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Species composition, spatial distribution and population dynamics of bats hibernating in Wisłoujście Fortress, Polish Baltic Sea Coast (Chiroptera: Vespertilionidae)

Skład gatunkowy, rozmieszczenie przestrzenne i dynamika populacji nietoperzy zimujących w Twierdzy Wisłoujście na polskim Pobrzeżu Bałtyku (Chiroptera: Vespertilionidae)

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Abstract. The structure and dynamics of bat assemblage in winter and transitional period was studied in the Wisłoujście Fortress (16th–19th century) located in Gdańsk city, northern Poland. The object was used partially as a commercial store (until 1995), later as a summer tourist attraction, protected in winter from human penetration. Serious threats for existance of this monument forced recently the local officials to the intensive renovation project, leading to deterioration of roosting conditions for bats. In total, nine species were recorded: *Myotis myotis*, *M. nattereri*, *M. mystacinus*, *M. brandtii* (rare in Pomerania region), *M. dasycneme* (EN in Poland), *M. daubentonii*, *Eptesicus serotinus*, *Pipistrellus nathusii* (first winter record in Poland) and *Plecotus auritus*. *M. daubentonii* predominated among bats counted in autumn (43.4%) and netted in the entrances to the casemates (60%). *M. nattereri* was the most numerous species during winter (67.3%) and spring censuses (71.0%). *M. dasycneme* composed 3.5% of all bats counted inside of the Fortress (n=2256 records) but about 18% of individuals captured in mist nets (n=67). Only 8–12 bats were counted during winter 1993/1994. The number of bats increased significantly ($r=0.86$, $p<0.02$) until 2005, reaching the total number of 313 individuals in the whole object; however this trend was severely interrupted by restoration works. The adaptation of formerly unprotected roost in the Fortress area (installation of bat grill, walls of air-bricks etc.) compensated this decline only in a limited way. In winter 2002/2003 we studied seasonal dynamics in bats' numbers. The highest number of *M. daubentonii* and *M. dasycneme* was recorded in September. The number of *M. nattereri*, after a peak in a half of September, declined almost to zero in October and increased again, reaching its maximum value in February. Natura 2000 site was established in the Wisłoujście Fortress, although its future remains uncertain.

INTRODUCTION

Several species of vespertilionid bats of the temperate zone spend winter in underground roosts maintaining optimal thermal conditions and humidity (Althringam 1996). Such roosts are mainly natural caves, widely distributed in mountain and upland areas. However, almost no shelters of that kind are available in the lowlands of Central Europe, thus many species need to hibernate

in their anthropogenic substitutes: cellars (Lesiński et al. 2004), wells (Bernard et al. 1998) and – among the most important – various military structures, often considered as historical monuments (Bogdanowicz 1983, Urbańczyk 1990, Bernard et al. 1991, Fuszara et al. 1996, Hebda & Nowak 2002, Sachanowicz & Zub 2002). The latter ones may serve as crucial sites for taxonomically rich bat assemblages, consisting of unusually large numbers of individuals (e.g. Urbańczyk 1990). Forts, castles, air-raid shelters, bunkers and tunnels of underground factories make an oportunity for long-therm monitoring of bat populations (Urbańczyk 1989), similar to that conducted in caves and abandoned mines of upland areas (for comparision see:

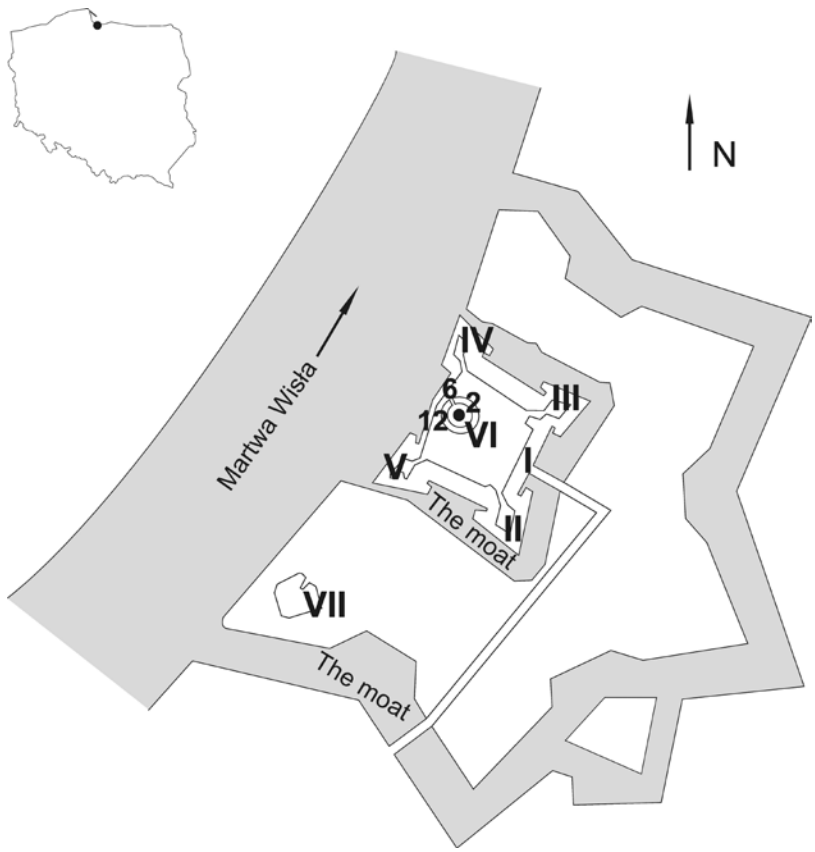

Fig. 1. Plan of the Wisłoujście Fortress. Explanations: I – the guard room of the postern tunnel, II – The Południowo-Wschodni (South-Eastern) Bastion, III – The Ostroróg Bastion, IV – The Artyleryjski (Artillery) Bastion, V – The Furta Wodna Bastion, VI – The Wreath (Arabic numbers refers to the controlled cellars), VII – the powder-magazine of The Eastern Entrenchment. Objects I–VI are parts of the Fort Carré.
Rys. 1. Plan Twierdzy Wisłoujście. Objaśnienia: I – wartownia poterny, II – Bastion Południowo-Wschodni, III – Bastion Ostroróg, IV – Bastion Artyleryjski, V – Bastion Furta Wodna, VI –Wieniec (cyfry arabskie odnoszą się do kontrolowanych piwnic), VII – prochownia Szańca Wschodniego. Obiekty I–VI stanowią część Fortu Carré.

Kowalski & Lesiński 1991, Weinreich & Oude Voshaar 1992, Řehák & Gaisler 1999). Although selection of roosts by some bat species in military objects is well known recently (Bogdanowicz & Urbańczyk 1983, Lesiński 1986), the factors affecting their population dynamics remained unexplained, even if patterns of this dynamics were described in many localities (Bagrowska-Urbańczyk & Urbańczyk 1983, Fuszara & Kowalski 1995, Fuszara et al. 1996). Several constructions have stopped to serve for military purposes just in the recent times, they became utilized commercially, abandoned or demolished; restoration works are started in some of them in order to save their historical values, however causing serious threats for wintering bats (e.g. Mitchell-Jones 2004). In contrast, unguarded sites are often under a serious pressure of uncontrolled human penetration, intensifying spontaneous bat arousals (Thomas 1995) or even acts of vandalism (Mitchell-Jones 2004). Thus, intensity of human disturbance in bat hibernacula may vary in space and time, however no case studies were published to document any effects of this factor on bat numbers.

The Polish Baltic Sea Coast is the area of special biogeographic significance. It is known not only as an important bat migratory path (Jarzembowski 2003), but also as a northern limit of distribution for some European species (Baagøe 2001, Güttinger et al. 2001, Bogdanowicz & Ruprecht 2004). However, the state of knowledge about distribution and size of winter bat colonies in that region remains insufficient, restricted only to a small portion of available underground constructions (Jarzembowski et al. 2000, Wojtaszyn et al. 2001, Dzięgielewska 2002). No detailed informations were published regardind bat hibernation in one of the most valuable monuments of military architecture – 16th-century Wisłoujście Fortress (Gdańsk City). Scattered data from transitional periods revealed significance of the object for some species recognized as endangered in Poland (*Myotis dasycneme* – Ciechanowski & Przesmycka 2001) or extremely rare in the region (*Myotis brandtii* – Ciechanowski & Sachanowicz 2003). Single winter records of only four species have been published until recently (Jarzembowski et al. 2000, Ciechanowski & Przesmycka 2001, Ciechanowski & Kokurewicz 2004).

The aim of this study was to describe the structure of bat assemblage using the Wisłoujście Fortress during winter and transitional period, as well as long-term and seasonal changes in the number of bats roosting in the monumental military object. The additional goal of the following paper was to document the effect of temporally varying human disturbance on the largest bat hibernaculum of Polish Baltic Sea Cost.

STUDY AREA AND HISTORY OF THE SITE

The Wisłoujście Fortress is located in the Gdańsk city, northern Poland (18° 40’ 43” E, 54° 23’ 39” N). Geographically, it lies in the eastern part of Baltic Sea Coast region – a border between Vistula Spit and Żuławy Wiślane (delta of the Vistula river). The main object – Fort Carré – was built in the 16th century, as a sea-fortress protecting the port of Gdańsk. It is composed of four Bastions: Południowo-Wschodni (South-Eastern), Ostroróg, Artyleryjski (Artillery) and Furta Wodna. They contain large casemates, built of bricks and covered by earth embankements. The lateral walls of the bastions are built of bricks and stones as well. The fortress was built almost on the sea level, thus neither the casamates nor most of the remaining bat hibernacula are the typical underground roosts, however the thick, brick walls made them well insulated, at least before the main renovation works in 2004–2005. Originally, the casemates were opened on the lateral sides, however the secondary walls were built in these openings in the 20th century, making the insides dark and partially free of frost; the effect was increased when wooden doors were installed in the main casemate gates. The remaining bat hibernacula of the Fort Carré are small cellars under the officers’ houses in so called Wreath and small guard-room in the fort’s postern. Outside of the central fort, the belt of external earthwork fortifications (The Eastern Entrenchment) was built in the 17th

century, enriched by the 19th century powder-magazine. The latter object, containing the narrow corridor with some ventilation shafts in the ceiling, maintain a significant bat hibernaculum as well. In February, the casemates and cellars were relatively cool (mean=3.7 °C, SD=2.2, range 0.6–9.0 °C, n=33) and moderately humid (mean=66.9%, SD=10.4, range 39.0–81.0%, n=19), although these figures may poorly reflect conditions inside of the crevices or ventilation shafts. Mean external temperature in the same period amounted 2.8 °C (SD=4.3, range –7.0–8.0 °C, n=8) (authors' unpublished data).

Both Fort Carré and The Eastern Entrenchment are surrounded by wide moats, filled by brackish waters from neighbouring Martwa Wisła – the dead branch of the Vistula River. Vegetation on The Eastern Entrenchment consists of shrubs, as well as unmanaged tree stand of maples *Acer platanoides*, old, partially dying black poplars *Populus nigra* and lane of monumental horse-chestnuts *Aesculus hippocastanus*. The earthworks of Fort Carré were densly overgrown by *Lycium halimifolium*, removed completely in 2003. The moat banks are covered by scattered beds of *Phragmites australis* and *Schoenoplectus tanbaermontani*.

The Wisłoujście Fortress was demilitarised after the First World War and heavily demolished in 1945. After a partial restoration it was used extensively as a store of paints, windows and vegetable preserves. The vertical ventilation shafts were closed by concrete plates or even fulfilled with soil and rubble what increased an insulation of internal parts of the casemates. The monument faced an increasing devastation as an effect of sea waves, penetration of walls by moat waters, precipitation of salt and air-polution by neighbouring "Siarkopol" company, which stored and processed large amounts of sulphur. Deep crevices appeared in the walls and ceilings of all casemates of Fort Carré, causing a serious threat to the buliding, although – both with loose fragments of plaster – maintaining crucial bat shelters during hibernation. After 1995, the Fortress stopped to be used as a commercial store. The monument, managed by The City of Gdańsk History Museum, became utilised only in summer, as a seasonal tourist attraction. The Fort Carré remained closed and guarded in winter, contrary to the powder magazine of the Eastern Entrenchment, facing uncontrolled human penetration and disturbance.

The Fortress was included on the list 100 most endangered cultural monuments by World Monument Watch in 2000–2001; the situation of the site resulted in starting of wide-scale restoration projects. First renovation works were performed since September 2003, in the same period, when bats used to aggregate in winter roosts. They included archeological excavations, prospecting drillings and removal of earth embankements in Bastion Artyleryjski, as well as temporary opening of ventilation shafts in all bastions (the latter was performed in October). In the same period the Fortress became recognized as an important bat site by Polish Ministry of Environment (established as Special Area of Protection PLH 220037 in Natura 2000 European network). All works were stopped during the winter 2003/2004, while the ventilation shafts were closed provisionally (with spreadsheets of plastic foil) after an intervention of environmental officials. Restoration started again in spring 2004, resulting in fulfillment of all crevices in internal walls of Bastion Artyleryjski with cement; in summer 2005 they became completely covered with desalination compress. The small room in its casemates was separated from their remaining parts with a provisional synthetic curtain (only in winter 2004/2005). Additionally, a secondary wall in South-Eastern Bastion was partially removed in 2005, resulting in appearance of ice-cover in one of the corridors. All works were stopped for the two last winter periods. As a partial compensation for negative results of renovation works, the powder-magazine of the Eastern Entrenchment was modified in order to increase its capacity as bat hibernaculum. Its entrance was closed with bat grills (Mitchell-Jones 2004), while walls of air bricks and water reservoir were built inside in summer 2005.

MATERIAL AND METHODS

All four bastions of the Fort Carré and cellar no. 12 of the Wreath were checked every February between 2000 and 2006 (7 checks). In winter season 2002/2003 these objects were checked every month (since September until April), in order to reveal seasonal dynamics in the number of bats (9 checks). Additional objects (cellars no. 2 and 6, guard-room of the postern tunnel) were checked irregularly until 2005, when all potential bat hibernacula in the Fortress area were controlled for the first time. Fort Carré was controlled also 5 times in winter 1993/1994 (December–March), on 27 November 1999, three times in the autumn

2003 (29 October, 18 September, 19 December) and on 8 April 2006. The powder-magazine of the Eastern Entrenchment has been checked during every visit since September 2003. In total, 28 controls of the Fortress were conducted between 1993 and 2006.

During each visit all visible bats were counted in the controlled objects, including those hidden in deep crevices and ventilation shafts. Potential shelters were checked using torches and head-lamps. We avoided handling of bats, except for species needing a careful examination of dental features or taking some measurments (*Pipistrellus* spp., *Myotis mystacinus*, *Myotis brandtii*).

Five times (6 October 2000, 21 October 2000, 14 September 2002, 14 September 2003, 15 October 2006) a mist netting was performed at the entrances of bastions of the Fort Carré. Two or four ECOTONE mist nets were set up since dawn until midnight. Captured bats were determined to the species, sexed, aged (in the case of *M. daubentonii* – RICHARDSON 1994), weighed and their forearms measured prior to release.

RESULTS

In total, nine bat species were recorded in autumn-spring period: Large mouse-eared bat *Myotis myotis* (Borkhausen, 1797), Natterer's bat *Myotis nattereri* (Kuhl, 1817), Whiskered bat *Myotis mystacinus* (Kuhl, 1817), Brandt's bat *Myotis brandtii* (Eversmann, 1845), Pond bat *Myotis dasycneme* (Boie, 1825), Daubenton's bat *Myotis daubentonii* (Kuhl, 1817), serotine *Eptesicus serotinus* (Schreber, 1774), Nathusius' pipistrelle *Pipistrellus nathusii* (Keyserling et Blasius, 1839) and brown long-eared bat *Plecotus auritus* (Linnaeus, 1758). Among them, *M. nattereri* was the most numerous, with a significant share of *M. daubentonii* (Table 1). Both species were found during almost every control since the beginning of the study. *M. dasycneme* appeared to be the third most numerous species, amounting not more than 5.2% of all bats, but regularly encountered since its first winter observation on 11 February 2002. Single *M. myotis* appeared irregularly (10 February 2001, 17 April 2003) until 2004, when it became a permanent element of bat assemblage wintering in Fort Carré. The remaining species were noted only sporadically: *P. auritus* (29 October 2003, 19 December 2003, 24 February 2004, 18 February 2005), *E. serotinus* (21 November 2002, 21 January 2003, 18 February 2005), *M. mystacinus* (1 male, 21 November 2002: Bastion Ostroróg), *M. brandtii* (1 female, 17 April

Table 1. The number and percentage of bat records from Wisłoujście Fortress. Autumn: 14 IX – 20 XII, winter: 21 XII – 20 III, spring: 21 III – 17 IV
Tab. 1. Liczba stwierdzeń i udział procentowy gatunków nietoperzy w Twierdzy Wisłoujście. Jesień (autumn): 14 IX – 20 XII, zima (winter): 21 XII – 20 III, wiosna (spring): 21 III – 17 IV

species	autumn		winter		spring		total	
	n	%	n	%	n	%	n	%
Myotis myotis	2	0.3	10	0.7	4	1.4	16	0.7
Myotis nattereri	225	37.6	927	67.3	198	71.0	1350	59.8
Myotis mystacinus	1	0.2	–	0.0	–	0.0	1	<0.1
Myotis brandtii	–	0.0	–	0.0	1	0.4	1	<0.1
Myotis dasycneme	31	5.2	41	3.0	8	2.9	80	3.5
Myotis daubentonii	260	43.4	239	17.3	50	17.9	549	24.3
Eptesicus serotinus	1	0.2	2	0.1	–	0.0	3	0.1
Pipistrellus nathusii	–	0.0	1	0.1	–	0.0	1	<0.1
Plecotus auritus	1	0.2	2	0.1	–	0.0	3	0.1
indeterminate	78	13.0	156	11.3	18	6.5	252	11.2
total	599	100.0	1378	100.0	279	100.0	2256	100.0

Table 2. The number and species composition of bats hibernating in Wisłoujście Fortress, counted on 18.02.2005. Explanations: I – the guard room of the postern tunnel, II – The Południowo–Wschodni (South-Eastern) Bastion, III – The Ostroróg Bastion, IV – The Artyleryjski (Artillery) Bastion, V – The Furta Wodna Bastion, VI – cellars of the Wreath, VII – the powder-magazine of The Eastern Entrenchment
Tab. 2. Liczebność i skład gatunkowy nietoperzy zimujących w Twierdzy Wisłoujście dnia 18.02.2005. Objaśnienia: I – wartownia poterny, II – Bastion Południowo-Wschodni, III – Bastion Ostroróg, IV – Bastion Artyleryjski, V – Bastion Furta Wodna, VI – piwnice Wieńca, VII – prochownia Szańca Wschodniego

species	I	II	III	IV	V	VI			VII	total	%
						12	2	6			
M. myotis	–	2	–	–	–	–	–	–	2	4	1.3
M. nattereri	3	53	8	143	13	3	2	4	18	247	78.9
M. dasycneme	–	10	–	–	–	–	–	–	1	11	3.5
M. daubentonii	–	11	2	2	4	–	–	–	11	30	9.6
E. serotinus	–	1	–	–	–	–	–	–	–	1	0.3
P. auritus	–	1	–	–	–	–	–	–	–	1	0.3
indeterminate		4	4	3	1	1	1		5	19	6.1
total	3	82	14	148	18	4	3	4	37	313	100.0
number of species	1	6	2	2	2	1	1	1	4	6	–

2003: Bastion Artyleryjski) and *P. nathusii* (1 male, 16 February 2003: Bastion Furta Wodna). In total 2256 bat records were noted (Table 1) and 313 bats were counted maximally in the whole Fortress (Table 2).

The species composition varied in time. In autumn, *M. daubentonii* predominated, but in winter and spring *M. nattereri* was a dominating taxon. The proportion of *M. daubentonii* compared to *M. nattereri* was significantly higher in autumn than in winter (Chi-square test with Yates' correction, $\chi^2=176.50$, $p<0.0001$), in autumn than in spring ($\chi^2=73.85$, $p<0.0001$), but did not differ between winter and spring ($\chi^2=0.00$, $p>0.9$).

The total number of hibernating bats in the Fortress has changed significantly since 1994. After closing of the commercial stores it began to increase progressively ($r=0.86$, $p<0.02$; $y=-41415.7626+20.7553957x$) until 2005, when it reach the maximum. This trend was interrupted only in winter 2003/2004, when first renovation works, excavations and prospecting drillings were performed in autumn. However, a year later, the number of bats roosting in the Fort Carré dropped about 77% in association with removal of secondary wall in South-Eastern Bastion and covering of the walls with desalination compress in Artillery Bastion. Although the number of bats counted in newly adapted powder-magazine of the Eastern Entrenchment increased almost twice, it did not compensate a population decline in the remaining objects.

Hibernating bats were unevenly distributed in the Fortress area, with 85% of the assemblage concentrated in just three objects. The highest species richness was observed in South-Eastern Bastion and powder-magazine of the Eastern Entrenchment, while the highest number of individuals appeared in the Artillery Bastion. Only a few bats were noted in the remaining six objects (Table 2). With respect to the species composition, the first two objects appeared to be the most vaulable bat hibernacula, where most individuals of *M. dasycneme* spend winter and mate in autumn (observations of copulating pond bats in 2002). Progressing restoration works strongly affected the spatial distribution of bats. After their first stage in 2003, performed in the autumn, bats number decreased more than one third in the Artillery Bastion, but increased in the South-

-Eastern Bastion (Fig. 3). However, the fulfillment of crevices in the Artillery Bastion did not cause any decline of bats number in the next winter season (2005). Moreover, they aggregated almost all in one place – a small chamber, separated by a plastic curtain, where three, large clusters of *M. nattereri* (59, 51 and 17 individuals) hanged directly on its walls and composing a majority (88%) of all bats wintering in this bastion. Such a behaviour was formerly unknown in the Fortress, where most of the animals hibernated hidden in ceiling cracks, dispersed among several, smaller clusters. Only after the second stage of restoration works, bats almost completely abandoned the Artillery Bastion, where not only crevices were filled, but also the temporary curtain was removed (Fig. 4).

The number of bats varied strongly through the season as well (Fig. 5). The largest aggregations of *M. daubentonii* appeared in early September. Contrary to the winter period (see above), they did not hide in the crevices, but covered the ceilings and walls of ventilation shafts in dense clusters. The number of *M. daubentonii* declined visibly in the third decade of September, later increasing again, but not reaching the earlier level. It remained relatively stable between October

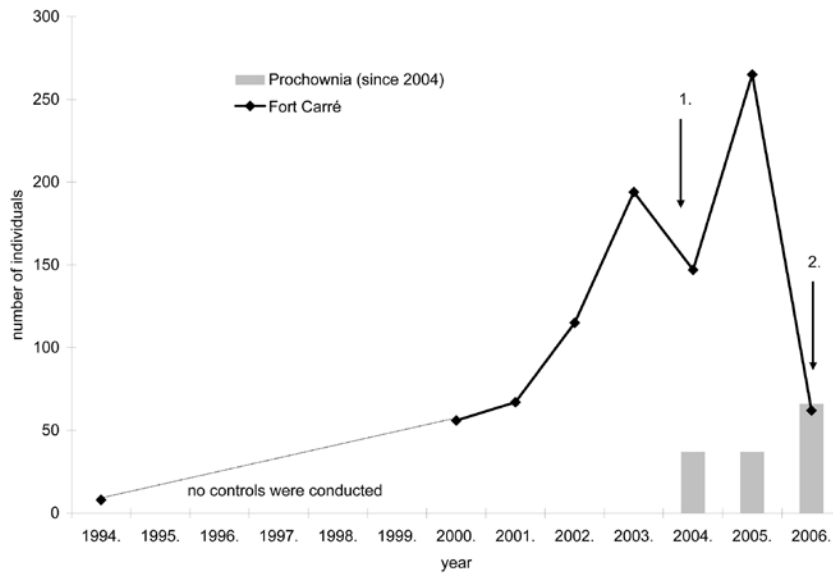

Fig. 2. Long-therm changes in the number of bats hibernating in the Wisłoujście Fortress in 1994–2006, based on February counts. Explanations: 1. Autumn works in Artillery Bastion (prospecting drillings, archeological excavations, opening of ventilation shafts, removal of earth embankements); 2. Summer renovation works (fulfillment of crevices and laying of desalination compress on walls in Artillery Bastion, partial removal of secondary wall in South-Eastern Bastion).

Rys. 2. Długoterminowe zmiany liczebności nietoperzy zimujących w Twierdzy Wisłoujście (lata 1994–2006), w oparciu o liczenia w lutym. Objaśnienia: 1. Jesienne prace w Bastionie Artyleryjskim (wiercenia rozpoznawcze, wykopaliska archeologiczne, udrożnienie przewodów wentylacyjnych, usunięcie nasypów ziemnych znad sklepienia); 2. Letnie prace remontowe (wypełnienie szczelin i pokrycie kompresem odsalającym wewnętrznych ścian Bastionu Artyleryjskiego, częściowe usunięcie wtórnego zamurowania w Bastionie Południowo-Wschodnim).

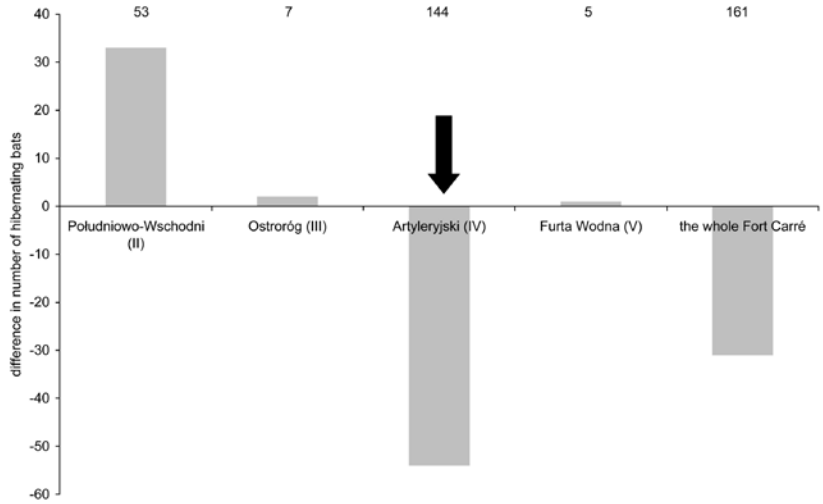

Fig. 3. Effect of works conducted in Artillery Bastion in autumn 2003 on bats number in particular parts of Fort Carré, expressed as a differrence in bat number between December 2002 and 2003.
Rys. 3. Wpływ prac prowadzonych w Bastionie Artyleryjskim jesienią 2003 na liczebność nietoperzy w poszczególnych częściach Fortu Carré, wyrażony jako różnica w liczbie osobników między grudniem 2002 i 2003.

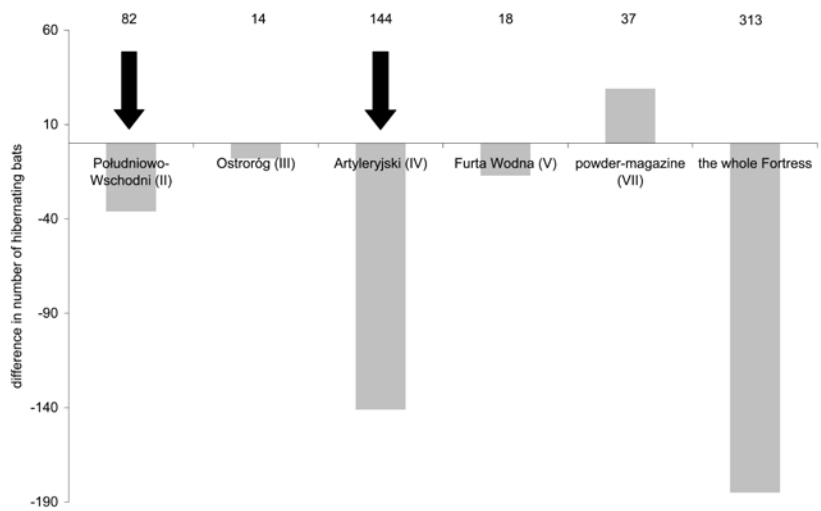

Fig. 4. Effect of works conducted in Artillery and South-Eastern Bastions in 2005 on bats number in particular parts of Wisłoujście Fortress, expressed as a differrence in bat number between February 2005 and 2006.
Rys. 4. Wpływ prac prowadzonych w Bastionach Artyleryjskim i Południowo-Wschodnim w roku 2005 na liczebność nietoperzy w poszczególnych częściach Twierdzy Wisłoujście, wyrażony jako różnica w liczbie osobników między lutym 2005 i 2006.

Table 3. The species and sex composition of bats netted in autumn in the entrances of casemates and powder-magazine of the Wisłoujście Fortress
Tab. 3. Skład gatunkowy i struktura płciowa nietoperzy odławianych w sieci jesienią przy wylotach z kazamat i prochowni Twierdzy Wisłoujście

species	males	females	total	%
Myotis myotis	1	2	3	4
Myotis nattereri	8	3	11	16
Myotis mystacinus	1	–	1	1
Myotis dasycneme	10	2	12	18
Myotis daubentonii	24	16	40	60
total	43	22	67	100

and February, decreasing finally in spring. A similar seasonal dynamics was revealed by *M. dasycneme*, however basing on a very small sample (n=39 records). The number of *M. nattereri* – after an early peak in the beginning of season – dropped almost to zero in October. However, it increased about 60 times until January, exceeding the number of *M. daubentonii* already in the late autumn. The highest number of *M. nattereri* was recorded in March (declining almost six times in the next month), but the highest total number of bats – in February.

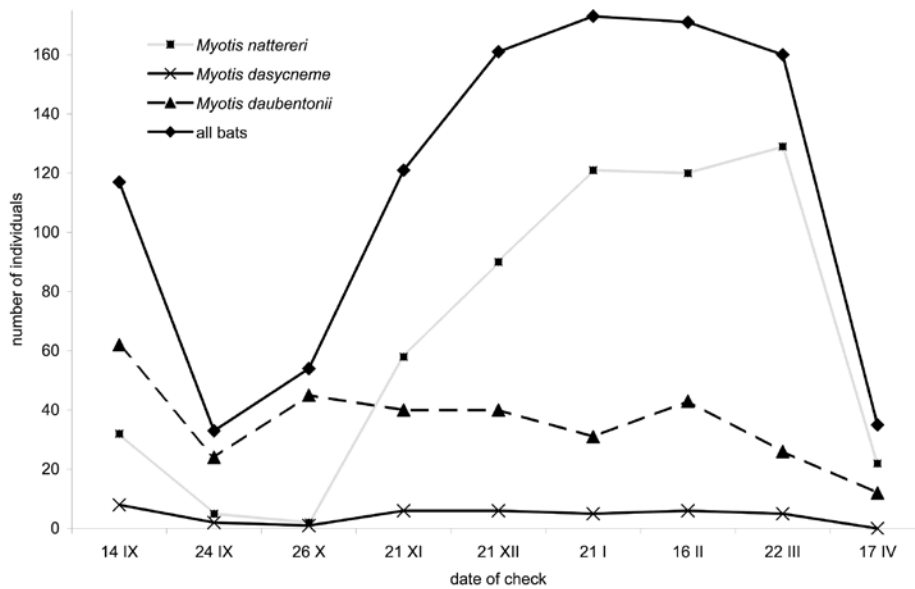

Fig. 5. Seasonal dynamics in the number of bats roosting in Wisłoujście Fortress in winter 2002/2003.
Rys. 5. Sezonowa dynamika liczebności nietoperzy wykorzystujących Twierdzę Wisłoujście jako kryjówkę zimą 2002/2003.

Among bats netted in the autumn (n=67), *M. daubentonii* predominated, but the high percentage of *M. dasycneme* (18%) was noticeable (Table 3). Most captured individuals were males, however a sex ratio did not differ significantly from 1:1 (χ^2=2.74, p>0.09). Among *M. daubentonii* 31 juveniles (yearlings) and 9 adults were captured; difference from 1:1 age ratio was statistically significant (χ^2=5.41, p=0.02). When the mist netting was conducted, several individuals of small *Myotis* were observed flying inside of casemates.

DISCUSSION

The number of bats roosting in the Wisłoujście Fortress during winter period placed it among the largest bat hibernacula in the Polish Baltic Sea Coast, at least in some seasons. Only one site – ruins of amunition factory in Police near Szczecin – appears larger, accumulating more than 1300 hibernating individuals (K. Drabińska, J. Żejmo, M. Dzięgielewska in Kepel et al. 2005). About 200 individuals were counted maximally in the castle of Teutonic Knights in Malbork (Stec & Kasprzyk in Kepel et al. 2005) and 120–150 individuals in bunkers of Kołobrzeg-Stadion and Szczecin-Zdroje (Wojtaszyn et al. 2001, Dzięgielewska 2002). No other bat hibernaculum located in Gdańsk city has ever been used by more than 90 animals (Jarzembowski et al. 2000).

Among the species recorded in Wisłoujście, some of them are of special significance, even if only exceptionaly encountered. *M. brandtii*, although considered as widely distributed in Poland, is extremely rare in the northern part of the country. It is only the second known locality of this species in the Baltic Sea Coast region (Ciechanowski & Sachanowicz 2003). *P. nathusii* is a long-distance migrant, known to leave Central Europe for winter and hibernating in hollow trees or houses located in milder climate of western Europe (Strelkov 1969). The Wisłoujście Fortress is the first known winter site of *P. nathusii* in Poland and quite an unusual type of hibernaculum, although the recent winter record of the species from Czech Republic is also associated with a similar object (a castle cellar, Benda & Hotový 2004). Among the regular inhabitants of the Fortress, *M. dasycneme* should be considered as the most interesting species. Regarded as globally vulnerable (Hutson et al. 2001) and nationally endangered (Wołoszyn 2001), it is included in Annex II of EU Habitat Directive, justifying designation of Natura 2000 site in Wisłoujście Fortress. Polish hibernacula do not concentrate large numbers of *M. dasycneme*. Its share in winter bat assemblages usually do not exceed 0.5% (Bagrowska-Urbańczyk & Urbańczyk 1983, Lesiński 1986, Kowalski & Lesiński 1991, Fuszara et al. 1996) and even in some large brick forts no pond bats are encountered (Bogdanowicz 1983, Fuszara & Kowalski 1995, Hebda & Nowak 2002). Wisłoujście Fortress is one of the largest winter sites of *M. dasycneme* in Poland, along with Fort Osowiec in Biebrza River Valley (at maximum 34 individuals – Lesiński & Kowalski 2002) and four other localities (including three fortification complexes), each concentrating no more than 6–15 individuals (Ciechanowski & Kokurewicz 2004, T. Kokurewicz in litt.). In fact, the real number of pond bats roosting in the Fortress can be even higher, what may be presumed from regular captures of *M. dasycneme* in autumn and observations of some individuals hiding deeply in narrow crevices. Bogdanowicz (1983) stated that *M. dasycneme* avoided winter quarters located in heavily urbanized areas, thus being a bioindicator of the changes in a habitat subjected to urbanization pressure. This hypothesis can recently be rejected, as the Wisłoujście Fortress – intensively used by this species both in autumn and winter – is located on the edge of densely populated city, where two large chemical factories have polluted the neighbouring area since 1969.

The species composition of bats wintering in Wisłoujście Fortress differed from that recorded in the other large, brick forts of Poland. In central and northeastern part of the country, forts are inhabited mainly by a barbastelle *Barbastella barbastellus* (Schreber, 1774) composing 50.8% of all bats (Fuszara et al. 1996). Also in the forts of Nysa (Lower Silesia) barbastelle is the most numerous species (Hebda & Nowak 2002), while in the forts of Poznań it composed at least 14.1–20.9% of winter bat colonies (Bogdanowicz 1983). Barbastelle is an oligothermophilous species, hibernating in 0.0–3.0 °C (Bogdanowicz & Urbańczyk 1983) and large forts are considered rather cool roosts with intensive air circulation (due to many entrances and windows), what explains high numbers of *B. barbastellus* spending winters there. Thus, the lack of any barbastelles hibernating in Wisłoujście Fortress seems astonishing, however the species does not occur anywhere in Gdańsk (Jarzembowski et al. 2000) and it is a very rare bat in the whole Pomerania region (Kowalski & Szkudlarek 2003). Instead, the winter bat assemblage of the studied locality is dominated by moderately thermophilous species, i.e. *M. nattereri* and *M. daubentonii*. However, they are known to find shelters in the deep, highly located crevices and ventilation shafts (Bogdanowicz & Urbańczyk 1983, Lesiński 1986), where the temperature may be significantly higher and more stable than in the corridors themsleves.

Low number of bats in the period, when object was intensively used as a commercial store, confirms their sensibility to repetitive disturbance (light, noise) during hibernation (Thomas 1995). Later increase in bat numbers appeared similar to that observed in roosts newly opened for these animals, e.g. the old mines, where exploitation came to an end (Lutsar et al. 2000, Bihari 1998 in Güttinger et al. 2001). Also in winter quarters, where bats were intensively banded, their numbers increased several times after the end of marking programm (Lesiński 1990, Řehák & Gaisler 1999). Spatio-temporal dynamics of bat numbers in the Wisłoujście Fortress suggest however, that human pressure restricted only to the part of fortification complex forced at least some bats to change roost for the nearest available, not to leave completely the area. Movements among hibernacula in one and the same winter season (apparently associated with flying outside) were reported during some banding programmes (Bogdanowicz & Urbańczyk 1983, Gaisler et al. 2003). Bats may change their shelter not only directly due to the human activity, but its subsequent effects on internal conditions. At least some elements of restoration works (removal of secondary wall, opening of ventilation shafts) might strongly affect microclimate in the casemates, causing bats not only hiding deeper in the crevices (reaction observed frequently in *M. daubentonii* when ambient temperature decreased – Kokurewicz 2004), but also moving into unaffected parts of the Fortress. The latter behaviour can be compared with that recorded in *B. barbastellus* wintering in small, concrete bunkers and regularly moving from the upper floor to the dried wells in the coldest months (Sachanowicz & Zub 2002). Our observations showed however, that alternative roosts could only partially compensate the effect of human pressure on hibernaculum, likely due to unpredictable character of this factor.

The phenology of bat occurrence in Fortress resembles that observed in the other fortifications of lowland Poland. *M. daubentonii* is a bat appearing earlier in the undergrounds that *M. nattereri* and the highest numbers of this species are observed in the autumn, decreasing later during winter months (Bagrowska-Urbańczyk & Urbańczyk 1983, Jurczyszyn 1998). However, the mentioned peak in the number of Daubenton's bats was reported a bit later – from October (Lesiński 1986, Fuszara & Kowalski 1995, Fuszara et al. 1996) or even from November (Jurczyszyn 1998). Thus, the mass occurrence of *M. daubentonii* in the Fortress in September is worth noticing, possibly representing a short-therm phenomenon shifting in time among years – we observed it on 14 September 2002 but not on 18 September 2003. The species composition

of bats netted in autumn resembled that recorded inside of the casemates, although it may not represent the latter ones (they remained in a deep torpor) but the animals visiting the Fortress in order to take part in a swarming behaviour (sensu Parsons et al. 2003). Several individuals of *M. daubentonii* visited the Modlin Fortress near Warsaw even in August, however they number dropped almost to zero in the first week of September and increased again. Most of the individuals appearing then in Modlin remained active, flying inside of the forts, and only 4% of bats ringed in the autumn (including those found in lethargy) stayed there in winter (Lesiński 1990). Thus it was possible that high numbers of *M. daubentonii* roosting in the Fortress in September did not refer to the animals counted later in mid-winter but to the bats using the site as a transitional shelter during autumn movements.

Contrary to *M. daubentonii*, the maximum numbers of *M. nattereri* in hibernacula are usually observed in mid-winter, mostly in January–February (Bagrowska-Urbańczyk & Urbańczyk 1983, Fuszara et al. 1996), sometimes in March (Fuszara & Kowalski 1995) or December (Jurczyszyn 1998). The earlier results are, thus, consistent with our observations, however an early peak in the number of Natterer's bats, revealed in the half of September, was recorded for the first time. These animals could also use the Fortress as a transitional roost, leaving it after a short time, what may be judged from the very low numbers of *M. nattereri* in October, confirmed also in the other sites (Lesiński 1986, Fuszara et al. 1996, Jurczyszyn 1998). There are almost no earlier studies to compare with our data on phenology of *M. dasycneme*. The two series of censuses conducted by Lesiński & Kowalski (2002) in northeastern Poland revealed the numbers of pond bats at least 2–10 times higher in November–December than in February. No such phenomenon was observed in Wisłoujście and the September peak in the number of *M. dasycneme* seems to reveal the same aspect of annual life cycle as in *M. nattereri* and *M. daubentonii*. It should be noted however, that some changes in the number of bats counted in underground hibernacula could be an artifact, unrelated to arrival or departure from roosts, but caused by movements of some individuals into the deep crevices (Jurczyszyn 1998). This effect in *M. daubentonii* was explained as a reaction to unfavorable thermal conditions (Kokurewicz 2004).

The future of the Wisłoujście Fortress as an important bat site remains uncertain. It would be hard to preserve such a large winter colony in the casemates of Fort Carré, because the prospecting restoration works – necessary to preserve the Fortress itself – will change the microclimate, as well as the number and quality of micro-shelters. Adaptation of the powder-magazine on Eastern Entrenchment may compensate these losses only in a limited way and there would be a need for a significant delay (about 2–4 years) in renovation of the South-Eastern Bastion, until more bats accept a new roost. The main purpose for the creation of Natura 2000 site on the Fortress' area – regular occurrence of *M. dasycneme* – seems possible to be maintained, as the powder-magazine became recently the most important shelter of this species (5 of 7 individuals were noticed there on 8 February 2006).

STRESZCZENIE

W latach 1994–2006 badaliśmy strukturę i dynamikę zgrupowania nietoperzy wykorzystujących Twierdzę Wisłoujście (Gdańsk, północna Polska) zimą i w okresach przejściowych. Obiekt, budowany w XVI–XIX wieku, do 1995 roku był częściowo użytkowany jako magazyny, w ostatnich latach zaś jako letnia atrakcja turystyczna, zabezpieczona przed ludzką penetracją w okresie zimowym. Poważne zagrożenia dla substancji zabytkowej Twierdzy, skłonily lokalne władze do intensywnej renowacji obiektu, co prowadzi jednak do obniżenia jego wartości jako kryjówki nietoperzy.

Łącznie na terenie Twierdzy stwierdzono 9 gatunków nietoperzy: nocek duży *Myotis myotis*, nocek Natterera *M. nattereri*, nocek wąsatek *M. mystacinus*, nocek Brandta *M. brandtii* (rzadki na Pomorzu), nocek łydkowłosy *M. dasycneme* (kategoria EN w Polsce), nocek rudy *M. daubentonii*, mroczek późny *Eptesicus serotinus*, karlik większy *Pipistrellus nathusii* (pierwsze w Polsce stwierdzenie zimowe) i gacek brunatny *Plecotus auritus*. Nocek rudy dominował wśród nietoperzy liczonych jesienią wewnątrz Twierdzy (43,4%) i odławianych w sieci przy wejściach do kazamat (60%). Nocek Natterera był najliczniejszym gatunkiem podczas liczeń zimowych (67,3%) i jesiennych (71,0%). Nocek łydkowłosy stanowił 3,5% wszystkich nietoperzy liczonych wewnątrz Twierdzy (n=2256 stwierdzeń), ale około 18% osobników odławianych w sieci (n=67).

Zimą 1993/1994 na terenie Twierdzy znajdowano zaledwie 8–12 nietoperzy. Łączna liczba tych zwierząt istotnie wzrastała do 2005 roku ($r=0,86$, $p<0,02$), osiągając wartość 313 osobników w całym obiekcie; jednak trend ten został przerwany na skutek prac renowacyjnych. Adaptacja wcześniej niechronionej Prochowni Szańca Wschodniego (instalacja kraty zabezpieczającej, ścian z cegły-dziurawki) tylko częściowo skompensowała spadek liczebności nietoperzy między latami 2005 i 2006.

Zimą 2002/2003 badaliśmy sezonową dynamikę liczebności nietoperzy. Najwięcej nocków rudych i nocków łydkowłosych odnotowaliśmy we wrześniu. Liczba nocków Natterera, po osiągnięciu szczytu w połowie września, spadła niemal do zera w październiku, po czym ponownie wzrosła, osiągając maksymalną wartość w lutym. Twierdza Wisłoujście uznana została za Specjalny Obszar Ochrony w sieci Natura 2000, jednak jego przyszłość, jako jednego z największych zimowisk nietoperzy na Pomorzu Gdańskim, pozostaje niepewna.

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