernation period, declined significantly: Whereas 77 individuals were banded previously, only 9 individuals were counted recently.

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Comparison of the number and proportion of each bat species in the two survey periods.

Species	Acro- nyms	total number 1939- 1952	total number 1995- 2008	propor- tion 1939- 1952	propor- tion 1995- 2008	Paired differ- ence in median	P Wil- coxon ranked signed test	cavity type (natural vs artificial cavity)	ecoregion
Rhinolophus ferrumequi- num (Schreber, 1774)	Rf	309	82	14,1%	11,0%	-3,00	P < 0,001	ns	ns
Rhinolophus hipposideros (Bechstein, 1800)	Rh	953	32	43,5%	4,3%	-10,50	P < 0,001	ns	ns
Barbastella barbastellus (Schreber, 1774)	Bb	64	0	2,9%	0,0%	-3,00	P < 0,001	ns	ns
<i>Eptesicus serotinus</i> (Schreber, 1774)	Es	19	1	0,9%	0,1%	-2,00	ns	ns	ns
<i>Myotis bechsteini</i> (Kuhl, 1817)	MB	0	4	0,0%	0,5%	1,25	ns	ns	ns
Myotis dasycneme (Boie, 1825)	MDa	77	9	3,5%	1,2%	-2,50	P < 0,001	ns	ns
Myotis daubentoni (Kuhl, 1817)	Md	17	93	0,8%	12,4%	2,00	P < 0,001	ns	ns
Myotis emarginatus (Geof- froy, 1806)	Me	14	63	0,6%	8,4%	0,75	P = 0,100	ns	ns
Myotis myotis (Borkhausen, 1797)	MMy	387	23	17,7%	3,1%	-3,00	P < 0,001	ns	ns
<i>Myotis mystacinus</i> (Kuhl, 1817) / <i>M. brandti</i> (Evers- mann, 1845) / <i>M. alcathoe</i> Helversen & Heller, 2001	Mmba	206	338	9,4%	45,2%	2,00	P = 0,001	ns	P < 0,001
<i>Myotis nattereri</i> (Kuhl, 1817)	MN	32	63	1,5%	8,4%	0,50	ns	ns	ns
<i>Nyctalus leisleri</i> (Kuhl, 1817)	NL	3	0	0,1%	0,0%	-	ns	ns	ns
Pipistrellus sp. Kaup, 1829	Рр	28	4	1,3%	0,5%	-1,50	ns	ns	ns
<i>Plecotus auritus</i> (Linné, 1758) / <i>P. austriacus</i> (Fischer, 1829)	PAa	81	36	3,7%	4,8%	-1,00	P < 0,05	P = 0,038	ns
Total		2190	748	100,0%	100,0%				

Twenty-three individual specimens of *M. myotis* have been seen in recent years compared with 387 in the past, and the proportion of this species in the counts has fallen off sharply, from 17.7 to 3.1%.

In contrast to these declines, numbers of some species increased significantly during the second survey period: counts of *M. daubentoni* and *M. emarginatus* increased from 70 to 93 individuals and from 14 to 63 individuals respectively.

A net rise was also observed for the number of *M. mystacinus/brandtii/alcathoe*: from 206 to 338 individuals. Whereas this species complex accounted for less than 10% of the bats that were banded in the past, it now accounts for almost half of the bats observed. This rise is not uniform across the territory and has occurred predominantly north of the Sambre and Meuse valleys.

Plecotus auritus and *P. austriacus* are declining: their abundance is halved after 50 years. Preferential occupancy of man-made cavities has been ascertained only for these taxa.

The small numbers of *M. bechsteini*, *M. nattereri*, and *Nyctalus leisleri* that are generally counted in the winter

make it impossible to draw significant conclusions concerning their demographic change. Data about *Eptesicus serotinus* and *Pipistrellus sp.* were not taken into consideration since these taxa do not tend to hibernate in underground cavities but are found more readily in crevices in buildings.

DISCUSSION

Our comparison of the total number of bats seen in the fifty-eight roosts studied both in the past and in recent years shows that total numbers have nearly been divided by 3, despite the fact that the number of censuses made recently was higher and benefited from improved detecting techniques. In addition, species richness and diversity showed a remarkable decrease.

The availability or accessibility of hibernation roosts in the Walloon Region and contiguous regions has changed over the past fifty years. Several sites were destroyed, notably by the extension of quarries or filling of entrances, but new sites were made available thanks to the cessation of various human activities or through active bat protection measures (LAMOTTE, 2007). Similarly, the size of the natural karst network accessible to bats increased over this period due to the activities of cavers to unblock passages, thereby creating new possibilities for hibernation in natural environments. One cannot rule out the possibility that the trends documented here result to a certain extent from a change in the availability of hibernation roosts and a redistribution of bat populations amongst them. However, this can only partially explain the trends in populations of *Chiroptera*. Otherwise, each taxon's proportion in the various roosts studied would have remained relatively stable, which is clearly not the case. What is more, the geographical comparison carried out by LAMOTTE (2007) using a much larger corpus than the data gleaned from the fifty-eight roosts analysed here does not reveal a change in the taxa's spatial distributions on the regional scale that could explain the variations seen locally.

This study confirms, quantitatively and on the regional scale, the findings of a number of other studies on this subject. Quantitative comparison between these old and recent data shows, for many species, major declines in numbers of individuals in persisting hibernation roosts. The species concerned in particular by this trend are *B. barbastellus, R. ferrumequinum, R. hipposideros, M. myotis,* and *M. dasycneme.*

In addition to the harmful consequences of disturbing hibernating individuals as a result of human activities, such as underground exploration and/or touristic visits (FAIRON, 1967; SPEAKMAN & RACEY, 1989; SPEAKMAN et al., 1991; THOMAS, 1995), including the banding of the specimens, many other factors have been suggested to explain the declines in the populations.

Apart from hibernacula disturbance, many other factors presumably impact resident bat populations: road traffic collision (LEMAIRE & ARTHUR, 1998), nocturnal light (ARLETTAZ et al., 2000; RICH & LONGCORE, 2005), decline of major insect prey species such as cockchafers for instance, disturbance in summer roosts.

R. ferrumequinum, for example, demands summer roost requirements. Its decline, which has also been underlined by FAIRON (1997), can be linked to the decrease of its preferred prey species such as *Aphodius rufipes* dung beetles, cockchafers, tipulids (RANSOME & HUTSON, 2000) in the Walloon Region (DELAHAYE & KERVYN, 2001). Antiparasitic treatment of cattle presumably negatively affects the abundance of *Aphodius rufipes* beetles, the only prey species upon which the greater horseshoe bat feeds in late summer (RANSOME & HUTSON, 2000). A negative impact of banding also needs to be considered for this species (VERSCHUREN, 2001; DIETZ et al., 2006).

Like *R. ferrumequinum*, *R. hipposideros* is particularly vulnerable when hibernating, given its hanging position from the ceiling of its roosts. FAIRON (1977) had already underlined some forty years ago *R. hipposideros's* sensitivity to recapture throughout the banding period and the mortality that could ensue. What is more, given its hunting strategy, which consists in flying constantly under the forest canopy or under the cover of hedges, *R. hipposi*

deros coped with a drastic reduction in the accessibility of its hunting grounds due to the destruction of the network of hedges and tree alignments in the Walloon landscape (MOTTE & LIBOIS, 2002; SCHOFIELD, 2008). Further research needs to be carried out on the impact of pesticide contamination and light pollution on this species (BON-TADINA et al., 2008). The latter could play a major role in food competition with the commonest species in Europe, the pipistrelle bat (ARLETTAZ et al., 2000).

The reasons *B. barbastellus* has almost disappeared from the Walloon Region (FAIRON & BUSCH, 2003) have not yet been elucidated. Nevertheless, its great sensitivity to disturbance, even in its forest summer roosts (RUSSO et al., 2004), must be underlined, as well as this species' highly selective diet (RYDELL et al., 1996; SIERRO & ARLETTAZ, 1997; SIERRO, 2003).

Causes for *M. dasycneme*'s decline have not yet been identified with certainty, although major changes in hunting habitats and a drop in the number of optimal summer roosts are suspected (LIMPENS et al., 2000).

The apparent increase of *M. emarginatus* could be attributed to methodological issues. It is plausible that banders previously under-estimated its presence because of its habit of clustering at the highest points of the ceilings in the underground cavities where it hibernates, i.e. where temperature is slightly higher. Given the small number inventoried, no clear statements about the evolution of the numbers of this species can be made.

Decline in the *M. myotis* population is most likely also due to the decline of some of its identified key prey species in the Walloon Region (KERVYN, 1996;). Limited accessibility to the vast summer roosts required by this species likely had an impact as well and is probably more important than that of the availability of optimal hunting grounds (GÜTTINGER, 1997). However, the detection of prey on its hunting grounds by this ground-gleaning bat could be hindered by noise, traffic noise especially (SCHAUB et al., 2008).

The decline of long-eared bats (*P. auritus / P. austriacus*) is probably also related to reduced roosts and prey availability. Further research needs to be carried on these species in order to monitor whether these two sibling species have similar ecological requirements and conservation status.

The taxa whose numbers apparently increased, i.e M. *daubentoni* and M. *mystacinus/brandtii/alcathoe*, are remarkable given that, over the past fifty years, they have become the most frequently observed taxa in underground cavities during winter. The possibility that the apparent increases in these taxa – which tend to hibernate in deep, narrow crevices – result from improved census techniques cannot be ruled out (FAIRON, 1999). Improved diagnostic criteria could also explain the increased abundance of M. *daubentoni* in recent counts (GILSON & MOES, 1982). Finally, the rise in the M. *daubentoni* population could be linked to eutrophication of aquatic habitats (WARREN et al., 2000), which is likely to increase the availability of Chironomidae that are consumed in great quantities by this species (BECK, 1995).

CONCLUSIONS

This long-term comparison of hibernating bat populations shows major changes that occurred in the composition of the bat community in Wallonia. The populations of five species have declined, whereas those of two others have increased. The fifty percent loss of species diversity observed in this study is both a reflection of the far-reaching ecosystem deterioration in the Walloon Region and the source of considerable change in the way these ecosystems function.

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