Summary of Professional Accomplishments

1. Name and Surname

Mateusz Ciechanowski

2. Diplomas or scientific degrees awarded, including the name, place and year of the award and the title of the PhD thesis:

29.06.2000 – **MSc in Biology**, Faculty of Biology, Geography and Oceanology, University of Gdańsk, MSc thesis: '*Bats (Chiroptera) of the Darżlubska Forest – species composition, selected aspects of ecology and morphometrics*', supervised by Prof. Dr hab. Bronisław W. Wołoszyn (Institute of Animal Systematics and Evolution, Polish Academy of Science).

2010 – **PhD in Biological Sciences: Biology**, Faculty of Biology, Geography and Oceanology, University of Gdańsk; PhD thesis: *"Spatial structure of the assemblage and dynamics of activity of bats (Chiroptera) in forest-agricultural landscape of northern Poland"*, supervised by Prof. Dr hab. Lech Stempniewicz (Department of Ecology and Zoology of Vertebrates, Faculty of Biology, University of Gdańsk).

3. Information on previous and current employment in research institutions:

15.01.2006 – present: **researcher and lecturer/assistant professor**; Department of Vertebrate Ecology and Zoology, Faculty of Biology, University of Gdańsk.

28.10.2004 – 30.01.2006: **research assistant**; Department of Vertebrate Ecology and Zoology, Faculty of Biology, University of Gdańsk.

4. Description of the Scientific Achievement set out in art. 219 § 1 point 1 of the Act on Degrees and Titles in Science and Arts from 20 July 2018 (Journal of Laws, 2020 no 85 with later amendments)

Habitat preferences of bats in a mosaic, anthropogenically transformed landscape

Introduction and hypotheses

The spatial use patterns and habitat preferences of animals are the focus of three main theories and concepts in ecology. The first of these is the optimal foraging theory, which tries

to predict the behavior of animals while obtaining food. Although a notable part of the hypotheses explaining the distribution of organisms is derived from it, its usefulness as a research program depends on six assumptions (e.g. Pyke 1984), which say that: 1) an individual's fitness depends on the behavior during foraging, 2) foraging behavior is at least partially heritable, genetically or culturally, 3) the relationship between foraging behavior and fitness is known and quantifiable, 4) the evolution of foraging is not prevented by genetic constraints, 5) the evolution of foraging is subject to functional constraints that may be realistically assessed, 6) foraging behavior evolve faster than the rate at which the factors that affect them change. Empirical tests of the assumptions of the original theory usually fall into four general categories, i.e. the type of food (diet composition), the choice of the habitat patch, the time after which the individual leaves the patch, and the frequency of movements between the patches. The fifth category of tests, sometimes distinguished, concerns central place foraging, i.e. a situation in which an animal uses the functional center of its home range, e.g. a nest, burrow or colony, from which it sets out for feeding grounds and to which it returns with at least a part of the collected food (Pyke 1984). The second pillar of the modern analysis of habitat selectivity is the concept of ideal free distribution (Fretwell and Lucas 1970), which predicts such a distribution of animals in a gradient of available resources that adopts the optimal pattern for each individual, without taking into account its modification by other factors, e.g. predation risk. This model is based on four basic assumptions that significantly simplify the scenarios observed in nature: 1) each individual can accurately estimate the resources, selecting the most abundant patches, which allows to maximize fitness, 2) each individual can freely move between the patches of habitats, without incurring any energy expenditure, 3) each individual has the same competitive abilities as other individuals, 4) the abundance and availability of resources does not change in any patch, so their production balances exploitation (Maszczyk 2008). The third element that makes it possible to place research on habitat selection in a broader theoretical framework is the ecological niche theory (Grinnell 1917, Hutchinson 1957), which places populations in a space described by resources and conditions that shape the range of ecological tolerance of a species (Holt 2009). This theory allowed to derive the concepts of resource partitioning that enable the coexistence of many different species in the same ecosystems (the history of the development of the concept and its current state was presented in Pocheville 2015). Since both natural factors and human activity lead to the formation of a mosaic landscape composed of patches of habitats that differ in terms of attractiveness to individuals that select them, all three of the above concepts are increasingly analyzed against the background of landscape

connections between adjacent ecosystems (Hanson et al. 1995). However, research on the habitat preferences of animals and their use of space are needed not only as exemplary models that allow to test theoretical ecological concepts, but also - as case studies - supplementing the knowledge of the biology of individual species, to the extent necessary for effective planning of their conservation.

Most terrestrial vertebrates with high locomotory abilities and large home ranges use a number of different habitat types in a mosaic landscape at the same stage of the life cycle, especially if they are food generalists. Such a resource use strategy is demonstrated especially by large carnivores (Gurarie et al. 2011) and ungulates (Allen et al. 2014), as well as by some animals endowed with the ability to fly actively, such as bats (Mackie and Racey 2007) and birds, especially raptors (Real et al. 2016) and aeroentomophages (Boynton et al. 2020). Since individual habitats differ in terms of their spatial structure and productivity, remaining within them may increase or decrease fitness of an individual, regardless of whether we consider the attractiveness of a given habitat as a source of food (foraging sites), water or essential minerals, as a shelter ensuring a favorable thermal balance, hiding against predators or a place of reproduction, and finally as a corridor ensuring free, safe and energetically optimal movements between patches of habitats performing the above-mentioned functions. Therefore, even the most opportunistic species with high locomotory abilities show clear habitat preferences in the mosaic landscape, making more intensive use of more attractive patches of habitats, while avoiding others (Sunde et al. 2014). However, these preferences can be modified in a result of interspecific competition (Reif et al. 2018), especially within assemblages that include a greater number of morphologically similar species (Katzner et al. 2003), precluding the interpretation of data on spatial behavior only in the light of optimizing foraging, thermal balance or limiting the risk of predation. In forest biomes, the fragmentation of habitats, and thus the mosaic nature of the landscape, increased significantly with the expansion of agriculture, and thus also with development of permanent settlements, resulting in an increase in infrastructure density (Bogaert et al. 2014). The consequence of this process was a decrease in the available area and connectivity of optimal habitats. Therefore, knowledge about the habitat preferences of individual species is nowadays one of the key elements necessary in contemporary nature conservation planning. Meanwhile, most species of birds and mammals still lack basic information on habitat and food preferences, or spatial behavior related to their use (IUCN 2021).

Habitat preferences of highly mobile animals may undergo strong changes in the annual cycle (Rehnus et al. 2013), which allows them to be adapted to the current energy needs, usually imposed by the reproductive status of an individual (Unterthiner et al. 2011), but also by the stage of seasonal migration, especially for long distance migrants (Lerche-Jørgensen et al. 2019). Therefore, the results of extrapolation of patterns of habitat and food preferences from the period of reproduction to other phenological periods may be highly biased, and establishing a full picture of resource use by a given species requires studies covering wider time windows or even the full annual cycle.

Bats (Chiroptera) occupy a unique position among small mammals due to their relatively large home ranges, compared to body size (Robinson and Stebbings 1997, Davidson-Watts et al. 2006, Mackie and Racey 2007, Flaquer et al. 2009). The ability to actively fly is responsible for this feature only partially – the home ranges of many bat species during the breeding period are many times bigger than the home ranges of small passerine birds of similar sizes during the nesting season (Whitaker and Warkentin 2010). However, they are comparable to the home ranges of much larger vertebrates, such as large predatory mammals (Kusak et al. 2005, Okarma et al. 2007) or birds of prey (Singh et al. 2015). As a consequence, bats can use a whole range of habitats with different functions during the day and night - daily roosts, feeding grounds, drinking sites, night roosts and corridors enabling their movement during the night (Lesiński 2006, Dietz et al. 2009). The ability to move quickly between various patches of habitats allows them to compare their resources in a relatively short time, bringing them closer to meeting the theoretical assumptions of the optimal foraging theory.

Strong attachment of lactating bats to breeding colonies, occupying daily roosts, where the young stay overnight, causes them to meet the assumptions of the central place foraging model (the time spent hunting in a given patch is positively correlated with the distance from the roost), even if they bring no part of their prey to the roost, but return there to feed their pups with milk (Daniel et al. 2008). Since pregnant females, and even males of some species, also live in colonies that occupy the same day roosts for a long time, to which they return almost every day (Henry et al. 2002, Safi et al. 2007), assumptions of the central place foraging model may be met in their case as well. As the energy demands of female mammals increase significantly in key stages of the reproductive cycle – pregnancy and lactation (Kunz 1974, Racey and Speakman 1987), it can be expected that also space use and habitat preferences are changing to meet those growing energy demand. The premise indicating such a possibility are significant differences in the size of home range and habitat preferences

between: 1) male and female bats during the reproductive period (Safi et al. 2007), and 2) females taking part in and not participating in breeding (Mackie and Racey 2007). If the used habitats serve as feeding grounds, such changes may also result in dietary change, which may act as an important adaptive function - an increase in percentage of more energetically profitable prey. As some bat species undertake long-distance seasonal migrations, they may appear during these migrations in areas where the landscape structure and habitat composition differ from those found in their summer range. As a consequence, the habitat preferences and space use of these mammals may also change significantly between the breeding season and the migration season. However, differences in habitat and food preferences between key phenological periods for many European bat species remain unrecognized. Moreover, even the so far available data on these elements of species' biology collected in the western part of Europe cannot be easily extrapolated to the conditions of the central and eastern part of the continent, mainly due to:

1) much lower degree of anthropogenic landscape transformation;

2) different climatic conditions (stronger continentalism);

3) a different landscape structure, especially in the young postglacial lakelands with much higher limnicity, which is manifested, for example, by differences in the diet of the noctule bat *Nyctalus noctula* between Great Britain (predominance of terrestrial insects; Jones 1995) and the Baltic countries (predominance of aquatic insects; Rydell and Petersons 1998);

4) more complex competitive relationships; e.g. a pair of morphologically similar species, *Pipistrellus pipistrellus* and *P. pygmaeus*, in Central Europe is accompanied by the much more numerous *P. nathusii*, while most research on the resource partitioning between the first two taxa has so far been carried out in the British Isles (Vaughan et al. 1997a; Russ and Montgomery 2002; Davidson-Watts et al. 2006; Nichols and Racey 2006; Sattler et al. 2007), where the third species did not even breed until recently.

Moreover, the role of various factors shaping the habitat mosaic shows great regional variation, but also variability over time. Most of the works to date indicate the importance of human activity as the main cause for diversification of the structure of landscape used by bats. However, in Central and Eastern Europe, other factors may also play an important role, including, at least locally, the expansion of European beaver *Castor fiber*, a keystone species and ecosystem engineer, significantly modifying the environment shared with bats (Rosell et al. 2005).

The basis of this habilitation dissertation is a series of five publications in peer-reviewed, international scientific journals, described below. The aim of the dissertation is to

determine the habitat preferences of bats in a mosaic landscape transformed by humans, in a specific Central European context, taking into account the influence of seasonal factors. The basic method, used today in research on the habitat use by insectivorous bats in various landscape types, is ultrasound detection. However, limiting ourselves to that method results only in exclusion of several species whose echolocation signals remain difficult or impossible to recognize, from the analyzes (Vaughan et al. 1997b, Walters et al. 2012), hence the need to supplement the study with radiotracking.

In my dissertation, I put forward the following main research hypothesis: the use of habitats by bats in a mosaic, human-transformed landscapes reflects not only their spatial structure, but remains a more complex phenomenon, not less dependent on the availability of food, stage of the life cycle, presence of the other, morphologically similar species within the assemblage and impact of keystone species that modify vegetation. Within it, I formulated the following partial hypotheses:

1. The most important feeding grounds of Central European insectivorous bats are deciduous forests, as well as water bodies (stagnant and running), i. e. the habitats considered to be characterized by the greatest availability of potential prey (paper 1).

2. Morphologically similar bats species of the genus *Pipistrellus* show patterns of resource partitioning, manifested by the selection of different habitats and low level of niche overlap (paper 1).

3. Water-surface foraging and trawling bat species select water bodies with the highest trophic state index or corresponding with their surface and structure to the needs of species-specific foraging tactics (paper 2).

4. The use of habitats as feeding grounds by insectivorous bats varies throughout the season, reflecting different energy demands at different stages of their annual cycle and/or the availability of specific prey taxa (papers 2 and 3).

5. In the temperate climate zone, the use of habitats and landscape structures avoided by bats in spring and early summer (pregnancy and lactation period) may increase significantly in late summer, due to the influx of individuals undertaking seasonal migrations or participating in dispersion after the reproductive period (paper 4).

6. The activity of the European beaver, leading to significant modification of habitats, mainly thinning of the tree stands and flooding (creation of ponds), increases the attractiveness of the small river valleys as foraging grounds for bats (paper 5).

Publications included in the Scientific Achievement – assumptions, methods, results and their discussion

1. **Ciechanowski M.** 2015. Habitat preferences of bats in anthropogenically altered, mosaic landscapes of northern Poland. European Journal of Wildlife Research 61(3): 415-428.

The insectivorous bats occurring in the temperate climate zone are an example of 'multi-habitat' animals - during their life cycle they use a number of different habitats that provide the functions of daily roosts, breeding sites, winter roosts, commuting routes, drinking and foraging sites. Despite significant plasticity in the choice of roost and foraging sites, as well as a broad spectrum of diet (Vaughan 1997), these mammals prefer some particular habitats during night-time activity (Vaughan et al. 1997a), including some prominent structures that appear only after heavy transformation of the landscape by humans, most notably tree lines (Verboom and Huitema 1997). Bats choose patches of landscape differing in land use, human modification, vegetation, geomorphology and underlying geology that all determine the productivity of an ecosystem and prey abundance (Threfall et al. 2012a, b). The aim of the first presented study was to investigate the habitat preferences of bats in the different landscapes of postglacial lakelands and coastal areas of the Gdańsk Pomerania.

The study was carried out in Gdańsk Pomerania (according to the definition by Markowski and Buliński 2004), within 69 randomly selected squares of the UTM 10 × 10 km grid (out of a total pool of 347 squares). In each of them, the evening recording of echolocation calls was carried out with the use of an ultrasound detector on a linear transect. Each transect was divided into sections assigned to one of the 36 distinguished habitat classes. The recorded echolocation calls were identified, as far as possible, down to the species level, with the help of the BatSound 3.31 bioacoustic program. The number of recorded bat passages in each habitat (use) was compared to the proportion of this habitat in the total length of all transects (availability). Habitat selection was tested based on the Z statistics with a Bonferroni correction (Byers et al. 1984). Breadth of habitat niche for every species was estimated using Levin's formula and niche overlaps between species using Pianka index (Przymuszny et al. 2007).

In total, 4063 bat passes (sequences of echolocation calls) were recorded; they belonged to at least 14 species. The most numerous species turned out to be: the common pipistrelle *P. pipistrellus*, Nathusius' pipistrelle *P. nathusii*, common noctule *N. noctula*, serotine *E. serotinus*, representatives of the genus *Myotis* (classified as *M. daubentonii* in 91 cases) and

soprano pipistrelle *P. pygmaeus*. These six taxa, each represented by more than 190 passes, were subjected to further analysis. Most of them are generalists, hawking prey in the air but close to vegetation, or (common noctule) high above the ground and far from obstacles, only the Daubenton's bat is a specialist gaffing prey from the water surface (Dietz et al. 2009). The distribution of passes among the habitat classes was extremely uneven, different from the pattern expected if these were used according to their availability. Bats preferred only water bodies, but avoided, among others. mixed forests and their edges, coniferous forests and roads through them, open areas and suburban buildings. Most of habitats (including woodlands) were used according to their availability.

Individual species differed in their habitat preferences. Serotine turned out to be a eurytopic and synanthropic taxon, selecting, as the only species, villages. It also selected roads in coniferous forests and treeless coastal dunes, while avoided open areas, tree lines and roads through broadleaved forests. It used the remaining habitats, even (as the only species) water bodies, according to their availability. Noctule strongly selected only water bodies and watercourses. It avoided mixed forests, arable land, tree lines, hedgerows and roads through coniferous forests. Most habitat classes, even settlements, meadows and pastures, were used according to their availability, giving the species the broadest habitat niche among the studied bats. All three species of pipistrelles revealed much narrower habitat niches when compared to the first two taxa. The most eurytopic species among them was the common pipistrelle. It not only strongly selected—as the only bat species to do so—tree lines but also stagnant and running waters, but avoided all open areas, mixed and coniferous forests, roads through the latter and suburb buildings, but not villages. The rarest representative of the genus, soprano pipistrelle, used a slightly narrower niche, preferring stagnant waters and roads in deciduous forests, while watercourses and villages were used according to availability. The second most frequent bat in the region, Nathusius' pipistrelle, occupied the narrowest niche within the *Pipistrellus* genus, strongly selected only waters but avoided open areas, tree lines, hedgerows, edges of mixed forests, villages and suburbs. *Myotis* spp. (represented mainly by Daubenton's bat) turned out to be the most stenotopic taxon - they preferred all types of waters, avoiding most forest habitats, arable land, tree lines of trees and villages.

The majority of the studied species revealed strong overlaps in habitat niches (Pianka indices for species' pairs reached values 0.72–0.93, mean 0.84). The exception was *E. serotinus*, which revealed much lower niche overlaps with other species than any other taxon (mean $O = 0.62$, range 0.38–0.76, with *M. daubentonii* and *N. noctula* as respective

extremes). Among morphologically similar *Pipistrellus* species, niche overlap between *P. pygmaeus* and *P. nathusii* was higher ($O = 0.92$) than between any of the two latter species and *P. pipistrellus* ($O = 0.78$ and $O = 0.77$, respectively)

This study has revealed that in the postglacial landscapes of central Europe, the only habitats strongly selected by bats (treated as a group) are water bodies, both stagnant and running—they are the crucial resource and place of concentration in the landscape (Ciechanowski 2002). Many other studies indicate the exceptional significance of water bodies and riparian habitats for bat fauna in the temperate zone of the Holarctic (e.g. Vaughan et al. 1997a; Menzel et al. 2005; Vindigni et al. 2009). It is usually associated with high abundance of flying insects, especially those undertaking their larval development in water (Fukui et al. 2006). The importance of water bodies for bats in lakelands of northern Poland appears to be higher than in Western Europe (Walsh and Harris 1996; Russ and Montgomery 2002), presumably due to much higher limnicity (Lehner and Döll 2004).

Contrary to the expectations, no clear selection of forests, including broadleaved ones, was disclosed; moreover, some habitat classes from the 'forest' group were even avoided. Hypothesis 1 was, therefore, confirmed only partially. Large-scale studies usually reveal that bats prefer patches of landscape with higher forest cover, usually broadleaved but sometimes coniferous stands (Ekman and de Jong 1996; Walsh and Harris 1996; Russ and Montgomery 2002; Mehr et al. 2011). All these studies, however, do not distinguish between various habitats inside the forest patch at a local scale – between the interior of tree stands and canopy gaps or forest roads. Function of the latter two types of structures was confirmed in the following study, although the earlier publications provided contradictory results (Hein et al. 2009, Loeb and O'Keefe 2006), similarly as in case of forest edges (Russ and Montgomery 2002, but also Cel'uch and Kropil 2008 vs. Vaughan et al. 1997a and the present study). The interior of intact, old-growth, multi-storey forests with closed canopy may provide a number of roosts (Kunz and Lumsden 2004, Ruczyński and Bogdanowicz 2004, 2008), but not foraging habitats for the majority of bats. Thomas (1988) provided an evidence for that, recording a relatively high number of bat passes inside the old-growth stands but only during the first 15 min after sunset and with a very low number of feeding buzzes. Only those species with very manoeuvrable flight, e.g. foliage gleaners, like some *Myotis* spp. and *Plecotus* spp. may forage in such forests through the whole night (Jung et al. 2012). Open areas are considered to be strongly avoided by bats (Walsh and Harris 1996; Russ and Montgomery 2002); this fact has been confirmed in this study – it can be explained by neither prey

availability nor constraints of spatial orientation, as at least, some bat species can easily cross the fields and meadows (e.g. Ekman and de Jong 1996). Probably, the avoidance of such habitats results mostly from predatory pressure. Avoidance of open areas by bats appears specific for pregnancy and lactation and cannot be extrapolated on seasonal, long-distance migrations of some species. In this period, bats regularly move even onto the open sea (Ahlén et al. 2009), they also appear frequently in the other habitats unattractive during nursing period (publication no. 4, Ciechanowski et al. 2016), thus it is highly unlikely that they did not cross e. g. vast patches of arable land then.

Habitat preferences of particular species mostly confirmed recent state of knowledge from the other parts of Europe, the study allowed, however, to reveal few specific features, unnoticed in earlier literature. Contrary to earlier papers (Lesiński et al. 2000, Bartonička and Zukal 2003), serotine appeared to be the only species that did not select waters. Also selection of pastures and forests (Robinson and Stebbings 1997) was confirmed only partially – in Pomerania region, the species preferred only roads in coniferous forests. Unusually strong association of that species with built-up areas might be explained by proximity to the species' daily roosts, i.e. almost exclusively buildings (Dietz et al. 2009). The position of common pipistrelle, as the only species specialized in utilization of tree lines crossing open areas, is astonishing, as the narrow habitat niche of Nathusius' pipistrelle, specialized in hunting in hunting above waters, even with no morphological adaptation indicating such preference. The latter was confirmed by earlier analysis of diet, dominated by Chironomid flies (Vaughan 1997). Analysis of habitat selection by rarer Myotis spp. was impossible due to significant similarity of echolocation calls among the particular representatives of that genus (Vaughan et al. 1997b, Walters et al. 2012) – to obtain that goal, application of radiotracking was necessary (publication no. 2, Ciechanowski et al. 2017).

The strong overlap of the habitat niches of the most numerous bat species (water bodies selected in five out of six cases) may induce questions about the significance of interspecific competition in the organization of bat assemblage. Part of that species, however, use different hunting tactics (Findley 1995) and forage in different microhabitats, defined by height above the ground or water surface and distance from vegetation (Baagøe 1987). The only group that might be expected to compete for food are morphologically similar species of *Pipistrellus*. However, the majority of earlier studies on habitat use by the two sibling, sympatrically occurring taxa, common and soprano pipistrelle, do not resemble the typical pattern of resource partitioning, but broad niche in the first one and specialization in the second one, but

the most preferred habitats are almost the same (Vaughan et al. 1997a, Davidson-Watts et al. 2006, Sattler et al. 2007).

The present study, for the first time, analyses in detail habitat preferences of all three, co-occurring in northern and central Europe, representatives of the genus *Pipistrellus*. It allows to compare them, what was, until recently, impossible in studies conducted in western part of the continent, due to too low share of Nathusius' pipistrelle in bat assemblages. That comparisons suggest that resource partitioning between *P. pipistrellus* and the remaining two *Pipistrellus* species may be based on partial differences in habitat preferences, confirming hypothesis no. 2, however, the strong overlap in habitat niche between *P. nathusii* and *P. pygmaeus* is astonishing. In the latter case, habitat partitioning may result from large differences in body size (Dietz et al. 2009: fifth finger length *P. nathusii* 41–48 mm and *P. pygmaeus* 33–40 mm) and in the frequency of echolocation calls (Skiba 2003: peak frequency *P. nathusii* 37–41 kHz and *P. pygmaeus* 50–60 kHz) that may indeed drive differences in the size of their prey (*P. pipistrellus* occupies intermediate values between the last two taxa, fifth finger 37–41 mm, peak frequency of the signals 42–51 kHz). Greater similarity in the forest microhabitat preferences between the largest and the smallest *Pipistrellus* species, than between them and their intermediate congeneric, was reported also by Jung et al. (2012).

My contribution to this paper included: developing the concept of the study, conducting all the field work, bioacoustic and statistical analyses, selecting and reviewing literature, interpretation of results, preparation of manuscript and figures and final edition of the text. The study was financed from the grant of Ministry of Science and Higher Education of the Republic of Poland N N304 131036 „*Habitat preferences of bats in mosaic landscapes of coastlands and lakelands of Northern Poland*" and the grant for individual research of University of Gdańsk BW1440-5-0369-8 „*Habitat preferences of bats in coastal and lakeland zones of Northern Poland*".

2. **Ciechanowski M.**, Zapart A., Kokurewicz T., Rusiński M., Lazarus M. 2017. Habitat selection of the pond bat (*Myotis dasycneme*) during pregnancy and lactation in northern Poland. Journal of Mammalogy 98(1): 232-245.

The pond bat *Myotis dasycneme* is a stenotopic, insectivorous vespertilionid species associated with some classes of riparian landscape and is considered to be of high conservation priority. Its distribution is extremely patchy across Europe, with high population densities in scattered centers of reproduction (Ciechanowski et al. 2007; Horáček and Hanák 1989). It is usually considered a specialized water-surface forager or trawling bat (Fenton and Bogdanowicz 2002). Until recently, it was believed that his specific hunting tactics – fast, relatively straight-line flight, low above water surface (Britton et al. 1997) restricts its foraging to large lakes, ponds and slowly flowing, lowland rivers, canals and dead river branches (Horáček and Hanák 1989, Boonman et al. 1995; Verboom et al. 1999). In spite of its high conservation status (Ciechanowski 2012), the biology and ecology of the species is astonishingly poorly studied. Moreover, the majority of research on the non-hibernation biology and ecology of the pond bat has been carried out in the heavily transformed, anthropogenic (mostly agricultural) landscape of the Western Europe (Britton et al. 1997; Boonman et al. 1995; Verboom et al. 1999; Van de Sijpe et al. 2004; Van De Sijpe and Holsbeek 2007). Meanwhile, this stenotopic species with specialized hunting tactics, remains an ideal model to test hypotheses about effect of structural parameters (surface – in case of lakes, width – in case of rivers) and trophic state index of water bodies on habitat selection, especially with help of radiotracking method. At the same time, similarly as any other insectivorous bat in our climate zone, it allows to test hypothesis about effect of stage of breeding stage on spatial behaviour and habitat preferences by comparing those parameters between periods of pregnancy and lactation. Earlier bioenergetic studies indicate that lactation significantly increases energy demands in females of insectivorous bats, compared to pregnancy (Kunz 1974). Animals may react on that increase by: 1) dietary shifts towards more easily available and more caloric insects (Jones 1995), 2) changes in hunting activity as well, as dynamic and timing of emergence from daily roost (Swift 1980, Maier 1992), 3) changes in use of space, manifested in shorter distances covered during lactation (Henry et al. 2002; Lučan and Radil 2010). In the present study, I focused on the third of reactions listed above (shifts in habitat and space use), interpreting them also based on earlier study on the first one (changes in diet composition, publication no. 3, Ciechanowski and Zapart 2012). This is the first ever study on habitat preferences of that species during period of its night-time activity.

The study was conducted in northern Poland, in the Bory Tucholskie forests, in three of the only eight known in our country, nursery roosts of pond bat. All studied roosts were

located between layers of house roofs. Females emerging from roosts in the evening were radiotagged. In total, 19 pregnant and 19 lactating females were equipped with radiotransmitters, and later tracked since dusk till dawn, using radio receivers with directional antennas. The majority of bearings were established by homing-in on animal and recordings actual position by GPS receiver, only in some cases we were able to use triangulation if the same individual with transmitter was recorded simultaneously by two field teams. Habitat availability was estimated by GIS analysis of topographic maps, while the lakes were classified to the particular trophic groups (eu-, meso-, oligo- and dystrophic) by means of phytoindication – every of those trophic types is characterised by specific vegetation. Habitat selection was tested using Z statistics with Bonferroni correction (Byers et al. 1984).

Pregnant females covered significantly longer distances between roosts and foraging sites (median 11379 m), than during lactation (median 2914 m). During pregnancy, the bats visited a chain of foraging sites (usually lakes) and spent only a short time (less than 10min) in each of them. The individual commuting path, calculated as a sum of line segments between particular locations, could cover up to 54 km, and the bat did not return to its roost until dawn During lactation, most pond bats visited usually only 1 or 2 main foraging sites, foraging there approximately 2h each time and returning to the maternity roost 1–2 times during the night to feed pups left there.

The main foraging sites of pond bats were lakes, rivers, canals, and fish ponds. During pregnancy, bats foraged mostly over lakes and only rarely over rivers, using both habitats in proportion to their availability Only the fish ponds were preferred in that period. Meanwhile, lactating females showed a strong preference for rivers and canals (foraging there for a longer time, over their relatively short – less than 1 km – sections), while avoiding lakes. Trophic classes of lakes were used unevenly. During pregnancy, bats selected eutrophic lakes and avoided mesotrophic ones, whereas, during lactation, mesotrophic lakes were selected and eutrophic ones were avoided. Dystrophic and oligotrophic lakes, usually small, were used in proportion to their availability in both periods.

Significant changes in the space use and pattern of movements between pregnancy and lactation appear to co-occur with rapid increase in energy demands after parturition (Kunz 1974), that results in need of reorganization of the energy budget of female bat organism (Racey and Speakman 1987). It allows to confirm the partial hypothesis no. 4. Lower energy demands in early pregnancy allow more energy to be spent on long-distance flights, associated with visits to several foraging sites and forced by low prey abundance in spring.

Pregnant females may spend the whole night commuting and foraging, not returning to the colony until dawn (Murray and Kurta 2004). Prey abundance in summer is probably much higher, however, so foraging bats may constantly exploit much smaller habitat patches with no need to travel long distances (Henry et al. 2002), saving their energy for the much higher demands of lactation (Racey and Speakman 1987). Moreover, lactating female bats exploit foraging habitats much closer to the nursery roosts because they must return to the colony to feed their pups (Henry et al. 2002; Murray and Kurta 2004). The observed reduction (of 74%) of flight distance in pond bats between pregnancy and lactation is much higher than that reported in another water-surface forager, the little brown bat, Myotis lucifugus (35% Henry – et al. 2002), presumably due to the larger body size and wing loading in *M. dasycneme* resulting in higher energy costs of flight.

The observed pattern of habitat use, with a predominance of water bodies, confirms our general knowledge about the hunting tactics of the pond bat (Britton et al. 1997). Shift in notable portion of female pond bats from lakes during pregnancy to narrow, fast-flowing rivers and canals during lactation, is, however, astonishing, similarly as shift from eutrophic to mesotrophic lakes in the same period. Thus, the hypothesis no. 3 should be accepted only partially. In spring, when the biomass of insects swarming above the waters is presumably low, pregnant females are forced to travel to the most productive patches of habitats, including either eutrophic lakes or their artificial counterparts, such as fishponds. On contrary, lactating females may maximize their energy gain by selecting large insects, consequently obtaining a larger portion of energy by a single capture effort. This change in foraging strategy could be confirmed by switch in diet from chironomids, that are much smaller in body size and predominant in eutrophic waters, to the much larger caddisflies, typically present not only in fast-flowing rivers but also in lakes with a lower nutrient content, e. g. mesotrophic ones, a phenomenon revealed in earlier dietary study in the same area. (publication no. 3, Ciechanowski and Zapart 2012). That shift remained unexplained until the radiotracking study revealed significant seasonal changes in habitat selection. In a similar way, analysis of habitat preferences based on acoustic survey of Nathusius' pipistrelle (publication no. 1, Ciechanowski 2015) allowed to interpret results of earlier dietary studies of that species (Vaughan 1997).

My contribution to that paper included: participation in the development of concept of the study, developing the concept of the manuscript, participation in the field work, review and

selection of literature, conducting all the statistical tests, interpretation of the results, writing the manuscript, participation in the preparation of figures and final edition of the text.

3. **Ciechanowski M.**, Zapart A. 2012. The diet of the pond bat *Myotis dasycneme* and its seasonal variation in a forested lakeland of northern Poland. Acta Chiropterologica 14(1): 73-79.

Contrary to the earlier views by Safi and Kerth (2004), dietary niche appears to significantly affect extinction risk in insectivorous bats (Boyles and Storm 2007). Thus, dietary studies might be important tool for recognition of potential threats (Arlettaz et al. 2000) and – presumably – conservation planning. However, due to the restricted range and abundance of many threatened bat species, several of them have their diet poorly studied, both in terms of sample sizes and geographical coverage (cf. Vaughan 1997). Meanwhile, diet composition remains one of the crucial elements of ecological niche of animals and allows to interpret data on habitat preferences of particular species, obtained by the other methods (Chattarjee and Basu 2018).

One of the bat species with the poorest state of knowledge on diet composition in European zone of temperate climate is the pond bat *Myotis dasycneme*. The species, endangered (EN) in Poland while near threatened (NT) in Europe and globally, is strictly associated with running and stagnant waters as foraging habitats. It hunts usually about 30 (10-60) cm above water surface, catching its prey by aerial hawking using wing membranes, or gaffing it from the water, using the tail membrane or feet (Britton i in. 1997). The diet of the pond bat is very poorly studied when compared to the other European bats (Beck 1995, Vaughan 1997). Until the moment of publishing of the present study, only two papers about its diet appeared – from the Netherlands (Britton et al. 1997) and Germany (Sommer and Sommer 1997). In both papers, only 50 faecal pellets were analyzed, thus the sample size was very limited, and only the German study provided some indication of seasonal variation (Sommer and Sommer 1997). There are no dietary studies of the species from Central or Eastern Europe, a major part of its geographical range. Chemical pollution of water bodies is sometimes considered a significant threat to the pond bat, and water quality may affect its habitat use (Van de Sijpe et al. 2004), as Biscardi et al. (2007) documented in another threatened trawling bat of Europe, the long-fingered bat *Myotis capaccinii*. The main component of its diet, non-biting midges, are often highly contaminated by either heavy

metals, PCBs, pesticides or polycyclic aromatic hydrocarbons. Concentration of these contaminants in tissues of insectivores increase along the food chain, accumulating in bodies of bats – secondary and tertiary consumers – as shown in pond bat itself (Reinhold et al. 1999). Nursery roosts of pond bats in Western Europe are often located in intensively used agricultural land with the network of canals and rivers. Therefore, the data on their ecology, including scarce dietary information, are of little use for understanding ecology of e.g. Polish or Baltic States' populations, occupying young, postglacial, forested lakelands with mesotrophic lakes. The diet of bats from these two landscape types may differ strongly, as Rydell and Petersons (1998) demonstrated for the noctule *Nyctalus noctula*. The aim of our study was to provide a first description of pond bat diet from Poland and to investigate seasonal variation of prey taxa.

The study material originated from a pond bat nursery colony located in the attic of an old forester's lodge near the village of Lubnia, Pomerania Lake District, Bory Tucholskie forests. The roost was visited 24 times between April and September 2006. Every time, bat droppings were collected from the entrance to the roost. In total, 20 samples were collected, consisting of 1725 individual faecal pellets that, at the moment of publication, remained the largest material regarding the diet of pond bat ever analysed. Content of droppings was studied under a dissecting microscope and the remains of invertebrates was determined to the order or family level. Frequency of occurrence (F%) was calculated for every taxon and sample, related to the total number of droppings (Flavin et al. 2001). Frequency of moth occurrence was calculated based on droppings containing limbs or proboscis, not only the scales, since those are known to remain in the gut long after eating the insect (Shiel et al. 1997). Prey remains appeared to be too highly masticated to use the percentage volume (V%) or the number of prey individuals (Whitaker 1988) as a measure of prey abundance within the time available for analysis of such a large sample of droppings.

The most frequent prey of pond bat from Lubnia were dipterans, and only slightly less frequent were caddisflies Trichoptera. The most frequent prey category among dipterans was non-biting midges Chironomidae, both imagines and pupae. Among caddis flies, members of Hydropsychidae family were recognized. Coleoptera were another relatively frequent taxon in the diet of the pond bat. F% of brown lacewings Hemerobiidae (Neuroptera) and moths Lepidoptera remained at similar level. Arachnids (excluding mites parasiting on bats) were slightly more frequently consumed – most of them belonged to spiders Araneae and harvestmen Opiliones, while Pseudoscorpionida were found only once The remaining taxa

(mayflies Ephemeroptera, greenflies Aphididae, three families of Hymenoptera) were noted in 1,9% of droppings

Frequency of particular taxa varied through the season. The highest F% of Chironomidae and Trichoptera was, respectively 88% and 86%, while the lowest was 38% and 29%. Up to 30th July the F% values of these two taxa were negatively correlated Since the end of May, frequency of caddisflies increased, replacing non-biting midges in their role of the most important prey during the majority of lactation period (24th June – 15th July). The highest frequency of Arachnida (excluding ectoparasites) was noted on 1st May (22.4%), frequency of moths peaked on 21st July – 12%, while F% of beetles varied between 10 and 33%. Frequencies of imagines and pupae of chironomids were significantly correlated with each other.

Possibility Direct comparison between dietary analysis from northern Poland and the two previous papers on the diet of the pond bat is limited, because of different measures used to express relative abundance of particular taxa (The Netherlands – percentage volume, Britton et al. 1997; Germany – percentage of prey fragments belonging to particular taxon, Sommer and Sommer 1997). However, all three methods applied, including frequency of occurrence (percentage occurrence) in our study, allow to reveal general importance of main prey taxa, and Polish data, based on the largest sample size ever collected for *M. dasycneme*, confirmed conclusions of the two earlier papers, clearly demonstrating pond bat's hunting tactics. The most frequent taxa – chironomids and caddis flies – complete their larval development in water, while after metamorphosis they swarm above the water surface, i.e. in habitats used by pond bats as the main foraging sites (publication no. 2, Ciechanowski et al. 2017). Chironomidae appeared to be the most frequent prey of the studied species in almost all studies, both based on morphological and molecular methods (Britton et al. 1997, Sommer and Sommer 1997, Krüger et al. 2012, 2013), except the unusual case of Russian paper (Smirnov and Vekhnik 2014). We revealed much higher frequency of chironomid pupae than in the other studies distinguishing among developmental stages of that family (Britton et al. 1997, Krüger et al. 2012, 2013), however their regular occurrence conforms to the species' hunting tactics, i.e. the ability to capture prey both by aerial hawking and by gaffing from the water surface (Britton et al. 1997). As frequency of imagines and pupae are correlated strongly, they must be taken in association with the same events in prey annual cycles, i.e. synchronized peaks of emergence of subsequent generations in particular chironomid species; pupae rise to the water surface, while imagines leave pupal exuviae and swarm above the

water (Tokeshi 1995). Growing popularity of molecular methods of dietary analysis (Krüger et al. 2013), allows to classify prey down to the taxonomic units of lower ranks (species and genera), however it excludes distinguishing among developmental stages of hunted invertebrates.

Large frequency of Trichoptera, almost as high as that of chironomids, is worth noticing. This taxon has previously been reported as of low or moderate importance in the diet of pond bat (Britton et al. 1997, Sommer and Sommer 1997). In the later material from northern Germany, caddisflies were, however, the second most important prey category, based of frequency of occurrence (Krüger et al. 2012, 2013), while at the Volga river in European part of Russia it became even the most important element of diet (Smirnov and Vekhnik 2014). In almost half of samples we found members of the family Hydropsychidae, generally associated with flowing water (Higler and Tolkamp 1982). Negative correlation between F% of chironomids and caddis flies shows that these taxa replace each other as the main prey during the season. The period of the highest F% of caddis flies in droppings of *M. dasycneme* coincided with the period of pond bat lactation (Dietz et al. 2009). Generally caddis flies reach larger body sizes than chironomids, thus they are more profitable prey, meeting the very high energy demands of lactating females (Racey and Speakman 1987), confirming hypothesis no. 4. The open question remained if the lactation of pond bat coincides with peak of caddis fly abundance, i. e. do phenology of species' reproduction is an adaptation to seasonal variation in food availability, while the bats make opportunistic use of available resources, or do they actively select larger prey when more abundant chironomids fail to fulfil their increasing energy requirements? Preference for large prey, when compared to avaiability of different body sizes, was revealed in Mediterranean *M. capaccinii* (Almenar et al. 2008). Only our radiotracking study on the very same population of pond bat revealed that the species optimizes energy gain during hunting by the another strategy – shifting between foraging sites during lactation period, moving, to a large degree, from lakes to rivers, i. e. from habitats dominated by non-biting midges to habitats being the main place of larval development for rheophilous caddisflies of the hydropsychid family (publication no. 2, Ciechanowski et al. 2017).

My contribution to that paper included: developing the concept of the study, developing the concept of the manuscript, review and selection of literature, conducting all the statistical tests, interpretation of the results, preparation of the manuscript including figures and final edition of the text.

4. **Ciechanowski M.**, Jakusz-Gostomska A., Żmihorski M. 2016. Empty in summer, crowded during migration? Structure of assemblage, distribution pattern and habitat use by bats (Chiroptera: Vespertilionidae) in a narrow, marine peninsula. Mammal Research 61(1): 45-55.

During seasonal migrations between summer and winter areas, some temperate-zone bats can travel large distances, sometimes exceeding 1900 km (Fleming and Eby 2004). Even large, open water bodies are not a permanent barrier for some migrating or dispersing bats (Baagøe 2001). Species that migrate on longer distances, like Nathusius' pipistrelle *Pipistrellus nathusii,* parti-coloured bat *Vespertilio murinus* and noctule *Nyctalus noctula*, leave Scandinavia in autumn and fly over the Baltic Sea from the southernmost points of Sweden (Alhén 1997). *P. nathusii* flying at a speed of about 20 km/h can theoretically reach the Polish coast in about 9 hours (Alhén 1997), using 8% of the fat reserves (Hedenström 2009). In that way, even the habitats extremely unattractive to bats during reproduction period, may play a significant role during the remaining stages of their yearly life cycle.

Data concerning the use of marine coastal habitats, as well as bat activity on coasts and the sea itself are, however, very scarce (Walsh and Harris 1996, Wermundsen and Sivonen 2008). The use of coastal habitats by bats is the most intensive during the spring and autumn migrations, when the narrow strips of coast, such as sand spits between sea and lagoons become migratory corridors (Jarzembowski 2003), while extending peninsulas act as starting points or stopovers between large bodies of water (Dzal et al. 2009; McGuire et al. 2012). Migrating bats seasonally enrich the fauna of both such peninsulas, and smaller islands, which are often poor in bat species and maintain low population density outside the migratory season, just as in case of Nathusius' pipistrelles regularly visiting Danish island of Bornholm in autumn (Baagøe 2001). They may even visit islands that are completely devoid of local bats (Cryan and Brown 2007, Petersen et al. 2014). Factors that restrict presence of bats on isolated, small islands and peninsulas during breeding period, include the small land surface, a scarcity of trees, a lack of roosts, and a low diversity and abundance of insect prey. On the smallest islands, no maternity colonies persist (due to the high energy requirements of lactating females – see: publication no. 1) and only adult males settle there (Johansson and De Jong 1996). Species richness and abundance of bat individuals increase with the area of island, while decrease with its distance to mainland, in agreement with predictions of classic

theory of island biogeography (Ahlén 1983). Both small marine islands and narrow, extending peninsulas can be treated as examples of landscape patches with limited possibilities of access and dispersal for bats, surrounded by large areas of unsuitable habitats, although the level of isolation in the case of islands is much higher.

To test hypothesis no. 4, the study was conducted on the Hel Peninsula, a sandbar 34 km long and 0.15-3 km wide, extending along a NW-SE axis, separating the Puck Bay from the open Baltic Sea. The majority of data about distribution and activity of bats were collected by evening recordings of echolocation calls with ultrasound detectors along linear transects in years 2007-2008. These transects were distributed evenly from the base to the end of Peninsula, to establish effect of distance from potential source of dispersal on presence of bats. Every research season was divided into two phenological period, distinguished by stages of bat life cycle: 1) late pregnancy, lactation and weaning of young (since half of June to beginning of August), 2) dispersal of nursery colonies, autumn migration and mating (August-September, to beginning of October). To establish effect of factors other than phenological period and distance from the base of peninsula on bat activity, weather data were acquired from meteorological station in the Hel city, while transects were divided into sections, classified into 8 habitat classes. Information was supplemented with results of roost survey, data about individuals captured accidentally on spring bird ringing station in Kuźnica and found grounded by local inhabitants in villages and towns.

Across the two seasons, 129 detector observations of six bat species were recorded on the Hel Peninsula, including serotine, *E. serotinus*; Nathusius' pipistrelle, *P. nathusii*; common pipistrelle, *P. pipistrellus*; soprano pipistrelle, *P. pygmaeus*; noctule, *N. noctula*; and an unidentified *Myotis* sp. In late summer and autumn, more than three times higher bat activity (98 observations, dominated by migratory Nathusius' pipistrelle) was recorded, compared to early summer (only 31 observations, mostly sedentary serotines and common pipistrelles). Except for numerous detector observations, only 10 bat records were ever obtained from the Hel Peninsula until the date of publication, among them only two ephemeral nursery colonies and single individuals of the two additional species – parti-coloured bat *Vespertilio murinus* (in spring) and Natterer's bat *Myotis nattereri* (in autumn).

In early summer, no significant correlation between the number of bat observations and the distance between the transect's centroid and the mainland was found – scarce, observed individuals were randomly distributed along the whole Peninsula. Such correlation was, however, revealed in late summer. The applied generalized additive mixed models (GAMM) revealed that the distribution of bat activity was uneven in space and variable in

time. Their occurrence varied among habitats in which the transect's were established, being the highest in deciduous and coniferous forests and the lowest in coasts and ports. Temperature positively affected the presence of bats, and increase of temperature by 1° raised the odds of bat occurrence by 37 %., contrary to the wind speed. Number of bats increased across the season (since spring till autumn) but that trend was affected by distance to the base on Peninsula (highly significant interaction between the last parameter and the number of day of the year). On the transects located in distal part of Peninsula (further than 20 km from its base) probability of bat's occurrence was rather stable over time and was below 0.1. On transects located close to the mainland (10 km and less), the probability of bats' occurrence was low at the beginning of the season but, after day 220–240 (ca. mid-August), increased rapidly exceeding 0.8 in late autumn (beginning of October). The numbers of bat observations differed significantly in relation to wind direction from expected; more bats than expected were observed in westerly winds, whereas fewer than expected bats were observed in southerly winds.

Bat assemblage inhabiting the Hel Peninsula during pregnancy and lactation appears to be poor in qualitative and quantitative terms. A relatively low number of bat observations (31 during 36 evenings) and, consequently, almost complete lack of bat activity on the majority of transects in early summer (median 0.0 passes/transect) support this hypothesis. For comparison, in mosaic landscapes of Pomeranian mainland, during 69 evenings in June–July, 4063 bat passes, roughly corresponding to 'bat observations' in the recent study, were recorded, with very similar research methods applied (Ciechanowski 2015, publication no. 1). Reasons for such low density and abundance of bats on the Peninsula in that period might be 1) strong gusty winds during the whole year and rapid weather changes resulting in unpredictable food resources and even being an obstacle for the movement between roosts, 2) scarcity of potential daily roosts, resulting in low number of tree cavities in pine forests growing on dunes, due to low height and circumference of trees, but also modernization of buildings to host increasing number of tourists, 3) the almost complete lack of fresh water bodies being the most frequently visited foraging sites (Walsh and Harris 1996, Russ and Montgomery 2002, publication no. 1 – Ciechanowski 2015), that restricts insect prey abundance but also results in the lack of drinking sites, which are crucial for the maintenance of bat populations (Adams et al. 2003, Adams and Thibault 2006). It should be presumed, that the observed individuals were mostly solitary males, or non-breeding females, as Johansson and De Jong (1996) suggested for the smallest islands on Scandinavian lakes. The breeding bat females require abundant and easily available prey due to their high energy requirements

(Racey and Speakman 1987); thus, they occupy roosts located as close as possible to optimal foraging sites (Dietz et al. 2006). The Hel Peninsula must be considered a geographical structure unattractive to bats during their reproduction period.

We confirmed hypothesis no. 5, revealing increase in importance of unattractive habitats and landscape elements for bats during their seasonal migrations and autumn dispersal. Random distribution of scarce individuals that used the Peninsula in early summer, with no larger concentrations of foraging individuals, typical for the neighbourhood of maternal colonies (Dietz et al. 2006), suggests lack of permanent, breeding bat populations. Significant correlation between the number of bat observations and the distance from mainland provides evidence that Hel Peninsula is not a migratory corridor for bats in autumn, although the dominant species in that period, *P. nathusii*, is a long-distance migrant (Petersons 2004). Increase in bat activity in that period must, therefore, be an effect of mainly, if not exclusively, on the Hel Peninsula. Probably, the majority of recorded individuals appeared in the study area during the dispersal of nursery colonies located on the mainland after the weaning of young, among which only few reach the tip of Peninsula. Some peninsulas can, indeed, act as stopovers and corridors for migrating bats but their orientation may have to align with the direction of the bats' migratory movements (Dzal et al. 2009; McGuire et al. 2012). Thus, one may expect that the Hel Peninsula is used more intensively as a migratory path by bats in spring, when they migrate along the coast from the west to the east, similarly as birds do during their return from winter sites (Busse 1976). However, we cannot exclude that a significant portion of individuals migrate along the coast of the Gulf of Gdańsk in autumn and might be brought to the Hel Peninsula accidentally by stronger winds from the adjacent mainland, similarly as in case of Nathusius' pipistrelle on oil platforms in the North Sea (Boshamer and Bekker 2008). The prevalence of bat observations during westerly winds (i.e. blowing from mainland) appears to support this hypothesis. The Vistula Spit, another section of the Polish Baltic Sea Coast with a similar origin and morphology, represents a different situation. It runs from the northeast to the southwest and thus acts as a main migratory corridor, mainly for Nathusius' pipistrelle, which results in a several-fold increase in their number in August and September (Jarzembowski 2003).

My contribution to this paper included: developing the concept of the study, training the second author in bat survey methods, participation in field work, review and selection of literature, interpretation of the results, writing of the manuscript and final edition of the text.

5. **Ciechanowski M.**, Kubic W., Rynkiewicz A., Zwolicki A. 2011. Reintroduction of beavers *Castor fiber* may improve habitat quality for vespertilionid bats foraging in small river valleys. European Journal of Wildlife Research 57: 737-747.

Insectivorous bats in mosaic, anthropogenically modified landscape, are dependent on spatially restricted habitat patches (publication no. 1, Ciechanowski 2015), strongly preferred due to prey availability or locomotorically and sensory advantageous spatial structure. They often concentrate their foraging activity in in river valleys, where they benefit from emerging aquatic insects (Fukui et al. 2006). Riparian zones and water bodies usually hold the highest diversity of bats and the highest density of foraging individuals (Rydell et al. 1994, Walsh and Harris 1996, Vaughan et al. 1997a, Grindal et al. 1999, Russ and Montgomery 2002, Ellison et al. 2005, Menzel et al. 2005a, Ciechanowski 2015), while in the diet of several species insects whose larvae develop in water may dominate (Vaughan 1997, Rydell and Petersons 1998, publication no. 3 – Ciechanowski and Zapart 2012). However, bats' adaptations to particular hunting tactics bring serious limitations regarding the use of various habitats, even those supporting extremely abundant prey. Aerial hawkers may capture prey only in some distance from obstacles, e.g., tree crowns (Baagøe 1987; Jones 1995; Kalko 1995). Therefore, their foraging might not be effective in dense tree stands and their activity is negatively correlated with stand density (Erickson and West 2003). Some species, like the Daubenton's bat, adapted to hawking insects just above the water or even gaffing them directly from its surface (Jones and Rayner 1988; Todd and Waters 2007), benefit from an acoustic mirror effect (Siemers et al. 2005). However, they cannot detect prey if water surface is turbulent, as frequently occurs in shallow and narrow streams (Mackey and Barclay 1989; Rydell et al. 1999), or if it is covered by floating vegetation (Boonman et al. 1998; Ciechanowski et al. 2007). Bats reveal clear microhabitat preferences, dependent on their foraging tactics. In forests, aerial hawkers hunt mostly in canopy gaps, on glades, in ecotones (Kusch et al. 2004), or in corridors formed by streams and trails (Lloyd et al. 2006). Some species prefer calm sections of rivers and avoid those with fast current (Warren et al. 2000).

Various keystone species, being simultaneously ecosystem engineers, may take part in modification of habitat structure and creation of attractive microhabitats, meeting the above requirements. One of such species is European spruce bark beetle *Ips typographus*, which outbreaks lead to thinning of spruce forest canopy and creation of optimal foraging habitats for western barbastelle *Barbastella barbastellus* (Kortmann et al. 2017). The other species

performing such a function might appear beavers – European *Castor fiber* and North American *C. canadensis* (Brazier et al. 2020). Damming of water courses by beavers reduces stream velocity and increases flooding outside the original channel (Rosell et al. 2005) while selective removal of trees (Zwolicki 2005) forms canopy gaps and reduces density of undergrowth (i.e., vertical obstacles). These modifications may increase attractiveness of a beaver-inhabited valley as a foraging site for several bat species, as their distribution long rivers and streams relates to the spatial structure of riparian vegetation (Warren et al. 2000; Downs and Racey 2006), physical characteristics of the current (Rydell et al. 1999; Warren et al. 2000), and water quality (Vaughan et al. 1996; Biscardi et al. 2007; Kalcounis-Rueppell et al. 2007), which are all features known to be modified by beavers. Their role as keystone species for several different plant and animal assemblage is well documented (Rosell et al. 2005), there were however no data about their effect on attractiveness of foraging sites of bats, whose presence in habitats modified by beavers was mentioned only marginally (Francl et al. 2004, Brooks and Fords 2005, Menzel et al. 2001). Only after publishing the following study (Ciechanowski et al. 2011), another paper, testing hypothesis about higher significance of beaver ponds for bats in Finland, appeared (Nummi et al. 2011). The objective of this study was to compare the foraging and commuting activity of vespertilionid bats among sections of small, forested river valleys modified and unmodified by European beavers.

The study was conducted in the forested valleys of two small watercourses in Bory Tucholskie (vicinity of Osiek, near the village of Stara Rzeka – 1 and Suchobrzeźnica – 2). Beavers were reintroduced in that area in 1971 and since then have colonized spontaneously almost the whole region. In each valley, a linear transect was marked parallel to the stream channel to record echolocation calls of commuting and foraging bats. Each of the transects was divided into sections modified by beavers (flooding, canopy gaps and their combination) and devoid of such modifications. Bat activity and their species identity was recorded with broadband ultrasound detector since spring until early autumn.

In total, seven species of bats were recorded on both transects: Daubenton's bat *Myotis daubentonii*, serotine *Eptesicus serotinus*, common pipistrelle *Pipistrellus pipistrellus*, soprano pipistrelle *Pipistrellus pygmaeus*, Nathusius' pipistrelle *Pipistrellus nathusii*, noctule *Nyctalus noctula*, and brown long-eared bat *Plecotus auritus*. The density of bat passes was significantly higher at site 1, regarding all taxa combined and the majority of individual species, but representatives of the *Myotis* genus were more active at site 2 The number of bat passes was significantly higher in sections of both valleys modified by beavers than in unmodified sections, similarly as the number of passes of four species (three

pipistrelles, noctule) at site 1. The highest bat activity at the last site was recorded in flooded forest with canopy gaps created by beavers. Significantly less passes were recorded in unflooded forest with canopy gaps and in dense, intact tree stand. Istotnie mniej przelotów zarejestrowano w niezalanym lesie z lukami i w zwartym, nienaruszonym drzewostanie. Meadows flooded by beavers were used more intensively than unflooded meadows. Identical or similar differences were revealed for particular species of pipistrelles, contrary to the noctule, for which the highest activity was recorded exactly over the flooded meadows.

We confirmed partially the hypothesis no. 5 – a keystone species, like the European beaver, affecting the spatial structure and productivity of habitats, may, through its activity, change the potential attractiveness of habitats as foraging sites for bats, thus affecting the abundance and distribution of hunting individuals. That impact was revealed only for aerial hawking species (pipistrelles, noctule) but not water-surface foragers (Daubenton's bat).

There are at least two main factors that may explain the higher activity levels of bats in sections subject to habitat modifications caused by beavers. The first, apparently more obvious, is damming of stream current and increase in water table that leads to flooding of former terrestrial habitats. All four species that revealed significantly higher activity on sections transformed by beavers (common pipistrelle, soprano pipistrelle, Nathusius' pipistrelle, noctule) are known to prefer water bodies as foraging sites (publication no. 1, Ciechanowski 2015). As beavers extend riparian habitats, they improve the habitat quality for bats and provide them with large areas where prey is much more abundant than over the shallow and narrow streams. Moreover, biomass of emerging chironomids, an important prey of pipistrelles and noctules (Vaughan 1997), increased in the valley section after construction of a beaver dam, at least during the first few years (Nummi 1989). Conducted in the same time and published slightly later, study in boreal forests of Finland revealed, anyway, that not only the fact of creation of water body, but also association of its genesis with construction activity of beavers, affect attractivity of foraging site for bats – both the activity of the latter and biomass of insect prey was several times higher over beaver ponds than over control ponds (Nummi et al. 2011). The second factor is related to a significant reduction of forest-associated clutter, being a serious limitation for aerial hawking species. Although woodlands, especially deciduous ones, are among the most preferred habitats by bats (Walsh and Harris 1996, Russ and Montgomery 2002), in the zone of young, postglacial lakelands of Central Europe, the majority of them is used only proportionally to their availability or even avoided (publication no. 1, Ciechanowski 2015). Aerial hawking bats usually avoid internal parts of dense, intact stands (Rachwald 1992; Lloyd et al. 2006), while their activity is negatively

correlated with the area of closed canopy (Kusch et al. 2004). In managed forests these bats frequently use thinned stands and clear-cuts (Patriquin and Barclay 2003, Węgiel et al. 2019), while in natural forests canopy gaps that are usually created by the aging of older trees, windthrows, outbreaks of phytophagous insects, and pathogenic fungi (Weiskittel and Hix 2003; Worrall et al. 2005). Cutting of trees that results from foraging of beavers may perform a similar function.

Based on obtained data, it cannot be established, which of the two effects of beaver activity described above has greater impact on insectivorous bats in small river valleys, moreover, the results indicate that these effects may act additively. The latter might manifest in higher activity of the most species in flooded forest with gaps than in non-flooded forest with gaps only. Flooding may also act independently as a factor promoting the use of habitat by bats, as evidenced by higher activity of all four species over the flooded part of the meadow than over the section outside of the beaver pond. This difference is especially important in noctule, an open-space forager with low manoeuvrability that hunts at high altitude, far from obstacles (Baagøe 1987; Jones 1995). Probably it relies more on wide meadows, subjected solely to flooding. On the contrary, pipistrelles, as the species that fly in quite a manoeuvrable style (Baagøe 1987; Kalko 1995) may prefer a combination of flooding and tree cutting, as their activity is usually the highest in close proximity to tree lines and gradually decreases at greater distances from them (Downs and Racey 2006).

We were unable to confirm our hypothesis that damming of the stream increase habitat use by water-surface foragers, like the Daubenton's bat, due to the formation of large areas of smooth water, which serve as an acoustic mirror for prey detection. The activity of the *Myotis* species was almost negligible at site 1, However, all beaver ponds at that site were completely covered by pleustophytic vegetation, mostly formed by duckweed (Lemnaceae). Such vegetation, by producing acoustic clutter that results in producing numerous background echoes, makes prey detection in Daubenton's bat impossible (Boonman et al. 1998), even if biomass of insects in such sites is high (Ciechanowski et al. 2007). At the site 2, much faster stream current almost completely eliminated duckweed, allowing much higher activity of *Myotis* species.

My contribution to this paper included participation in developing of the concept of the study, training of the co-authors in methods used later in field work, participation in bioacoustic analyses, interpretation of the results, writing of the manuscript and final edition of the text.
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/1440-5-0230-5 „*Impact of foraging and construction activities of beaver Castor fiber on spatial distribution of bats Chiroptera in small river valleys*".

Summary

In papers included in submitted scientific achievement, I analysed the effect of habitat variability in anthropogenically transformed landscapes on space use by bats (Chiroptera). These analyses covered various spatial scales (Gdańsk Pomerania region, Hel Peninsula, communal home range of one maternal colony, a valley of local water course), various levels of biological organization (multispecies assemblage, local population, individually marked animals) and various phenological periods (pregnancy, lactation, autumn migration). To test the proposed hypotheses I applied various research methods – detection and recordings of ultrasounds, radiotelemetry, dietary analysis based on morphological identification of prey remains in bat faecal pellets and Geographical Information Systems (GIS). Application of dietary analysis (publication no. 2, Ciechanowski and Zapart 2012), although not delivering any distributional information directly, allowed to interpret later results of radiotracking study (publication no. 3, Ciechanowski et al. 2017). The results presented in papers included in the Scientific Achievement allowed to confirm the main research hypothesis. They revealed also notable differences in habitat use by populations and assemblage of bats in Central Europe, dominated by youngi, postglacial landscapes, compared to, strongly transformed by humans, landscapes of western part of the continent. I manager also to confirm the majority of partial hypotheses:

1. The most important foraging habitats for the majority of Central European bats, at least aerial hawkers, are water bodies and water courses. Only serotine remains an outlier in that group, as villages and roads in coniferous forests appear to be the most important foraging sites for that species. Some species, apart from waters, prefer some terrestrial habitats, like tree lines in open areas (common pipistrelle) or roads in deciduous forests (soprano pipistrelle). The majority of woodland habitats are, however, used only proportionally to their availability or even avoided, a phenomenon that differs bat assemblage in northern Poland from those already studied in Western Europe.
2. Habitat preferences of morphologically similar, sympatric species of the genus *Pipistrellus* are elements of supplementary mechanism of niche partitioning. Very strong niche overlap between soprano pipistrelle and Nathusius' pipistrelle, extremely

differing in body size, while much smaller overlap between both of them and common pipistrelle, a species of moderate size, attest to that. The species more distant in terms of morphology and bioacoustic reveal more possibilities for niche partitioning based on use of prey belonging to different size classes or hunting in different distances from obstacles..

3. The pond bat, as a representative of water-surface foraging or trawling specialists, reveal pattern of habitat selection only partially in accordance with expectations. In May, it forages mostly over large eutrophic lakes, i. e. habitat known to be the most productive and optimal for the species moving by fast and not very manoeuvrable flight, adapted to hunting over large water bodies. In June, however, it selects narrow, fast-flowing rivers and (among lakes) mesotrophic waters, i. e. habitats of much lower productivity.
4. Seasonal changes in habitat use by insectivorous bats are dependent on their energy demands but also on availability of particular prey taxa. Pregnant females of the pond bat hunt during the whole night, visiting several foraging sites, located usually a dozen or so kilometres from a daily roost and preying mostly upon small non-biting midges, associated mostly with eutrophic lakes that are the main foraging habitats in that period. On contrary, lactating females return to the roost during night, using 1-2 foraging sites, usually located less than 3 km from the colony, and preying upon large caddisflies, associated mainly with, selected in that period, rivers and mesotrophic lakes. Those shifts result from both increase in energy demands during that stage of life cycle and need for feeding the young offspring in the middle part of the night.
5. Use of landscape structures avoided by bats during pregnancy and lactation increased significantly after the breeding period. It is associated with their dispersal and/or migrations of some species. Moreover, the pattern of use of that structure changes. Seasonal variation in activity and distribution of bats on the Hel Peninsula may serve as an example for that. During pregnancy and lactation, the activity of bats is extremely low there, while foraging individuals distributed evenly. In late summer and autumn, the activity of bats increases several-fold, also clear gradient of their density appears, with maximum values near its base and gradual decline of them towards its tip.
6. Significance of particular habitats in mosaic landscape may be subjected to modification due to activity of keystone species. The example of such relationship are the results of European beaver activity – mostly thinning of a tree stand by cutting and

creation of ponds by damming of small water courses. These processes increase attractivity of the valleys of small streams and rivers as foraging habitats for bats, although only partially as expected. Transformations caused by beavers resulted in increase of activity of aerial-hawking bat species but not the trawling or water-surface foraging bats. The reason for that, probably, was abundant occurrence of pleustophytes, overgrowing the water surface, thus making prey detection by bats impossible.

Distribution of bats, heterogenic in space and changing in time, is affected by several environmental and biotic factors, like weather conditions, food abundance, predation risk and ability to detect prey, that was all revealed in the local scale (Ciechanowski et al. 2007). The same factors are probably responsible for identical variability in larger spatial scales, although following their impact on activity and distribution of bats in much more difficult. Despite that, even uncovering only the patterns of distribution, habitat preferences and their seasonal changes provides important tools for conservation of these mammals (Razgour et al. 2011, Amorim et al. 2018). However, these patterns, in case of species with large geographical ranges, reveal often huge regional variation (Fabianek et al. 2015) that should be included in regionally prepared conservation guidelines. The picture of habitat use and selection by bats in young, postglacial landscapes of Central European lowlands that I obtained, precisely allowed, for the first time, to prepare such, profiled for regional needs, guidelines, with no need to rely on data from western, geographically and ecologically different part of continent.

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5. Presentation of remaining scientific achievements

Research projects, activities and publications not related do the Scientific Achievement set out in art. 219 § 1 point 1 of the Act

Starting from MSc studies in Biology on the Faculty of Biology, Geography and Oceanology, University of Gdańsk in years 1995-2000, my research interests have focused on ecology and biogeography of bats (Chiroptera), although part of my papers related also to small terrestrial mammals – rodents (Rodentia) and soricomorphs (Soricomorpha – shrews, moles etc.). My first research notes were published already during MSc studies, they covered small mammal fauna of Trójmiejski Landscape Park in *Przegląd Przyrodniczy* (Ciechanowski 1998) and winter bat surveys in *Przegląd Zoologiczny* (Ciechanowski and Jarzembowski 1999). Since the first year of graduate study (1995), I engaged myself in activities of Student Bat Research Group of the University of Gdańsk and associated Academic Bat Research Group of the Polish Society of Nature Protection „Salamandra", a notable Polish environmental NGO, participating in, conducted since 1989 till now, long-term monitoring program, devoted to populations of bats hibernating in underground roosts of Pomerania Gdańsk region (recently I remain its coordinator). That program resulted in another publication, with me as co-author, presenting its preliminary results, in journal *Studia Chiropterologica* (Jarzembowski et al. 2000).

Preparing myself to work on MSc Thesis, I established cooperation with Prof. Bronisław W. Wołoszyn from Institute of Systematics and Evolution of Animals, Polish Academy of Science, who agreed to become its supervisor. In my MSc Thesis, I covered both topics of faunistics (first ever survey of bat fauna in the northernmost intact forest complex on Poland – the Darżlubska Forest), habitat preferences, occupation of bat boxes, and even social structure and morphometrics of selected species, especially sexual dimorphism. I applied

several research methods, mostly bat mist netting, ultrasound detection and survey of diurnal roosts. That study (1998-1999) resulted in my first paper indexed in the Web of Science (Journal Citation List), printed in *Mammalian Biology*, dealing with use of different types of water bodies by bats (Ciechanowski 2002) and two other – analysing the size of mating groups of Nathusius' pipistrelle *Pipistrellus nathusii*, also in *Mammalian Biology* (Ciechanowski and Jarzembowski 2004) and comparing occupation of bat boxes in three different types of forest in *Folia Zoologica* (Ciechanowski 2005). The series of publications based on materials collected during work on my MSc Thesis includes also the paper about bat fauna of the Darżlubska Forest in Polish journal *Nietoperze* [*The Bats*] (Ciechanowski 2003), and the article about dynamics of sexual structure of Nathusius' pipistrelle population in Swiss bat research journal *Le Rhinolophe* (Ciechanowski and Jarzembowski 2009).

The subject of my PhD Thesis, prepared under supervision of Prof. Lech Stempniewicz, was the structure of bat assemblage, spatial and temporal variability of their activity and factors shaping its dynamics; I conducted the study devoted to that subject at the edge of Darżlubska Forest, i. e. the area covered by earlier research associated with my MSc Thesis. For that purpose, I applied broadband ultrasound recordings, bat mist netting and insect sampling with sticky traps as a method of prey abundance assessment; during that project I led a team of four MSc students. I conducted the field study in years 2001-2004, financed from supervisor's grant 3 PO4F 065 24 „*Spatial organization of assemblage and dynamics of bat (Chiroptera) activity in forest-agricultural landscape*" led by Prof. Lech Stempniewicz, under which I was contracted as the main investigator. To the data analysis, except univariate statistics, I implemented also stepwise multiple regression and canonical statistics (particularly RDA). The direct effects of that project were three publications indexed by Web of Science. The most important among them and still the most frequently cited among my papers (82 citations by Web of Science, 160 by Google Scholar), printed in *Canadian Journal of Zoology*, analysing the effect of weather conditions, lunar phase, phenology of aquatic vegetation and prey abundance on spatiotemporal variation in activity of seven co-occurring bat species (Ciechanowski et al. 2007). The most interesting among its findings was discovery of lunar phobia (i. e. avoidance of moonlight) by Daubenton's bat, a phenomenon which existence in insectivorous bats inhabiting temperate climate zone was generally not accepted among scientific community. Among important findings it should be listed also completely different set of factors affecting the activity of aerial-hawking bats, like pipistrelles, noctules, serotine (air temperature, biomass of insects) compared in water-surface foraging Daubenton's bat (moonlight, cover of water surface by vegetation, fog) and

revealing of very high hunting activity of the latter species in sub-zero ambient temperatures. The next article based on results from PhD thesis, published in *Acta Theriologica*, presented patterns of seasonal changes in activity of the same seven bat species in the comparative aspect on the background of available knowledge of their breeding phenology and migratory behaviour (Ciechanowski et al. 2010). The third paper, published in *Mammalia*, revealed nightly changes in habitat use by Nathusius' pipistrelle, probably being an anti-predatory adaptation (Ciechanowski et al. 2009). The series of publications based on material collected during preparation of PhD thesis, included also the short note about daily foraging of Natterer's bat (Ciechanowski and Anikowska 2007). In 2002 I obtained a grant from Foundation for Polish Science (FNP), that allowed me to participate in my first ever international scientific symposium (IX European Bat Research Symposium) in Le Havre, France, where did I present the preliminary results of my PhD project (in form of poster). In 2007, thanks to the support of H. M. Rector of the University of Gdańsk, I presented final results of that project, as an oral presentation, during XIV International Bat Research Conference in Merida, Mexico.

In 2004, I was hired as research assistant in the Department of Vertebrate Ecology and Zoology, University of Gdańsk, while after obtaining PhD degree in 2005, as an assistant professor (*adiunkt*) Shortly after getting that position, I established cooperation with Dr Christian Voigt and Dr Aną Popa-Lisseanu from Leibniz Institute for Zoo and Wildlife Research in Berlin, in order to participate in pan-European project devoted to tracking bat migrations by analysis of stable isotopes in fur of those mammals. It resulted in three papers with my co-authorship – in *PLoS One* (Popa-Lisseanu et al. 2012), *Biodiversity and Conservation* (Voigt et al. 2014) and *Proceedings of the Royal Society Series B* (Lehnert et al. 2018). Among a dozen or so authors of those publications, affiliated in research institutions scattered across the whole Europe, I was one the only two Polish scientists. In 2012 I was invited by Dr Andrzej Węgiel from the Faculty of Forestry, University of Life Sciences in Poznań, to participate in development of idea and methodology of research project „*Occurrence of bats in forests in relations to age, spatial structure and species composition of tree stand*" (the investigation no. 27/2012 commissioned by General Directorate of State Forests in Warsaw), I conducted also preliminary statistical analysis of data collected during that project, and, in consequence, I became a co-author of the two articles about part of the obtained results – in *Sylwan* (Węgiel et al. 2016) and *European Journal of Forest Research* (Węgiel et al. 2019). In cooperation with Dr Konrad Sachanowicz (then affiliated in Museum and Institute of Zoology, Polish Academy of Science), Prof. Piotr Tryjanowski and Dr hab.

Jakub Kosicki (Adam Mickiewicz University of Poznań) I prepared also the analysis of European range of wintering Nathusius' pipistrelle, a bat participating in long-distance migrations and hibernating in poorly insulated roosts – until very recently, almost exclusively in western and southern part of the continent. Based on spatial modelling of all cases available winter records, we were able to reveal a significant increase in frequency of cases of species' hibernation in Central Europe, including Poland and to link them to warming climate but also to use of urban heat islands. We published the article about that in *Mammalia* (Sachanowicz et al. 2019), similarly as earlier short note about the first ever case of Nathusius' pipistrelle wintering in Poland (Sachanowicz and Ciechanowski 2006).

Since 2003, in cooperation with Dr Konrad Sachanowicz, Dr hab. Aleksander Rachwald (Forest Research Institute) and Dr Michał Piskorski (Marie Curie-Skłodowska University of Lublin), I was involved into extensive survey of bat fauna of Albania, one of the least studied, with respect to bats, countries in Europe. Within that project, we organised 8 scientific expeditions, during which we conducted bat mist netting, ultrasound recordings and survey of potential daily roosts across the whole country, including hardly accessible mountainous regions of its northern part, from where no faunistic data were ever collected. W ramach tej eksploracji zorganizowaliśmy 8 wypraw naukowych, podczas których prowadziliśmy odłowy nietoperzy w sieci, rejestrację ultradźwięków i kontrolę potencjalnych kryjówek dziennych na terenie całego kraju, również w trudno dostępnych rejonach górskich jego północnej części, skąd nie zebrano wcześniej żadnych danych faunistycznych. These data we collected also in neighbouring countries of former Yugoslavia. Thanks to that activities, I became a co-author of five articles, presenting the first ever records of 11 bat species for Albania and 2 species for Montenegro, Bosnia and Herzegovina, in *Journal of Natural History*, *Acta Chiropterologica, Mammalia* and *Lynx* (Ciechanowski et al. 2005, Niermann et al. 2007, Sachanowicz et al. 2006, Sachanowicz and Ciechanowski 2006, Sachanowicz et al. 2016). We published whole collected material about bat fauna of Albania, including the analysis of earlier data from earlier literature, in the monograph entitled „*Bats of Albania*" by Bogucki Wydawnictwo Naukowe, a Polish publishing house (Sachanowicz and Ciechanowski 2019). Additional effect of Albanian expeditions was rich material of bat ectoparasites, being the subject of the next publication, prepared in cooperation with Dr Ján Krištofík from Institute of Zoology, Slovak Academy of Sciences in *Journal of Natural History* (Sachanowicz et al. 2014), but also ornithological observations and data about distribution of edible dormouse *Glis glis*, being subject of separate papers in journals

Acrocephalus (Sachanowicz et al. 2008) and *Acta Zoologica Bulgarica* (Ciechanowski and Sachanowicz 2014).

In some research, I used also molecular methods, what resulted in a paper about variability of control region of mitochondrial DNA in Nathusius' pipistrelle in Poland (Jarzembowski et al. 2004). In 2006 I led a project, financed by internal grant of the University of Gdańsk, no. BW 1440-5-0321-6 *„Development of efficient and cheap method of identification of morphologically similar bats from genus Pipistrellus, based on restriction fragment length polymorphism analysis of mitochondrial DNA"* (in cooperation with Anna Biała, then affiliated in Department of Genetics, University of Gdańsk). We developed, indeed much cheaper in those times, method of determination of all pipistrelle species in continental part of Europe (Nathusius' pipistrelle, soprano pipistrelle, common pipistrelle and two populations of Kuhl's pipistrelle *Pipistrellus kuhlii*, that might represent two separate, allopatric species), presented on 11th European Bat Research Symposium in Cluj-Napoca, Romania in 2008.

When preparing environmental expert opinions, plans of management of various protected areas, environmental impact assessments for construction projects, performing interventions associated with bat conservation, participating in monitoring of animal species, finally organizing field camps for members of Student Bat Research Group, I always tried to gradually publish the faunistic data gathered during such works. Thanks to that, I became an author or co-author of papers devoted to bat fauna of 9 landscape parks and 1 national park, published in journals *Myotis*, *Nietoperze* and *Parki Narodowe i Rezerwaty Przyrody* (Ciechanowski et al. 2000, Sachanowicz et al. 2001, Ciechanowski et al. 2002, Ciechanowski and Duriasz 2005, Ciechanowski et al. 2006a, 2006b, 2008), or as the chapters in monographs (Wojciechowski and Ciechanowski 2007, Bidziński et al. 2020, Ciechanowski 2020). Based on smaller portions of material and single records I published also 20 short notes, describing occurrence of bat species new for the Gdańsk Pomerania region or rarely encountered, addenda to bat fauna of already surveyed protected areas, but also observations of unusual summer and winter roosts, printed in journals *Nietoperze*, *Studia Chiropterologica* and *Chrońmy Przyrodę Ojczystą* (Ciechanowski 2001, Ciechanowski and Przesmycka 2001, Ciechanowski and Sachanowicz 2003a, 2003b, Ciechanowski and Szkudlarek 2003, Ciechanowski et al. 2003, Ciechanowski et al. 2004, Sachanowicz et al. 2004, Ciechanowski et al. 2005, Ciechanowski 2008a, 2008b, 2008c, Narczyński and Ciechanowski 2008, Zapart et al. 2008, Ciechanowski and Przesmycka 2009, Ciechanowski and Sadowska 2010, Ciechanowski et al. 2011a, 2011b, Ciechanowski 2013, Ciechanowski et al. 2013).

Multiannual monitoring of bats in the area of Natura 2000 site allowed to analyse long-term and seasonal dynamics of population and species composition of bats, including effects of restoration works and active protection; the paper about that subject in the journal *Lynx* (Ciechanowski et al. 2006). Both maintaining own faunistic database and broad cooperation with bat workers in the whole country, allowed me to become a co-author of few syntheses, like those summing up the knowledge about wintering of noctule, common pipistrelle and soprano pipistrelle within the borders of Poland in the journal *Nietoperze* (Wojtaszyn et al. 2004, Łupicki et al. 2007), about the status and distribution of pond bat in a Dutch journal *Lutra* (Ciechanowski et al. 2007), finally about the status and distribution patterns of all the other representatives of Polish bat fauna in a Czech journal (Sachanowicz et al. 2006). I continued that research trend, participating in the project *Atlas ssaków Polski* [*The Atlas of Polish Mammals*], directed by prof. Henryk Okarma and prof. Wiesław Bogdanowicz, for which I prepared databases and distribution maps of five bat species, i. e. greater mouse-eared bat *Myotis myotis*, Bechstein's bat *M. bechsteinii*, pond bat, northern bat *Eptesicus nilssonii* and Nathusius' pipistrelle[1]. Benefiting from bat mist netting, I also participate in multidisciplinary parasitological research, covering ecto-, meso- and endoparasites, allowing me to became a co-author of four next publications (Izdebska et al. 2009, Sachanowicz et al. 2017, Mierzyński et al. 2018, Cierocka et al. 2022). In the last paper, published in the journal *Animals*, we described a new-for-science species of mite from the family Demodecidae – *Demodex pusillus* Izdebska, Cierocka, Rolbiecki et Ciechanowski, 2022, collected from dead bats found during one of interventions in Pomerania region, 16 years earlier.

Preparing expert opinions, especially mammal surveys, allowed me, also, to publish some number of papers of local or regional importance, e. g. about distribution of small terrestrial mammals – rodents and soricomorphs, printed in *Przegląd Przyrodniczy* and *Badania Fizjograficzne nad Polską Zachodnią Seria C* (Ciechanowski 2001a, 2001b), but also, in cooperation with Dr Jan Cichocki and Dr Agnieszka Ważna from University of Zielona Góra, a broad synthesis about the structure of assemblage inhabiting raised and transitional peat bogs in Poland and factors affecting them, in the journal *Biological Letters* (Ciechanowski et al. 2012). Thanks to taking part in such tasks, I also published, as an author or co-author, results of complex surveys of mammalian fauna for selected nature reserves, in journals *Chrońmy Przyrodę Ojczystą, Parki Narodowe i Rezerwaty Przyrody*, *Acta Botanica Cassubica* and peer-reviewed monographs (Ciechanowski et al. 2003, Ciechanowski 2004,

[1] https://www.iop.krakow.pl/Ssaki/gatunki

Ciechanowski 2009, Ciechanowski and Antczak 2011, Ciechanowski 2012a, Wikar and Ciechanowski 2019), among which outstand the synthesis of long-term research on mammal fauna of „Jezioro Drużno" nature reserve, where, since 1970., the field station of our Department is located (Ciechanowski et al. 2013). Finally, my involvement as a coordinator of large, interdisciplinary teams, composed of naturalists specialized in various fields, resulted in being co-editor of monographs of three nature reserves in Gdańsk Pomerania region, together with Prof. Jacek Herbich and Prof. Wiesław Fałtynowicz (Ciechanowski et al. 2004, Herbich and Ciechanowski 2009), co-authorship of comprehensive, interdisciplinary evaluation of some areas in our region that were important for nature conservation (Ciechanowski et al. 2001a, 2001b), and proposal of delimitation of new protected areas in Tricity Metropolitan Area (Buliński et al. 2006).

Few times I was invited to write chapters in handbooks and guidebooks, being the synthesis of actual state of knowledge in particular field, necessary in the academic learning, practice of nature conservation, and even acting as a reference material, making scientific work easier. The first of them were chapters about Bechstein's bat and pond bat in „*Guidelines to conservation of habitats and species Natura 2000*", commissioned by the Ministry of Environment (Ciechanowski and Kokurewicz 2004, Ciechanowski and Piksa 2004). Later, I prepared methodologies for national monitoring of that species, used in methodological guidebooks published by Chief Inspectorate of Environmental Protection (Ciechanowski 2012b, 2012c). Together with Prof. Wiesław Bogdanowicz, I prepared characteristics of Polish mammal fauna, along with species checklist for 4th volume of „*Fauna Polski*" [*The Fauna of Poland*], a publication of Museum and Institute of Zoology PAS in Warsaw (Ciechanowski and Bogdanowicz 2014). Finally, invited by late Prof. Czesław Błaszak from Adam Mickiewicz University of Poznań, I wrote a chapter about bats, summarizing knowledge on their morphology, anatomy, ecology, ethology, evolution and systematics, for the volume of „*Zoology*", basic academic handbook for teaching that subject in our country, printed by Polish Scientific Publishers PWN (Ciechanowski 2020).

My studies on bats and publication activity associated with that subject resulted in frequent invitation to reviewing submitted manuscripts in the numerous, international scientific journals: *Global Change Biology* (1), *Canadian Journal of Zoology* (1), *Annales Zoologici Fennici* (1), *European Journal of Wildlife Research* (1), *Acta Chiropterologica* (12), *Mammal Research* (1), *Acta Theriologica* (1), *Mammalia* (2), *Acta Zoologica Lithuanica* (1), *Central European Journal of Zoology* (1), *Biologia Bratysława* (1), *Restoration Ecology* (1), *Polish Journal of Ecology* (2), for which, in total, I prepared 27 peer-reviews. I also wrote

26 reviews of scientific papers for national or regional journals: *Animal Science* (1), *Chrońmy Przyrodę Ojczystą* (8), *Forest Research Papers* (1), *Parki Narodowe i Rezerwaty Przyrody* (2), *Przegląd Przyrodniczy* (5), *Przyroda Sudetów Zachodnich* (4), *Roczniki Bieszczadzkie* (1), *Studia i Materiały CEPL w Rogowie* (1), *Zoologica Poloniae* (1), peer-reviewed monograph (2). In years 2018-2020 I work voluntarily as an editor with powers to decide about manuscript acceptance in the journal *Mammal Research*, published by Springer and Mammal Research Institute PAS. In years 2004-2012 I was also a member of Editorial Board of the journal *Nietoperze* [*The Bats*], published by Polish Society Of Wildlife Friends "pro Natura", for which I prepared 46 reviews of submitted manuscripts. I also reviewed student research-conservation project for US-based, non-governmental organization *Bat Conservation International*.

Presentation of significant scientific or artistic activity carried out at more than one university, scientific or cultural institution, especially at foreign institutions and other forms of research activities carried out abroad

My scientific activity in the other institutions was strictly associated with characteristics of the conducted research, especially the field ones, associated with participation in scientific expeditions. It allowed to collect materials from geographical regions distant from Poland or even Palaearctic, but also obtaining new skills, used later in scientific and teaching work in my home university.

On 19.07-14.08.2009 I worked, as a volunteer on the research ship s/y OCEANIA, belonging to Institute of Oceanology, Polish Academy of Sciences in Sopot. The cruise route runs along the coasts of Western Spitsbergen. My job during that cruise was to conduct seabird count (every 2h) and preliminary analysis of their results, including basic univariate statistics.

On 28.03.2015-15.03.2015 I participated, as a volunteer, in field research of National Museums of Kenya and Karatina University (project leader: Dr Paul Webala), conducted in Kenyan national parks: Kakamega, Mount Elgon, Lake Elementaita and Kisumu, as well as their direct surroundings. My duties covered bat mist netting, conducting morphometric measurements of captured individuals, survey of daily bat roosts, but primarily training of Kenyan scientists and students in bioacoustic methods (recording, detection and analysis of ultrasounds).

In 2006 I visited HS Skovoroda Kharkiv National Pedagogical University in Kharkiv, Ukraine (research group led by prof. Anton Vlaschenko) in order to acquire tissue samples for

genetic study on Kuhl's pipistrelle. During that trip, I participated in bat mist netting in Kharkiv and National Park „Gomolsha Forest".

In 2012, I was invited by dr Gunars Petersons and dr Jurģis Šuba to give a lecture about bat ecology on Faculty of Biology, University of Latvia, Riga. I gave that lecture, titled „*From sensory ecology and wing shape to maps and landscape: habitat use by European bats*" on 27.11.2012. It presented part of the results of my recent Scientific Achievement (point 4, above) on the background of the current knowledge on bat ecomorphology.

In years 2003, 2004, 2005, 2006, 2007, 2010, 2011 and 2012 I co-organized (together with Konrad Sachanowicz – Institute of Biology, Nicolaus Copernicus University in Toruń, later Museum and Institute of Zoology PAS, Aleksander Rachwald – Forest Research Institute and Michał Piskorski – Institute of Biological Sciences, Maria Curie-Skłodowska University of Lublin) a series of scientific expeditions to Albania, focused on, as comprehensive as possible, survey of bat fauna, inhabiting that country. Their results, including scientific publications based on them, were described in the previous chapter („*Research projects, activities and publications not related do the Scientific Achievement set out in art. 219 § 1 point 1 of the Act*"). My duties during that expeditions covered bat mist netting, recording of their echolocation and social calls, collecting samples for genetic studies and gathering geolocation data.

In March 2019 and February 2020 I co-organized (together with Zuzanna Wikar and Marta Szurlej) two scientific expeditions to Sibundoy, Colombia in cooperation with Foundation "Biodiversitatis" and Faculty of Biology, University of Łódź. The main aim of the expeditions was preliminary survey of bat assemblage in a patch of humid Andean forest, bought by Foundation to protect it as a nature reserve and a site of the future, first ever, Polish research station in tropical zone. My duties during that expedition covered bat mist netting, recordings their echolocation calls, conducting morphometrical measurements, collecting bat ectoparasites, faecal pellets for dietary analysis and samples for genetic studies. Additionally, I conducted preliminary survey of bird fauna of the reserve, handled camera traps for recording of larger mammals and collected moss samples for the study of tardigrades (Tardigrada) prepared by Prof. Łukasz Kaczmarek, Adam Mickiewicz University, Poznań.

Presentation of teaching and organizational achievements as well as achievements in popularization of science or art

I have given classes on the University of Gdańsk since 2001, first as a PhD, since 2004 as a research assistant, and, finally, since 2006, as an assistant professor. In total, I gave **21** different classes (approximately 210 hours/year) on degree courses: Biology, Nature, Evaluation and Protection of Natural Areas and Conservation of Natural Resources (Faculty of Biology), Bioinformatics (Faculty of Mathematics, Physics and Computer Science), Environmental Protection (Faculty of Chemistry), Geography (Faculty of Geography) as well as Forensic Science and Forensic Biology (Faculty of Law and Administration), both at the level of undergraduate (bachelor's degree), graduate (master's degree) and postgraduate education. They have covered ecology, especially animal ecology, systematics, field diagnostics, biogeography, conservation of nature and biodiversity. Since 2009 I have given original, personally designed class *„Biology and ecology of bats"*, at which the attending students can acquire detailed knowledge on evolution, anatomy, morphology, bioacoustics, ecology, ethology, systematics, research methods and conservation of the second most speciose mammalian order in the world. I give special attention to the quality of field classes that I consider crucial to teaching natural sciences, both basic and applied ones; nine classes among subjects taught by me, included field work in their syllabuses. I was also given a task of looking after a scientific collection of vertebrate specimens in Department of Vertebrate Ecology and Zoology, University of Gdańsk.

In total, I was a supervisor of 26 MSc theses and 15 BSc theses on degree courses: Biology, Environmental Protection and Nature. Recently, I provide direct, informal, scientific supervision to the two PhD students on the University of Gdańsk; subject of their research cover molecular identification of prey in foliage-gleaning bat species and morphological indicators of niche partitioning in sibling species belonging to genus *Myotis*. Since 2005 I have been also a supervisor of Student Bat Research Group of the University of Gdańsk (in years 1997-2000, during my own graduate studies, I was a Chairman of that group). Within that function, I co-organised and supervised 23 bat research scientific-training field camps for our students and gave lectures about biodiversity of Mexico, Costa Rica and Kenya, based on experience from my trips. In years 2013-2014 I was in chargé of preservation, arranging and cataloguing of the zoological collection in the Department of Vertebrate Ecology and Zoology, University of Gdańsk, which are used, recently, e. g. for the educational purposes.

Since 1997, I carried out, and later also coordinated projects associated with environmental consulting – project documentations, management plans and outlines of

conservation goals for protected areas (nature reserves, landscape parks[2], Natura 2000 sites, ecological sites[3], nature-landscape complexes[4]), the species' monitoring reports but also environmental impact assessments for various construction projects. The effect of that activities is authorship or co-authorship of at least 128 documents and reports, mostly regarding mammals, especially bats, but also (in cooperation with other experts) providing comprehensive, interdisciplinary evaluation of natural values, commissioned by, among others, Regional Directorates of Environmental Protection in Gdańsk and Olsztyn, General Directorate of National Roads and Motorways, Regional Directorate of State Forests in Gdańsk, PGE Polish Energy Group, Pomeranian Metropolitan Railways, Park of Culture and Entertainment 'Grodzisko' (today: 'Hewelianum'), Departments of Environment of the Gdańsk, Sopot and Gdynia Magistrates, Maritime Office in Gdynia, Tricity Landscape Park and several private investors or consultancies hired by them (mostly from wind energy industry). Three times, in 2011, 2016 and 2021, on behalf of Institute of Nature Conservation PAS, carrying out the task commissioned by Chief Inspectorate of Environmental Protection, I worked as national coordinator of monitoring of pond bat and Bechstein's bat, for which I developed an official methodology (being mandatory in Poland until now). On request of General Directorate of Environmental Protection, together with Dr Andrzej Kepel for Polish Society for Nature Protection „Salamandra", I prepared a draft of guidelines to pre-construction surveys and post-construction monitoring for environmental impact assessments associated with impact of wind farms on bats.

Since the beginning of graduate studies, I have engaged myself in non-profit social activism, focused on conservation of nature and biodiversity, mostly withing structures of Polish Society of Nature Protection „Salamandra", which I have been an active member since 1996 and in which Programme Board I sit since 2021. Recently, I am a chairman of Academic Bat Research Group of PTOP „Salamandra" in Gdańsk. I also engaged in conservation activism under the aegis of Naturalist Club from Świebodzin, another prominent, Polish conservationist NGO. As part of involvement in activities of the first organization, for many years, I conduct interventions associated with protection of bats in the built-up areas. Few times, I also led the projects focused on bat conservation in Gdańsk Pomerania region,

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[2] *Park krajobrazowy* – in Polish environmental law, large-scale protected area with relatively mild conservation regulations, devoted to protection of cultural landscape along with bio- and geodiversity.
[3] *Użytek ekologiczny* – in Polish environmental law, small protected area of local significance, securing patches of valuable habitats or localities of rare, threatened or protected species; roughly corresponding to Site of Special Scientific Interest (SSSI) in the United Kingdom.
[4] *Zespół przyrodniczo-krajobrazowy* – in Polish environmental law, protected area of local significance, securing natural, landscape/aesthetic and cultural values.

financed, among others, by Small Grants Program of Global Environment Fund (GEF/SGP – years 2007-2008), and Regional Fund for Environmental Protection and Water Management in Gdańsk[5]. In cooperation with the city of Sopot and Regional Directorate of Environmental Protection, I brought about the creation of 8 protected areas in the rank of ecological site. I also coordinated (in cooperation with PTOP „Salamandra" and the Association for the Protection of Owls) gathering the scientific and legal documentation to support the social protests against construction of the regional road Wejherowo-Celbowo through the Natura 2000 site Darżlubska Forest. For many years, I was also a member of the Rarities Committee at the Agreement on Protection of Bats in Poland (verifying the amateur observations of rare or hard-to-identify bat species), and Interview Panel of Bat Survey Licenses at the same organization (conducting exams confirming qualifications of trained amateur bat workers). Since 2005 I have been a member of the Regional Council for Nature Conservation, an advisory body to the Regional Director of Environmental Protection in Gdańsk, since 2014 – in the Council of Pomeranian Landscape Park Complex, since 2014 – in the Scientific-Social Council of the Forest Promotional Complex "Oliwsko-Darżlubskie Forests".

My involvement in sharing knowledge and popularization of science covers mostly the subject of bat biology and – in a broader sense – problems of nature and biodiversity conservation. I am a co-author of the book „*Nietoperze Polski*" (*Bats of Poland*, together with Konrad Sachanowicz and drawings by Tomasz Cofta), printed first in 2005 by MULTICO publishing house and saw a second edition in 2008. For many years, it was the most popular field guide to identification of Polish bat species and the most frequently used source of knowledge about their biology. I am also a co-author of content of three guides to the natural values of the Sopot city and Tricity Landscape Park, three educational booklets about valuable natural locations in Sopot and Gdynia cities, as well as several educational signs about flora, fauna and protected areas, distributed across the whole Tricity metropolitan area. I wrote also at least a dozen or so articles and news to the *Biuletyn Polskiego Towarzystwa Ochrony Przyrody „Salamandra"* [*Bulletin of the Polish Society for Nature Protection „Salamandra"*] and its successor - *Magazyn Przyrodniczy „Salamandra"* [*„Salamandra" Nature Magazine*]; recently I have a permanent column „*Skróty ze świata nauki*" [*Science World Digest*] in the latter. In years 2003-2015 I led educational walks devoted to observation of bats and bioacoustics, targeted at citizens of the Tricity agglomeration, as a part of the 13 subsequent Baltic Festivals of Science (events entitled „*Night hunters*" and „*Walking with*

[5] *Wojewódzki Fundusz Ochrony Środowiska i Gospodarki Wodnej* – a Polish public fund, functioning in every region/district (*voivodship*) of the country, devoted to supporting environmental and conservationist initiatives.

bats"). Four times, I also participated an educational event „*BioBlitz*", organized by Institute of Oceanology PAS in Sopot, which aimed at survey of biodiversity of selected area in the shortest time possible (usually 24h) and spread knowledge about it to the local community. I participated in the, organized by Faculty of Biology, project „*Invite a scientist to Your school*", during which I presented, in secondary schools of Pomeranian voivodship, lectures about three subjects – biology and conservation of bats, advances in mammalian taxonomy, including the discoveries of new species in last years, and function of deadwood in forest ecosystems. The first of the subjects was also presented during many lectures I gave in Tricity schools, during several, consecutive projects of bat conservation in Pomeranian region, financed by Regional Fund of Environmental Protection and Water Management in Gdańsk. Twice, on the invitation of Tucholski Landscape Park, I led workshops on bat conservation, with field classes, targeted at, among others, teachers from regional schools. I also conducted workshop on the same subject, for staff of the Słowiński National Park. In years 2020-2021 I gave also three webinars, commissioned by Centre of Ecological Information and Education in Gdańsk, entitled: „*Mess in the forest? Deadwood and biodiversity*", „*Purring apocalypse. Are house cats a threat to wild nature?*" and „*Into the Andes for... bats. Photographic-naturalist expedition to Colombia*". In 2009, Polish Public Television (TVP) made an episode of natural-educational series „*Wild Poland*" entitled „*The well full of bats*", devoted to, among others, winter bat census in „Słupia Valley" Landscape Park. In 2016, in TVP3 channel, an episode of the series „*Mission Nature*" entitled „*Kurze Grzędy*" was broadcasted, in which I presented natural values and biodiversity in one of the wetland reserves of Pomeranian region, covered by interdisciplinary faunistic survey, coordinated by me. Many times, I have also given interviews about bats, especially their conservation, in Radio Gdańsk and the Gdańsk Television but also in „*Gazeta Wyborcza Trójmiasto*" and „*Dziennik Bałtycki*" newspapers.

SUMMARY

Summing up, my scientific achievements consist of **26 original, peer-reviewed papers** published in English (including 21 after obtaining a PhD), in journals indexed by Web of Science (Journal Citation Report 2020) and **88 other peer-reviewed publications out of JCR** (1 English-language monograph, edition of 1 Polish-language monograph, 27 chapters in Polish-language monographs, 6 English-language papers in journals indexed by Master Journal List, 3 English-language papers in other journals, 1 English-language paper in post-conference proceedings, 47 Polish-language scientific papers), including 51 after obtaining a

PhD. I am also a co-author of **128 environmental expert opinions and reports**, in which mostly I participated as coordinator of works. My **Hirsch index** according of **SCOPUS** database is **11** (according to **Web of Science** database – **10**), while my papers **were cited 394 times** (including 373 times without autocitations). Summary ***Impact Factor*** of all my papers according to the list of Journal Citation Reports (JCR) for the year of publication, amounts **32.351**, while ***Source Normalized Impact Paper*** (SNIP) amounts **19.081**. According to **Google Scholar**, all my works were cited **1147** times, **Hirsch index** is **15**, while **i10-index** – **23**. Summary number of points for all publications, both indexed and unindexed, according to scoring of the Ministry of Science and Higher Education for the particular year of publication amounts: **981** (without papers published in years 2019-2022 – **691**), while according to new scoring (in operation since 2019) – **2435**.

I presented results of my studies on several conferences and symposia, being an author or co-author of **85 oral presentations or posters**. I was also **a head of 1 scientific project financed from grant of National Science Centre**[6], the main investigator in the next such project and a head of three projects financed from grants of the University of Gdańsk, acquired for the Individual Research. I was also a **supervisor** of **26 MSc theses** and **15 BSc theses** but also conducted a direct, informal supervision for three PhD students. For many years, I have been also a member of the Regional Council for Nature Conservation, an advisory board to regional environmental protection authority.

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(Applicant's signature)

[6] A grant agency that took duties of Ministry of Science and Higher Education with respect to financing of research projects.