

Structure of Nests and Colony Sizes of the European Hornet (*Vespa crabro*) and Saxon wasp (*Dolichovespula saxonica*) (Hymenoptera: Vespinae) in Urban Conditions

by

Jerzy Nadolski¹

ABSTRACT

Studies of different groups of insects in urban areas sometimes show large populations, greater than in non-urban areas. The reason for this is a presence in the cities some of dominating species which often occur almost en masse. This group includes, inter alia, hymenopterans and especially social wasps (Vespinae). Colonies and nests of two wasp species, the European hornet (*Vespa crabro*) and Saxon wasp (*Dolichovespula saxonica*) in areas of the city of Łódź in Poland were studied. Whole colonies positioned both in buildings as well in natural places, size of societies, parameters their nests, differentiation of cells in combs and their location were investigated. We also studied the correlation between the size of the nest and societies of these insects. It was found that nests established in the buildings are much larger, produced more individuals of reproductive castes and thus obtained a better reproductive success especially for the hornet colonies whose queens prefer the buildings as a place to nest.

Key Words: Urban fauna, social wasps, *Vespa crabro*, *Dolichovespula saxonica*, Hymenoptera, Vespinae, nests of wasps.

INTRODUCTION

Due to the diversity of habitats and wealth of species as well their small size, there is often a lack of information regarding insects existing in urban areas. Individual insect species react differently to urbanization pressure and mosaics of environment within cities and only some of them are able to effectively inhabit these areas with very specific ecological niches. Studies conducted so far on various groups of insects in urban areas sometimes showed large total populations which were higher than those known from

¹ Natural History Museum, University of Łódź, Kilińskiego 101, 90-011 Łódź, POLAND, e-mail: nadolski@biol.uni.lodz.pl

non-urban areas. The reason for this is a presence in the cities of dominant species which often occur almost en masse. This group includes, inter alia, hymenopterans and especially ants (Formicidae) and social wasps (Vespinae) (Chudzicka, Skibińska 1994). The presence of wasps (Vespidae) in urban areas is commonly known. (Czechowski 1979; Haeseler 1982; Skibińska 1982; Skibińska 1987; Ahrné 2008), including the city of Łódź in Poland (Kowalczyk 1991; Nadolski 2004; Kowalczyk & Kurzac 2005; Kowalczyk & Szczepko 2008; Nadolski *et al.* 2011). Numerous and large-scale studies determined the species composition of this group of insects, their proportions as well as the dynamics of quantitative changes in the urbanized areas (Pawlikowski 1998; Nadolski 2000b; Nadolski 2001; Pawlikowski *et al.* 2005; Hermes & Köhler 2006; Christie & Hochuli 2008; Langowska *et al.* 2010). The study of this group of insects is important because wasps in the city can be hazardous for people. They can inflict dangerous stings (McGain *et al.* 2000; Nadolski 2000a) and they can cause the spread of pathogens (Nadolski *et al.* 2000).

Organization of insect societies for many years is of interest to many study centers. An excellent example of this is the study of honey bee (*Apis mellifera*) societies. Special scientific centers whose research interests are focused solely around this species of insect are known. Moreover, there are many papers on the subjects of the organization of wasp societies, of which a classical model of these studies are paper wasps – species of the genus *Polistes*. Their nests, built without protective envelopes, are easy to observe and therefore have become a common source of information on the behavior of wasps (Strassmann 1989; Tibbetts 2004; Starks & Fefferman 2006). The observations of Vespinae are definitely more difficult, although not impossible even in the case of hornets (Yamane & Makino 1977; Bunn 1988; Nakamura & Sonthichai 2004). However, it is often difficult to accurately determine the quantitative parameters of colonies of these animals. The specificity of their nests, tightly surrounded by layers of envelopes, whose aim is to protect the colony and maintain an adequate microclimate, constant humidity and temperature (Klingner *et al.* 2005; Klingner *et al.* 2006), as well high number of individuals and aggressiveness of their societies may often pose serious impediments. Hence sizes of colonies of these insects are often subject to speculation. Parameters of Vespinae nests are occasionally determined, during studies of these insects'

biology (Brian 1965; Haeseler 1997; Leathwick & Godfrey 1996), however, exceptionally little is known about the real size of societies of these wasps, especially in urban conditions. Therefore, the author undertook this difficult task, whose aims were to obtain information about the structure and the real size of societies and nests of two species of Vespinae in an urbanized area. The main purpose of these studies were therefore to determine the parameters and structures of their nests characterizing the size of their colonies and tracking the steps of the building of nests and development of societies in the aspect of adaptation of this group of insects to urban conditions. Studies were conducted on two species of social wasps – the European hornet - *Vespa crabro* (Linnaeus, 1758) and Saxon wasp - *Dolichovespula saxonica* (Fabricius, 1793). Both species differ in size of individuals, as well as colonies, and their nests are convenient for research because they are built in places relatively easy to locate. The typical habitat both of these wasps is deciduous woodland. They usually build their nest in hollow trees, on branches of the trees, sometimes in natural burrows. In the city, their colonies are established usually in different buildings and urban infrastructures, and also in bird nest-boxes (Nadolski 2004; Langowska *et.al* 2010).

Recent studies greatly increased the scope of various activities aimed at reducing the urban populations of social wasps (Nadolski 2001). Numerous media campaigns increase interest in this issue and heighten concerns about the city's inhabitants caused by the presence of colonies of wasps. This fear, which is not always fully justified, causes that people massively inform municipal services about practically all of the observed colonies of wasps and a large part of the nests is removed.

METHODS

The studies were conducted in the area, located within the administrative boundaries of the city of Łódź as well as within areas directly adjacent to it. Łódź is a city in central Poland covering 294.4 km² (Diehl 1997) of which green areas including parks and forests comprise a significant area 55.5 km², which constitutes about 19% of the whole administrative area of the city. The climate is intermediate between the continental climate – Eastern European and maritime climate – Western European, with the average annual rainfall of 573 mm (Dubaniewicz 1990). Łódź as a city has a specific concentric and

regular arrangement of streets and buildings, which is sometimes disturbed by traffic routes. This system of street, led to the creation of characteristic three zones each with a different character. The correlation between the area classified to the given zone, and the qualitative and quantitative composition of the studied different groups of organisms was found (Kuziel & Halicz 1979; Markowski *et al.* 1998; Nadolski 2000b; Nadolski 2001, Markowski *et al.* 2004). In recent years, the expansion of residential areas as well as conducted road investments gradually changed the original layout of the zones. However, their general character and separateness still exist. The first zone this is a center of the city with the rest of the former Lodz at the turn of the 19th and 20th century. This zone, consisting of a old, historic areas, is cut by a chessboard streets running perpendicular to one another, where historic Art Nouveau buildings are located. This area is replenished by newly residential and office buildings. This zone is poorly differentiated biologically, and only to a small extent this area is enriched by the urban green. However, the presence the old city parks, forming a sort of enclave of greenery, enriched by the old, centuries-old plantings, create very specific living conditions for different animal groups, including insects. These parks are often a number of discrete and bounded through the streets and buildings and often form specific, partially isolated ecosystems. The second zone, formed by areas occupied by modern blocks including skyscrapers and their infrastructure as well as by industrial sites, despite the presence of large number of young trees and large green areas, makes an impression of rather poor and monotonous. By its specificity, in a very small degree, it allows for free migration of animals from the area of the city center to suburban and non-urban areas. Therefore in this area observed, as in the city center, large qualitative impoverishment of many taxonomic groups of animals, including insects (Markowski *et al.* 2004). The third zone runs along the administrative border and surrounds whole of the city and thus other zones also. This is an area of detached houses and old farms, which is in direct contact with agricultural lands and forests located outside the city. Therefore, this area may be regularly replenished by migrating species of animals. Green belts, which connect in some places all three of zones, as well as railway lines, which run deeply even into the dense urban development, also allow for limited migration of species to places, located within the very city centre (Kowalczyk & Nadolski 2007).

Information about the location of nests came, in most cases, from the municipal services, especially from the Fire Brigade Department to which all such information are reported, forest services as well as from the telephone notification and other survey data obtained from citizens of Łódź, as well as especially from author's own observations. *Vespa crabro* and *Dolichovespula saxonica* colonies came from different places in all zones of the city. The European Hornet is a large, easily distinguishable wasp and finding and identification of colonies of this insect are very easy. However, all incoming information was checked. Being aware of possible defects of these methods of search of nests, but the only usable, it was necessary to estimate the possible their error. We must be aware of the fact that Łódź has a surface of almost 300 km², with a dense urban structure, with multiple industrial regions, agricultural areas, forests and parks. The author of this study has decided to carry out detailed inventory all of wasps nests in of randomly selected 10 squares, each with an area of 1 km². Efforts were made in these areas to record all nests of Vespinae, particularly colonies of *Vespa crabro* and data obtained in this way compare from the number of colonies of the same squares noted as a result of notification, surveys, and data obtained from all of the municipal services. It turned out that in case of *Vespa crabro* only a few nests established on the premises of abandoned factories and fallow lands were not included in the notifications. These studies showed very high over 90% effective registration all of colonies of hornet in the city. Locate and recognize the nest of *Dolichovespula saxonica* is much more difficult, and hence the above described method could not be used. Therefore, the total number of nests of this species in the city of Łódź was not specified. After verified, received data were entered into a specially created database in Access (Microsoft Inc 1997 and 2000). Only part of nests was included in further research which was dependent on the adopted procedure. Some vibrant and active colonies were removed, along with all individuals of wasps who remained in it. To collect all individuals of societies of wasps, the liquidation of these nests was carried out at night. Studies of social wasps' nests are limited due to technical reasons. The choice of the nest is dependent on many factors which are essential to use it for further study. For most of these analyzes could be used only complete and undamaged nests. For this reason, underground nests of wasps, as well as placed high in the branches of trees, could not be used.

For further detailed analysis were selected the appropriate number of nests collected from all study areas and zones in the city, that met the necessary requirements. For comparative analysis of some parameters of nests and castes were used all collected colonies at the final stage of their development, derived with two or three consecutive years. After freezing, whole nests were kept at a temperature -18°C for further study. Both active as well as the empty nests, were subjected to a thorough analysis. Graphics and statistical analyses were made using STATISTICA 9 (StatSoft, Inc. 2009). Standard statistical methods were used. For better clarity, precise description of the used methods sometimes will complement the information about the results achieved that were obtained relating to specific topics included in this paper.

RESULTS

The place of establishment of the colony

In spring, the young new queens of wasps, born and mated the previous autumn begin the building of nests, choosing for this places which are often characteristic for the given species. Based on the material obtained within the years 2000-2008 which was recorded in the database, the preferences in this aspect were analyzed. Every recorded place was qualified into two categories. To first category was classified 'natural places', the typical and characteristic for particular species which were not places inhabited by humans or arising as a result of human activity. The only exception were the breeding boxes for birds, which because of their characteristic construction resemble hollows of trees, therefore they were classified to places in 'natural' groups (photo 1). To the other category - "buildings" were included places directly related to the structure of the urbanization of the city - residential buildings and outbuildings with the associated infrastructure. Within years 2000-2008 in the area of Łódź and its immediate neighborhood, based on the conducted research, 365 developed nests with workers of *Vespa crabro* (table 1) were recorded.

From the obtained results, the fact of a large number of nests established in residential or utility buildings, which as the 'unnatural' places included in the second category, really deserves attention. Most often, wasps' colonies were found in unused attics of buildings and in cellars (photo 2 and 3). They were often found in layered walls, in the insulation of roof or flat roof, as



Photo. 1. *Dolichovespula saxonica* nest in a breeding box for birds.

Table 1. The choice of place for nests of *Vespa crabro* within the particular zones of Łódź

species	City centre			Housing estate			Suburban area including forests				nests total		
	natural places	%	buildings	%	natural places	%	buildings	%	natural places	%		buildings	
<i>Vespa crabro</i>	3	0.8	33	9.0	24	6.6	130	35.6	11	3.0	164	45.0	365

Photo. 2. *Vespa crabro* nest in an attic

well in the chimney or ventilation flues. It happened that nests were formed directly on windowsills and window blinds, on balcony grilles and various objects left over in cellars, in clothes being on balconies, coca-cola containers kept at the back of shops, window curtains or even in bullet-proof firewall of military shooting range.

Study of the structures of nests.

The catalogued and collected nests underwent a thorough quantitative and qualitative analysis. 34 nests of *Vespa crabro* and 93 nests of *Dolichovespula saxonica*, at the final stage of development, were accurately investigated both active colonies and empty nests. For the statistical analysis of parameters of cells and combs, only such nests were used which possessed fully developed



Photo. 3. *Vespa crabro* nest in a cellar during a rebuilding

and not damaged combs. Size of whole nests (diagonals), thickness of envelopes, size and shape of combs, number and size of individual cells (diagonals and depth of 10-50 randomly selected cells, depending on the size of combs, sequentially counted every fifth cell), the utilization of the cells in different stages of colonies development, location of meconium (fecal pellets in cells) and the number and proportions of castes. The surfaces of combs were calculated using the model of a geometric Fig. most resembling the shape of the comb. These were most often the surfaces of a circle, ellipse, triangle or rectangle. The volume of the nest was calculated, depending on the shape, with the use of the formula for the volume of a sphere, ellipsoid, cylinder and sometimes cuboids. Table 2 presents size of nests of *Vespa crabro* and *Dolichovespula saxonica* coming from both types of places (natural and buildings).

Values of parameters of cells (width and depth) in nests of studied wasp's species were subjected to statistical analysis. As a result of these analyzes three types of cells, referred to herein as (small, medium and large) were distinguished. Table 3 presents the results of the analysis of parameters of nests (combs and cells) of the studied wasps' colonies. No statistically significant differences between parameters of combs and cells of the nests from natural places and buildings. For all nests of *Vespa crabro*, analysis of the width of cells

Table 2. Mean volumes of nests of *Vespa crabro* and *Dolichovespula saxonica* in the final stage of their development from the city of Łódź in years 2000 - 2008.

species	nests in buildings volume (dm ³) ± SE	nests in natural places volume (dm ³) ± SE
<i>Vespa crabro</i>	21.00±11.31	4.37±0.24
<i>Dolichovespula saxonica</i>	1.32±0.29	0.78±0.12

Table 3. Values of parameters of nests of *Vespa crabro* and *Dolichovespula saxonica* within the area of Łódź at the final stage of their development.

species	surface of comb (cm ²)		dimensions of small cells (mm)		dimensions of medium cells (mm)		dimensions of large cells (mm)				
	Max.	min.	N	width.±SE	depth.±SE	N	width.±SE	depth.±SE	N	width.±SE	depth.±SE
<i>Vespa crabro</i>	1963	9	100	7.65±0.038	17.69±0.88	140	8.7±0.032	20.34±1.63	170	10.15±0.029	28.41±5.78
<i>Dolichovespula saxonica</i>	177	2	110	3.89±0.035	9.78±0.65	200	5.51±0.025	12.85±0.98	160	7.06±0.030	17.97± 2.65

conducted using Levene's test showed homogeneity of variances ($F_{2,407} = 1.64$, $p = 0.196$, $\alpha = 0.05$), the differences between mean values of the width of cells are statistically significant (ANOVA: $F_{2,407} = 1448.6$, $p < 0.00001$). The post-hoc analysis with Fisher's NIR test demonstrated important statistical differences between the mean values of the width of small, medium and large cells (MS intergroup = 0.145, $df = 407.00$, for all variants $p < 0.05$). For the second studied species *Dolichovespula saxonica* the diversification of these variables was also statistically significant (Levene's test ($F_{2,467} = 1.830$, $p = 0.162$) (ANOVA: $F = 98655.13$ $p < 0.0001$) Fisher's NIR (MS intergroup = 0.135, $df = 467$, for all comparisons $p < 0.05$). The statistical analysis of the depth of cells in the nests of both species demonstrated lack of homogeneity of variance. Nonparametric test also confirmed the variation within the studied cells into three types (ANOVA Kruskal-Wallis test for *V. crabro*: $H_{2,410} = 233.52$ $p < 0.0001$ and for *D. saxonica*: $H_{2,470} = 363.06$ $p < 0.0001$).

The distributions of mean values of width of cells, present in consecutive combs and different nests of *Vespa crabro* are presented in graphs in Figs. 1 and 2. We can clearly see the differences between cell types. Parameters of

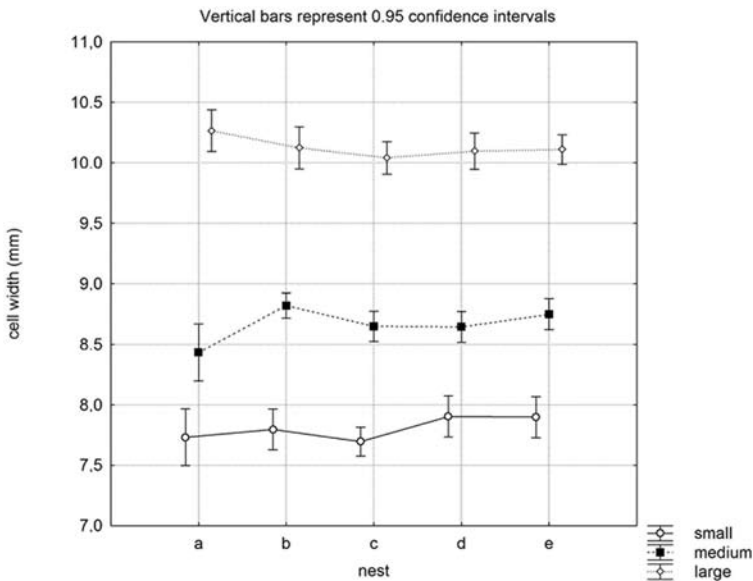


Fig. 1. The distribution of mean values of the width of different types cells, in several nests of *Vespa crabro*, in the final development stage of colonies.

a given type of cell are similar but not identical in different combs and also between different nests of hornets.

Diversity and location of particular type of cells both within a single nest and between various nests were studied. The parameters of one type of cell of the same species are subject to minor changes. The study showed little difference of cells size between nests, but much more noticeable are the differences between the combs, even within the same nest. To examine the distribution of mean values of parameters of different types of cells under the influence of two factors grouping: combs and nests (*Vespa crabro*), statistical analysis was performed using a hierarchical ANOVA. Levene's test demonstrated homogeneity of variance for statistics – the width and the depth of cells for particular their types, in hornet's nests. Statistical analysis - univariate test of significance for the variables - the width of small cells of two, two-stage grouping factors (nest and comb) are shown in Fig. 3 (Hierarchical ANOVA). The obtained results acknowledge the statistically significant differences of the mean value of this parameter. Small cells differ in width, both in particular combs in a nest and in combs between nests. Graphical illustration of the distribution of mean values of cell width is shown in graphs (Figs. 4 and 5).

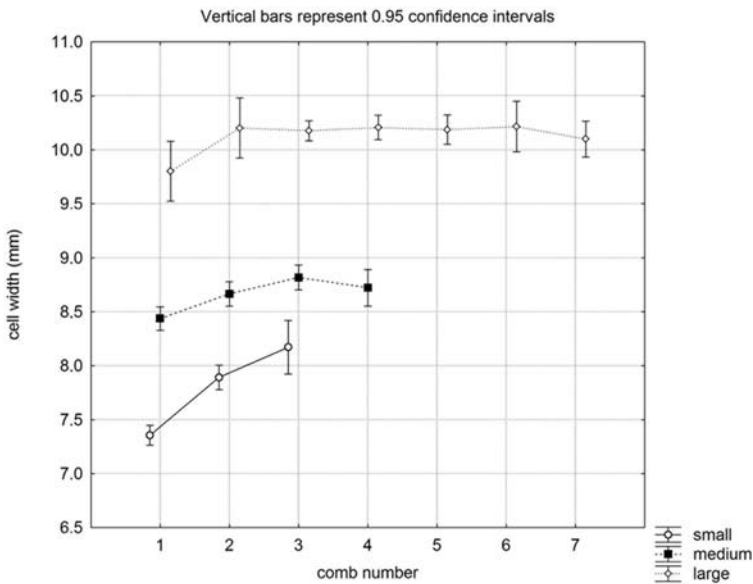


Fig. 2. The distribution of mean values of the width cells in particular combs of nests of *Vespa crabro* in the final development stage of colonies.

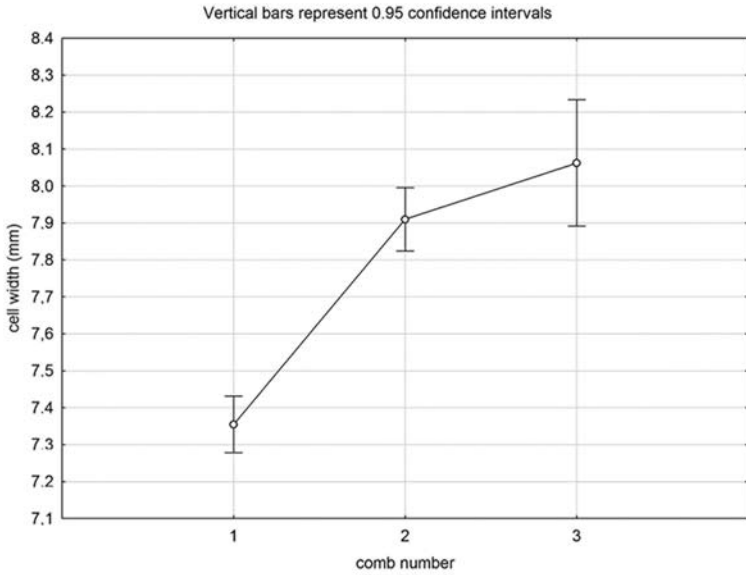


Fig. 3. Distribution of the mean values of the width of small cells in different combs for the nests of *Vespa crabro* at the final stage of development of colonies (hierarchical ANOVA $F_{2,90} = 59.040$, $p < 0.00001$)

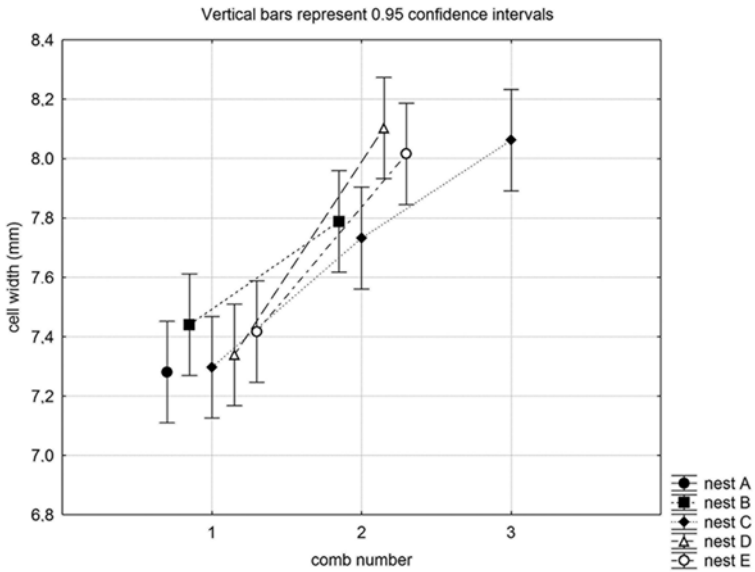


Fig. 4. Distribution of the mean values of the width of small cells in consecutive combs and separate nests of *Vespa crabro* at the final stage of development of colonies (hierarchical two-factor ANOVA, $F_{7,90} = 2.221$, $p = 0.04$)

These graphs clearly show the differences of mean values of analyzed variables, especially between successive combs.

The distributions of mean values of depth of all the identified types of cells have also been analyzed. Analyses have shown that the differences between the mean values of depth of small cells are not statistically significant, both between combs in one nest and combs of different nests of *Vespa crabro* (hierarchical ANOVA).

For medium-sized cells, also were observed a similar variation, although cells in the last combs are smaller than in previous (Fig. 6). The carried out analysis - one-dimensional test of significance for the variable- the width of medium cells for two two-stage grouping factors (nest and comb) is presented in Figs. 7 and 8 (hierarchic ANOVA). The obtained results confirm the statistically significant differences of the mean value of this parameter. Medium cells differ in width both between combs in a given nest and in combs of various nests.

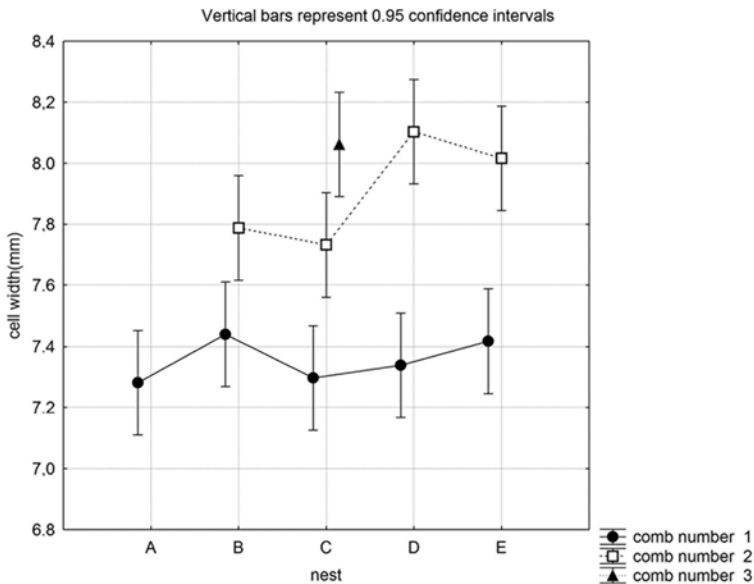


Fig. 5. Distribution of the mean values of the width of small cells in different nests and separate combs of *Vespa crabro* at the final stage of development of colonies (hierarchical two-factor ANOVA, $F_{7,90} = 2.221$, $p = 0.04$)

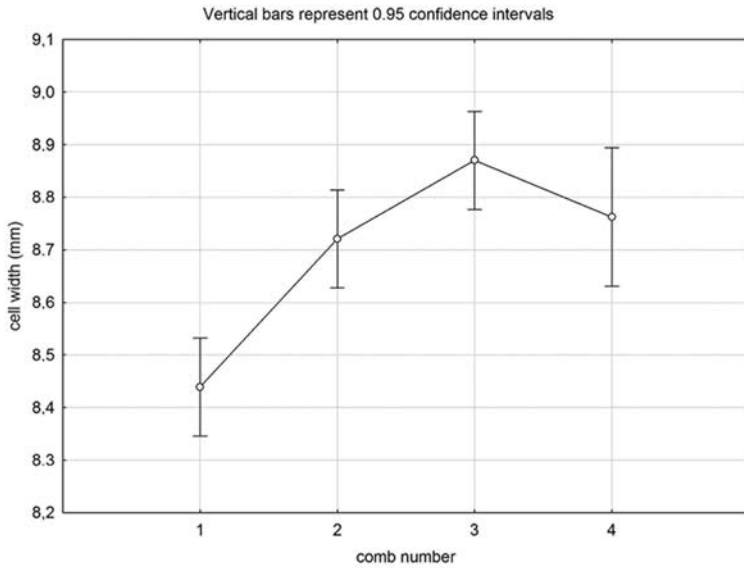


Fig. 6. The distribution of mean values of the width of medium cells in different combs in all study nests of *Vespa crabro* in the final stage of development of colonies (hierarchical ANOVA $F_{3,126} = 14.899, p < 0.00001$)

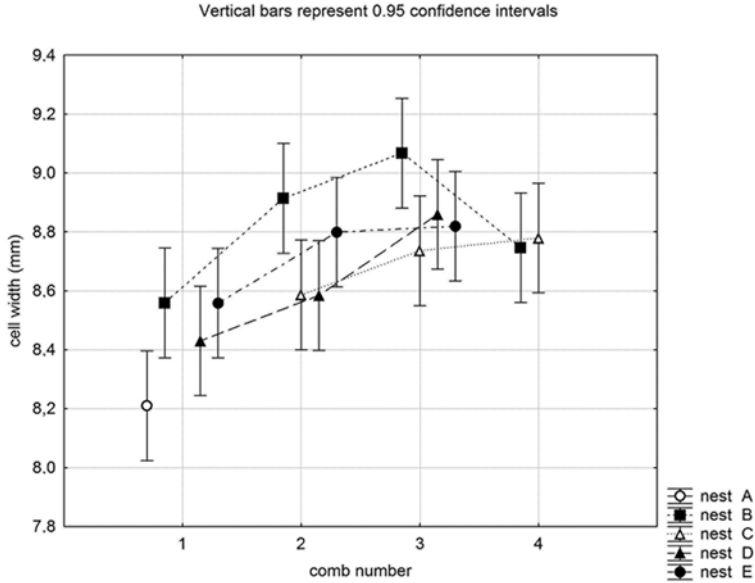


Fig. 7. The distribution of mean values of width of medium cells in different nests and consecutive combs of *Vespa crabro* in the final stage of development of colonies (hierarchical two-factor ANOVA, $F_{10,126} = 2.501, p = 0.009$)

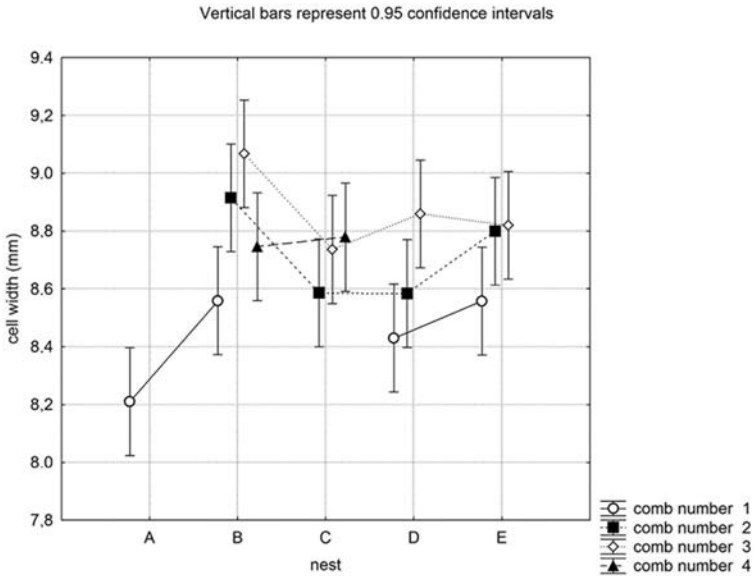


Fig. 8. The distribution of mean values of width of medium cells in different combs and separate nests of *Vespa crabro* in the final stage of development of colonies (hierarchical two-factor ANOVA, $F_{10,126} = 2.501$, $p = 0.009$)

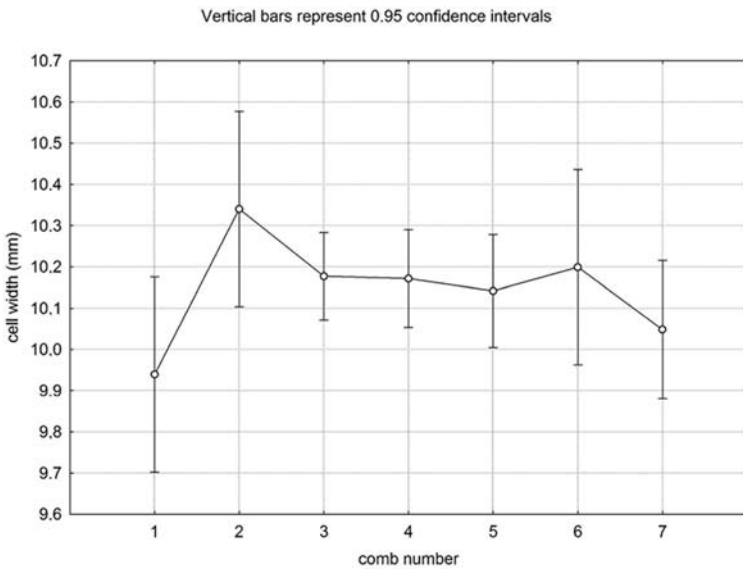


Fig. 9. The distribution of mean values of the width of large cells in combs in nests of *Vespa crabro* in the final stage of development of colonies (hierarchical ANOVA $F_{6,153} = 1.272$, $p = 0.27$)

This graph shows the differences between mean values of the analyzed variable – the width of medium cells. The observed mean values of this parameter in fourth combs are smaller than in third. This is probably associated with the disorder of structure of these combs caused by appending to them the large cells, in later stages of developing of colony, and the necessity of small changes in the size of medium-sized cells adapting them to the further stages of extension of combs.

The two last graphs demonstrate more precisely the complexity of structure of consecutive combs in nests of *Vespa crabro*. One can see clearly, that differentiation of this parameter is greater for various nests than for different combs.

The differences between the mean values of the depth of medium cells, as it is in the case of small cells, are not statistically significant, both between combs of a given nest and for various nests of *Vespa crabro*.

Width of large cells proved to be a constant parameter, both between different nests of hornets, as well as the combs within the same nest. The results of conducted analysis - one-dimensional test of significance for the variable – the width of large cells for two two-stage grouping factors (nest and comb) – is presented in Figs. 9-11 (hierarchical ANOVA). The obtained results do not confirm statistically significant differences between mean values of this parameter. Width of large cells do not differ significantly both among combs in the nest as well as in combs between nests and the observed differences are not statistically significant ($p > 0.05$).

The obtained results of the statistical analysis of this parameter show its great conservatism clearly. It is understandable because these cells are built in the last phase of the development of a colony and they are used for development of castes which are the most precious for wasps' societies – reproductive castes. Because the size of the imago individuals depends on the size of the cell in which they grow (author's own unpublished observations), therefore, the stability of this parameter, which determines the normal development of future queens (*gynes*) and males (*drones*) is very important for the colony and one can expect that natural selection favors just such a solution. The observed higher, than in other cases, dispersion of the values defining the confidence intervals, is probably associated with differentiation of large cells into two types used for, future queens and *drones*, which have various sizes.

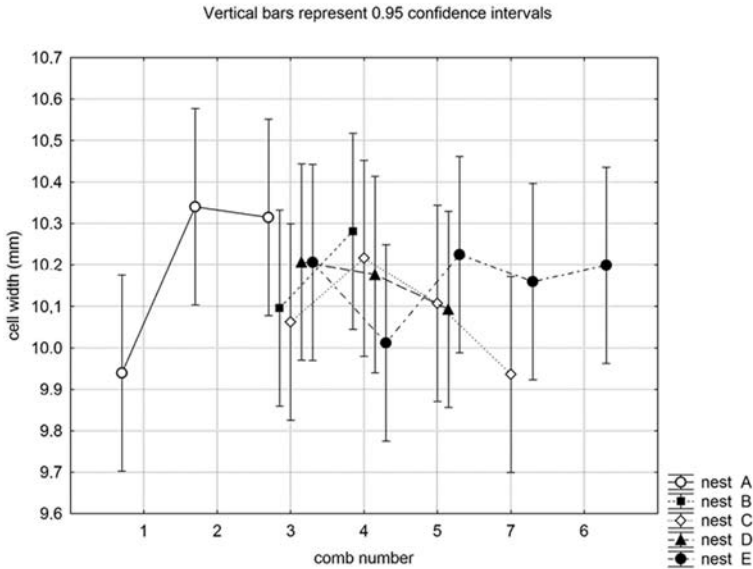


Fig. 10. The distribution of mean values of width of large cells in consecutive combs and different nests of *Vespa crabro* in the final stage of development of colonies (hierarchical two-factor ANOVA, $F_{10,153} = 0.805$, $p = 0.62$)

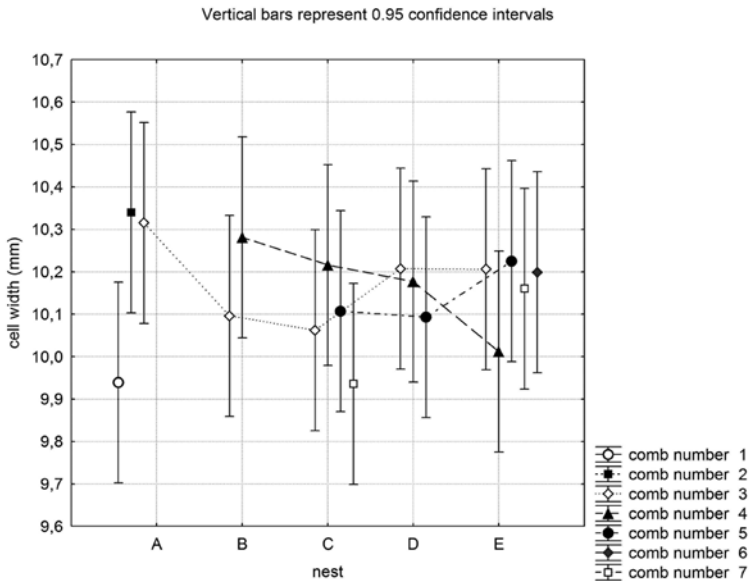


Fig. 11. The distribution of mean values of width of large cells in different nests and consecutive combs of *Vespa crabro* in the final stage of development of colonies (hierarchical two-factor ANOVA, $F_{10,153} = 0.805$, $p = 0.62$)

The obtained results for depth of large hornet's cells, not confirm statistically significant differences between the mean values of this parameter also. Large cells no differ from one another significantly in depth both between consecutive combs in a given nest and in combs from various nests.

Similar statistical analyses were conducted for nests of *Dolichovespula saxonica*.

Levene's test demonstrated homogeneity of variance for statistics – the width of cells for particular their types, *D. saxonica* nests. The statistical analysis of this variable - one-dimensional test of significance for two two-stage grouping factors (nests and combs) is presented in Figs. 12-15 (hierarchical ANOVA).

The differences between the mean values of the width of small cells are statistically significant both between combs of the same nest and various nests of *Dolichovespula saxonica*.

The graph in Fig. 13 shows the distribution of mean values of the width of small cells in the nests of distorted structure, which was caused by the presence of reproductive workers, which build additional cells from which

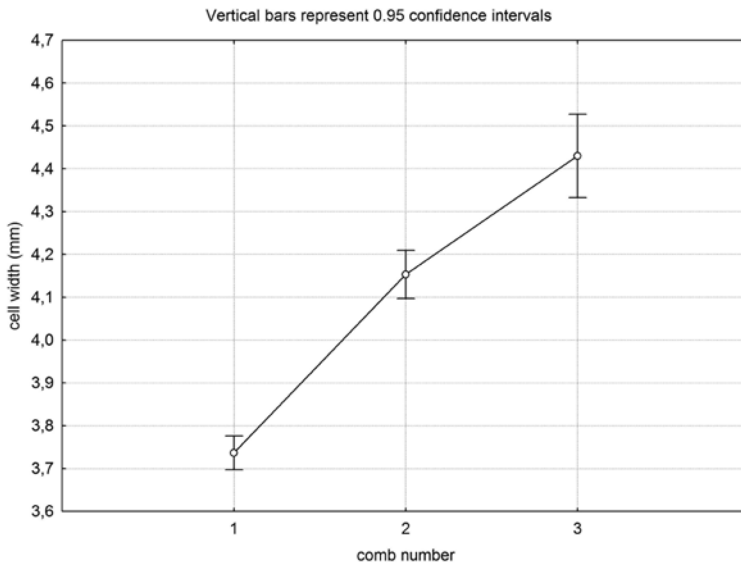


Fig. 12. The distribution of the mean values of the width of small cells in consecutive combs in nests of *Dolichovespula saxonica* in the final stage of development of colonies (hierarchical ANOVA $F_{2,90} = 129.92$, $p < 0.00001$)

drones of workers will develop. In the graph are clearly seen small cells also in 4th comb. In the nests where 'worker policing or queen-controlled' (Foster & Ratnieks 2001; Foster *et al.* 2001) is effective, such cases are rare.

For further analysis, small cells from the fourth comb were not included.

The presented graphs demonstrate that the occurrence of small cells is limited mainly to the two first combs; rarely can they be found in the third one. Their presence in the remaining indicates certain anomalies in the structure of social organization of a colony.

For width of medium cells statistical analysis of this variable - one-dimensional test of significance for two two-stage grouping factors (nest and comb) is presented in Figs. 16-18 (hierarchical ANOVA).

The conducted analysis indicates that the differences between the mean values of the width of medium cells are statistically significant both between combs of the same nest and various nests of *Dolichovespula saxonica*.

The presented graphs indicate that medium cells, used for the growth of worker caste, are located mainly in combs 1 - 4, rarely in the last ones.

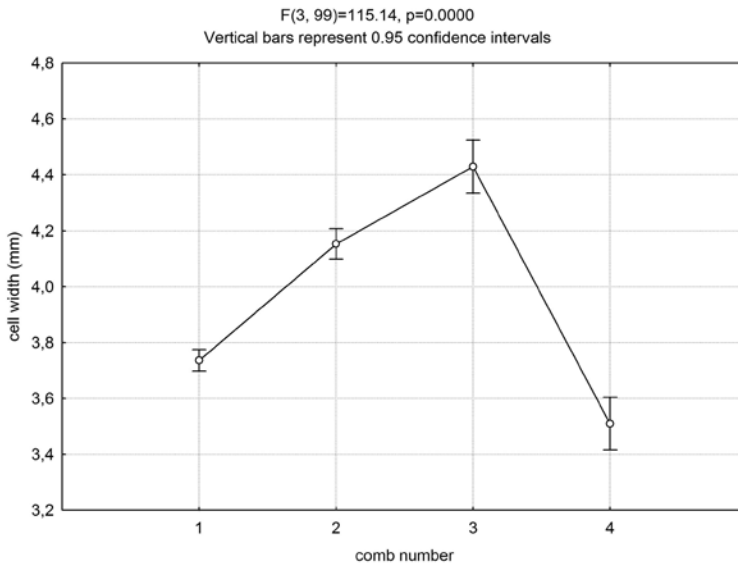


Fig. 13. The distribution of mean values of the width of small cells in successive combs in the nests *Dolichovespula saxonica* in the final stage of the colony. The graph illustrates the presence of small cells built on the fourth comb probably by "reproductive" workers (limited 'worker policing') (Foster *et al.* 2001; Wenseleers *et al.* 2005a).

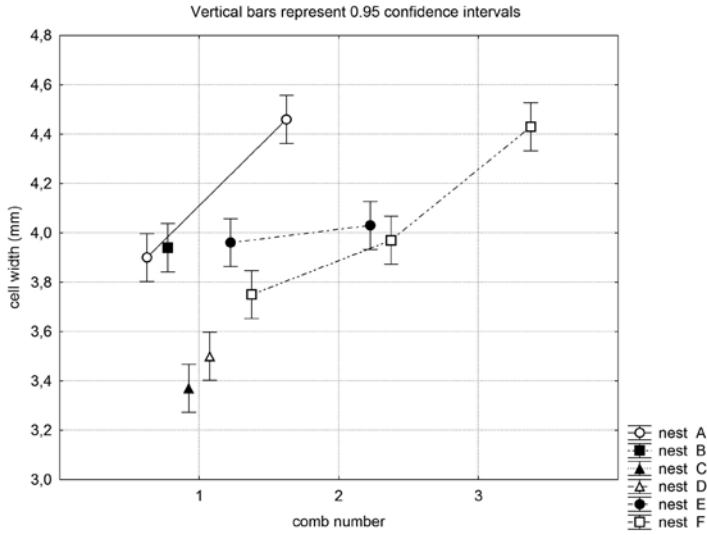


Fig. 14. The distribution of mean values of the width of small cells in particular nests in consecutive combs of *Dolichovespula saxonica* in the final stage of development of colonies (hierarchical two-factor ANOVA, $F_{7,90} = 26.857$, $p < 0.00001$)

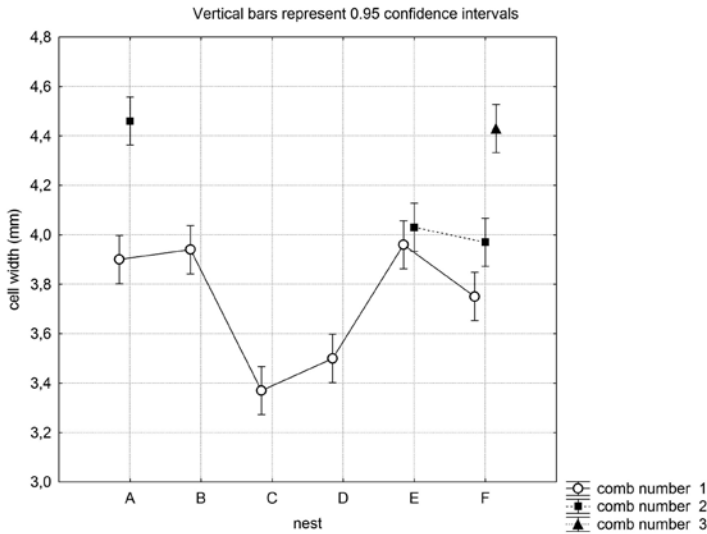


Fig. 15. The distribution of mean values of width of small cells in consecutive combs in different nests of *Dolichovespula saxonica* in the final stage of development of colonies (hierarchical two-factor ANOVA, $F_{7,90} = 26.857$, $p < 0.00001$)

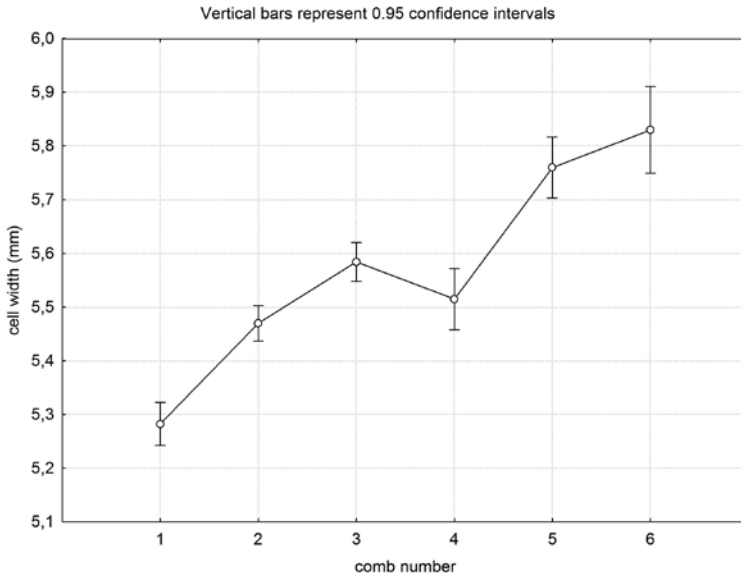


Fig. 16. The distribution of mean values of the width of medium cells in consecutive combs in nests of *Dolichovespula saxonica* at the final stage of development of colonies (hierarchical ANOVA $F_{5,180} = 56.541$, $p < 0.00001$)



Fig. 17. The distribution of mean values of the width of medium cells in different nests in consecutive combs of *Dolichovespula saxonica* at the final stage of development of colonies (hierarchical two-factor ANOVA, $F_{14,180} = 74.737$, $p < 0.00001$)

Moreover, their width is varied and differs among colonies of *Dolichovespula saxonica*, but its parameters depend also on the location in a particular nest. The differences are statistically significant.

For width of large cells, statistical analysis of this variable - one-dimensional test of significance for two two-stage grouping factors (nest and comb) is presented in Figs. 19-21 (hierarchical ANOVA).

The differences between the mean values of the width of large cells are not significant statistically, both between combs of a particular nest and various nests of *Dolichovespula saxonica*. In nests of this species, widths of large cells are similar in all studied colonies.

Attention should be paid to the great similarity of the results of statistical analyses of cell parameters of nests of *Vespa crabro* and *Dolichovespula saxonica*. For both species one can observe significant statistical diversity of parameters of small and medium cells as well as their similar, though not identical, location within a nest. For both species one can observe stability of sizes of large cells for reproductive castes, but their function associated with the use of them for two types of castes (*gynes* and *drones*), makes, that values

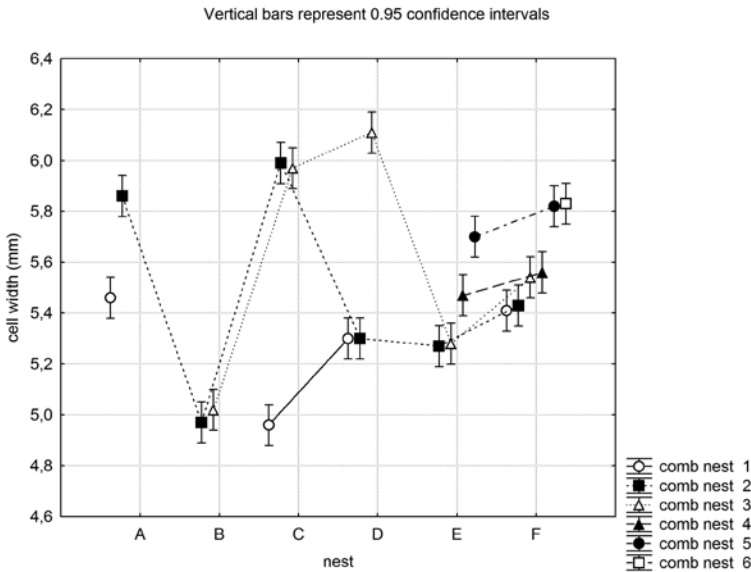


Fig. 18. The distribution of mean values of the width of medium cells in consecutive combs in different nests of *Dolichovespula saxonica* in the final stage of development of colonies (hierarchical two-factor ANOVA, $F_{14,180} = 74.737$, $p < 0.00001$)

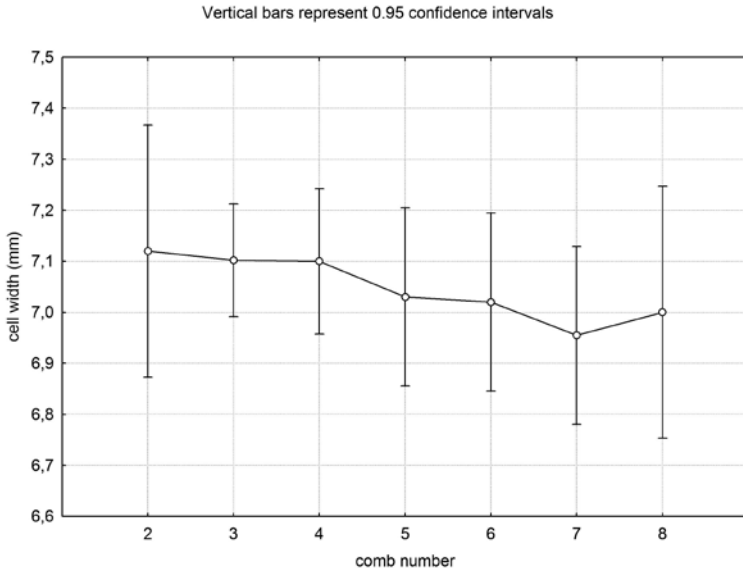


Fig. 19. The distribution of mean values of the width of large cells in particular combs in nests of *Dolicho-vespula saxonica* in the final stage of development of colonies (hierarchical ANOVA $F_{6,144} = 0.511, p < 0.8$)

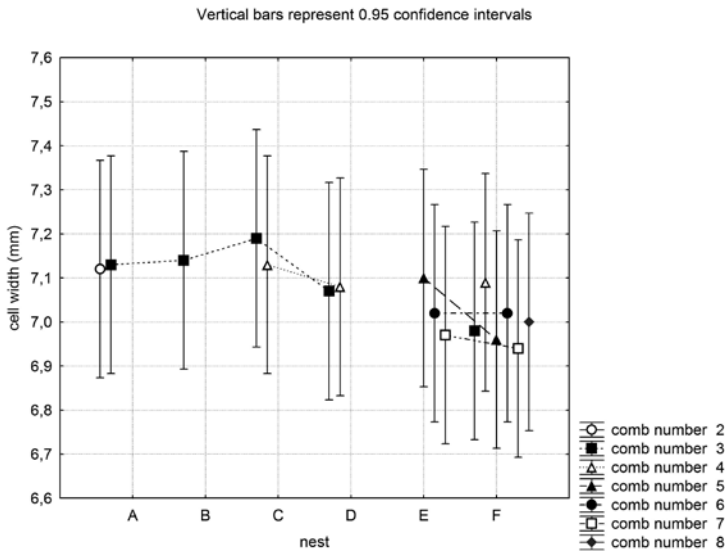


Fig. 20. The distribution of mean values of the width of large cells in consecutive combs of different nests of *Dolicho-vespula saxonica* in the final stage of development of colonies (hierarchical two-factor ANOVA, $F_{9,144} = 0.267, p < 0.99$)

of their mean and confidence intervals are relatively high.

Based on the analysis of location and size different forms of wasps development in colonies, so eggs, larvae, pupae, as well quantities of meconium in individual cells (Yamane & Makino 1977; Star & Jacobson 1990) attempt was made to reconstruct the sequence of formation and exploitation of the combs and cells by wasps. Fig. 22 shows the results of these analyses for *Vespa crabro*. The presented schematic drawings show the results these studies, demonstrating the sequence built of rings of cells in successive combs. The newly built ring is the basis of choice of area of combs, as places for eggs lying by the queen. The same color indicates areas of different combs formed more or less simultaneously. The schematically, real number and location of individual cells in consecutive combs in one of the studied nests of *Vespa crabro* were shown in (Fig. 23). One can clearly see here the ring system of distribution of individual forms of development of these insects. Characteristic here is primarily creating and use and gradual increasing of the number of cells in few combs simultaneous (2-3), and after a certain stage of their formation (ring 4 - 6 cells), further continuing of their construction, with the growth of colonies.

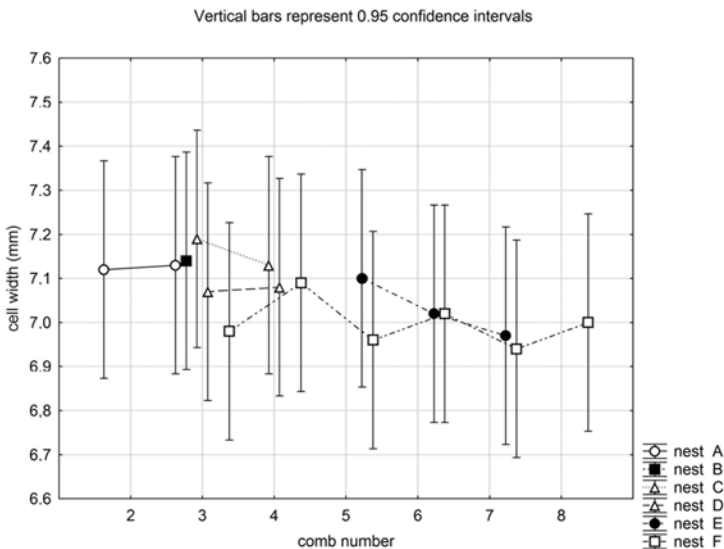


Fig. 21. The distribution of mean values of the width of large cells in particular nests in consecutive combs of *Dolichovespula saxonica* in the final stage of development of colonies (hierarchical two-factor ANOVA, $F_{9,144} = 0.267$, $p < 0.99$)

At the maximum number of combs (6-8), wasps do not build each of them separately till the end, but they are gradually and annularly expanded (photo 4). The cells in first combs are used for the development of larvae and pupae usually two or three times, especially around the central point, which is the place of start construction of the primary comb, further cells are used usually twice, in last combs (6, 7 and 8), containing reproductive castes, only once. Of course, there are often deviations from this typical pattern which result from disruptions in the working of insect's societies related with the shape and volume of the place where the nest is located (construction obstacles, the place too small, narrow, etc.) (photo 5), presence of parasitoids (photo 6), including social usurpers or the death of the queen.



Fig. 22. *Vespa crabro* nest analysis - schema forming combs (different colors mean areas of cells built at the same time)

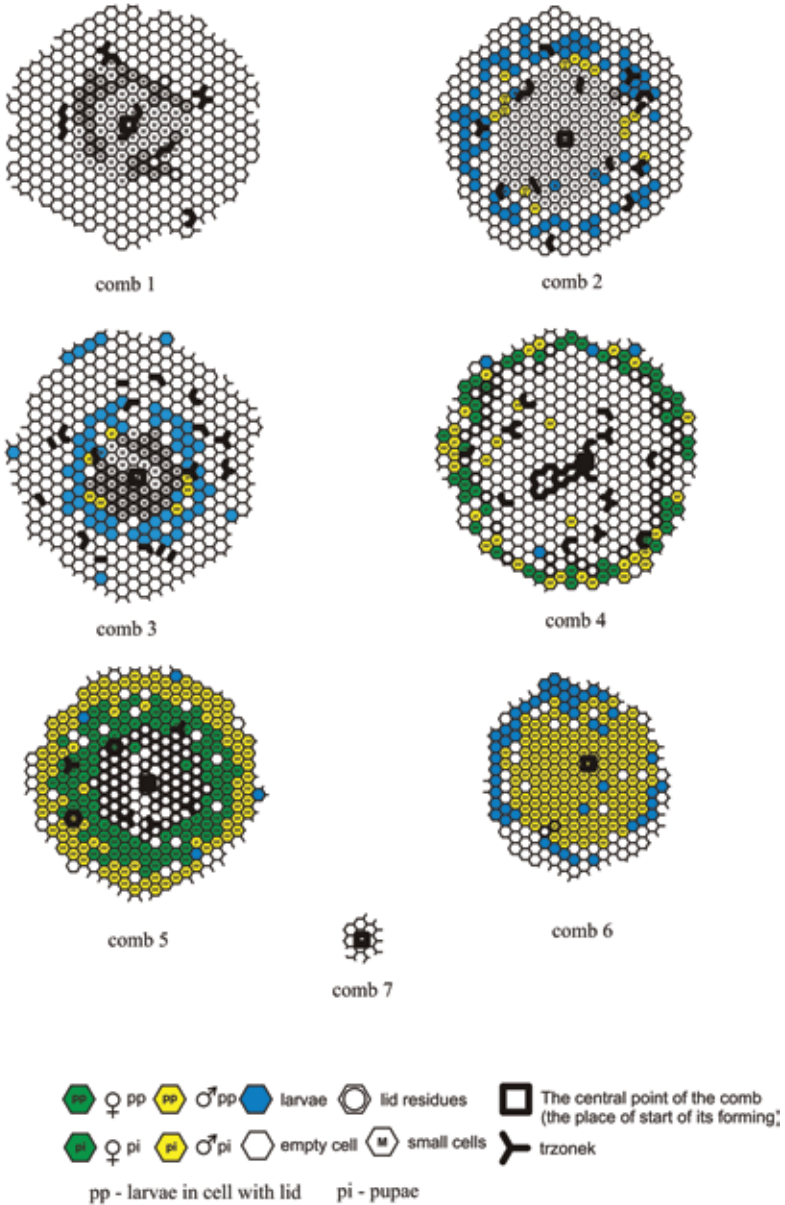


Fig. 23. Detailed analysis of one of the *Vespa crabro* nests in the final stage of development of the colony with the location of the individual cells



Photo. 4. *Vespa crabro* comb showing successive rings of cells



Photo. 5. *Vespa crabro* nest in the attic showing nest structure disorder caused by an obstacle in the roof structure

Colony size

Studies of colony size in the nests of the social wasps were based on data obtained by counting the individuals of each caste, the number of eggs, larvae and pupae as well as meconium in cells (Yamane & Makino 1977). Based on the number of meconium, how many times used different groups of cells was studied. After analyzing the data, the potential number of all wasps of different castes presented in a given society over a full season was obtained. Table 6 presents examples of exceptionally large societies of *Vespa crabro* and *Dolichovespula saxonica* in the area of the city of Łódź. For these calculations 24 largest nests were used, in the final stage of development, both from 'natural'



Photo.6. *Dolichovespula saxonica* nest destroyed by *Aphomia sociella*, showing combs built crosswise

Table 6. Abundance of castes in the example of two large colonies of *Vespa crabro* and *Dolichovespula saxonica* from the vicinity of Łódź (total number of all individuals from different castes, which were born and lived in the nest)

species	workers	queens	males	total number of individuals	nest volume
<i>Vespa crabro</i>	1018	497	546	2061	23.552 dm ³
<i>Dolichovespula saxonica</i>	937	156	251	1344	3.203 dm ³

Table 7. The summary of mean values of the number of hornets from the castes, number of cells and the volume of *Vespa crabro* nests in the final stage of development of colonies, which were established in natural places (Nat.) and buildings (Bld.) in the area of Łódź (N = 24)

workers ± SE		gynes ± SE		males ± SE		number of cells ± SE		nest volume (dm ³) ± SE	
Nat.	Bld.	Nat.	Bld.	Nat.	Bld.	Nat.	Bld.	Nat.	Bld.
767±62	915±138	56±8	238±59	80±10	270±63	708±56	1281±207	1.37±0.13	21.00±11.31

places and ‘buildings’. In table 7 there are presented mean values of volume of nests coming from both types of places as well as the mean values of the number of individuals of castes and number of cells in nests of *Vespa crabro*.

Number of individuals in the colony should be dependent on the size of the socket, and above all on the number of cells. Correlations between the number of individuals, and the quantitative parameters of the nest were examined. A statistical analysis of linear correlation – Pearson r test between the size of the nest and various parameters determining the size of the studied societies of *Vespa crabro* and *Dolichovespula saxonica* was conducted. For these analyzes, only fully developed nests were used.

There is a strong correlation (Spearman test) between the total number of worker’s cells and the number of workers both in the nests of *Vespa crabro* established in natural places ($r = 0.69$; $p < 0.05$) and in buildings ($r = 0.80$; $p < 0.05$) (Cohen 1988). There were very strong correlation between the total number large cells and counts of *drones* and *gynes* together in the nests of *Vespa crabro* established in natural places ($r = 0.95$; $p < 0.05$) and in buildings ($r = 0.97$; $p < 0.05$). These results reflect the effective use all of large cells. The determine count of meconium showed, that these cells, for the development of reproductive castes are used only once.

The results of these studies are so interesting that require additional discussion. Not surprisingly there is strong correlation between the number of various cells in the nest, and the number of individuals in the colony. But it

is worth noting difference in r value between the nests from 'natural' places and from 'buildings'. These differences are results from the limitations of the size of nests, connected with the volume of natural places in which colonies were established (nesting boxes and tree hollows) and the lack of such limitations in cases of nests in buildings. Societies of wasps whose development of nests are limited by capacity of the place, are somehow forced to eliminate potential losses through additional use of the same cells, which is done more often than in the case of nests built without these restrictions, and located in the buildings (while maintaining the similar number of workers). The total number of individuals of all castes also should therefore be correlated with the overall size of the whole colony - the volume of the nest both for *Vespa crabro* as well as *Dolichovespula saxonica* (Figs. 24 and 25).

The very strong correlation (Cohen 1988) between the basic parameters of a nest its volume of a nest and the count of imago individuals is so understandable, although it must be noticed that the parameter - nest volume cannot be the value directly proportional to the size of the society, as the volume of a sphere is not directly proportional to its radius (exponential function). Moreover, the aforementioned fact that the same cells are used many times

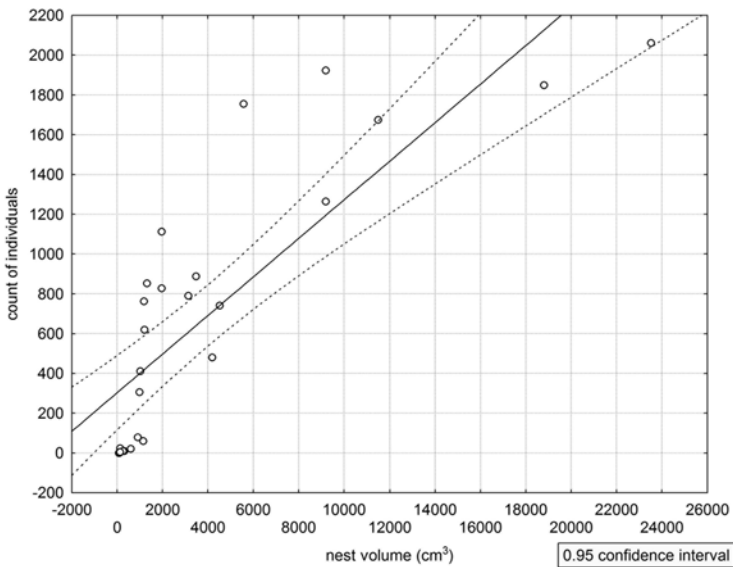


Fig. 24. The correlation between the volume of a nest and the total count of individuals of *Vespa crabro* ($N = 27$; $r = 0.83$; $p < 0.05$)

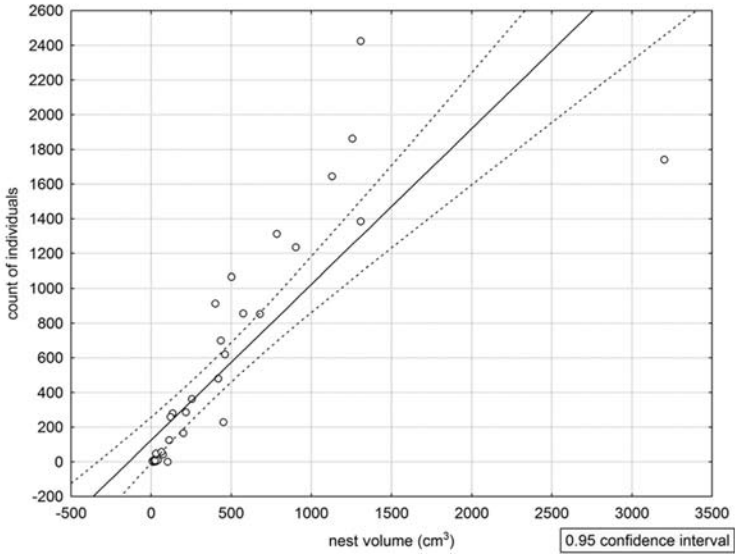


Fig. 25. The correlation between the nest volume and the count of individuals of *Dolichovespula saxonica* (N = 41; $r = 0.84$; $p < 0.05$)

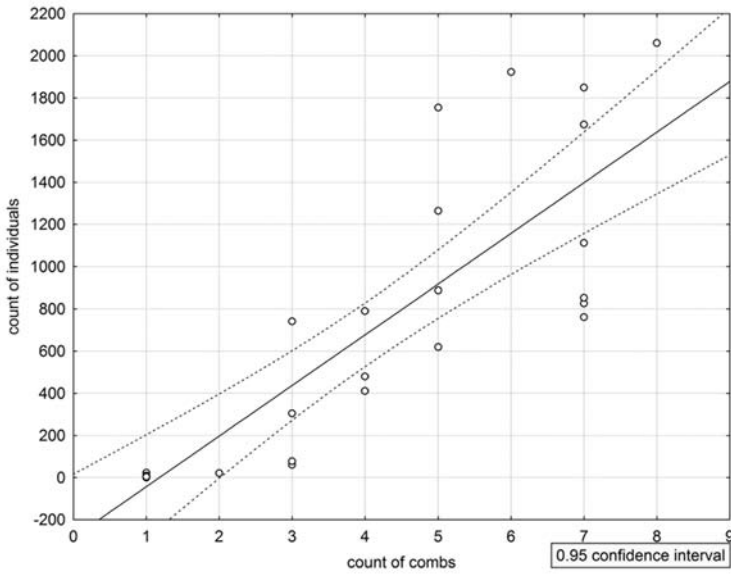


Fig. 26. The correlation between the count of combs and the count of individuals of *Vespa crabro* (N = 27; $r = 0.84$; $p < 0.05$)

for the development of larvae has a fundamental importance here as well. The number of combs, though strongly correlated with the number of individuals (Fig. 26) is not a parameter that can be used uncritically to assess the size of the colony. It is so because in some special cases, the volume of the place where the nest is located (low attic, flat roofs or narrow slits) necessitates the construction of only 1-2, a maximum of 3 combs, but with much larger surfaces on which all cell types are located

The comparison between the success of *Vespa crabro* nesting in natural sites and buildings - ranks of the total number of large cells in studied nest, established in both types of places were compared. The differences were statistically significant (ANOVA nonparametric Mann-Whitney U test) (Fig. 27). To assess the effect of nest site for potential reproductive success of Vespinae, hornet's nests were used only. Nests and colonies of *Dolichovespula saxonica* are so small that their location in a 'buildings' or 'natural places' has no practical significance for future size of the colony.

Differences in the number of workers between colonies in both types of places are not statistically significant.

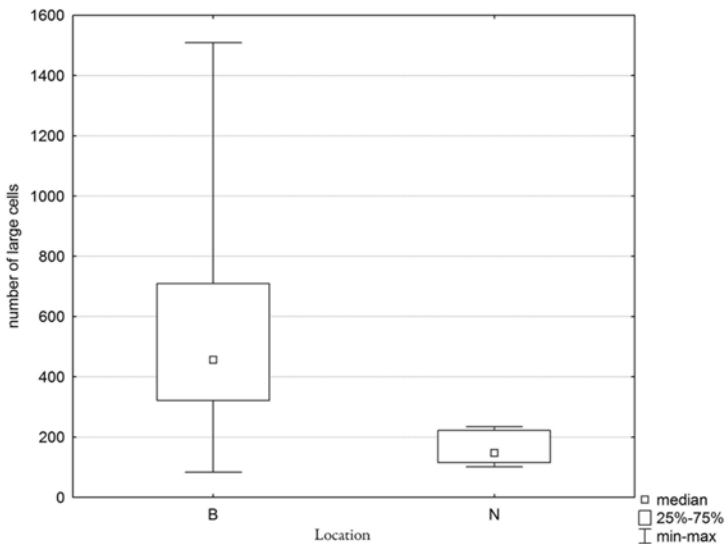


Fig. 27. The number of large cells of the nests of *Vespa crabro* established in buildings and natural places in 2006-2008. ANOVA nonparametric Mann-Whitney U test. $U = 9.00$; $p = 0.002$.

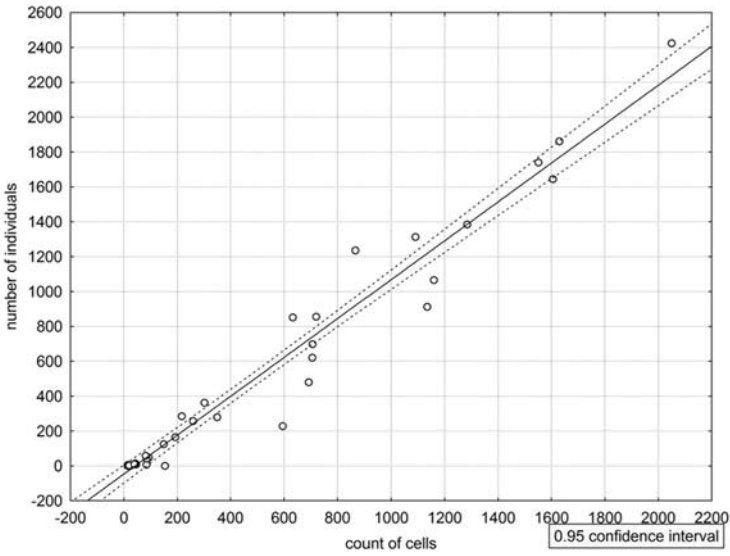


Fig. 28. The correlation between the total count of cells and the count of individuals of *Dolichoivespula saxonica* (N = 41; $r = 0.98$; $p < 0.05$)

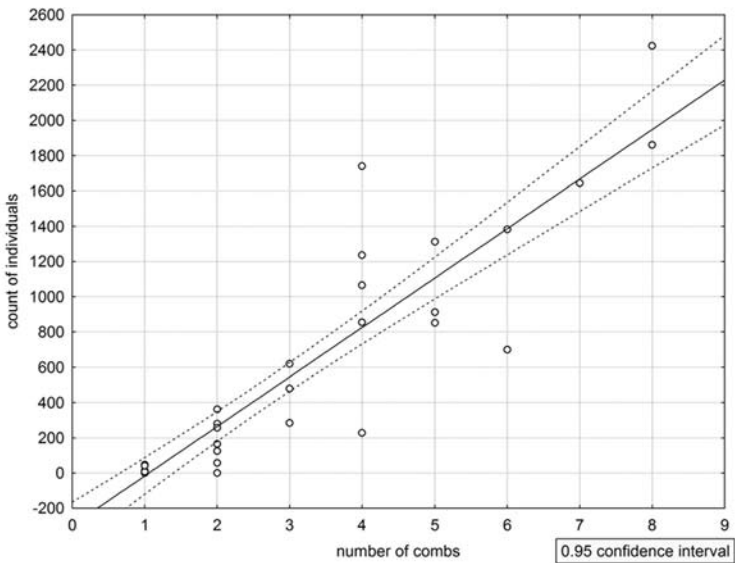


Fig. 29. The correlation between the number of combs and the number of individuals of *Dolichoivespula saxonica* (N = 41; $r = 0.92$; $p < 0.05$)

For nests of *Dolichovespula saxonica* analysis showed no differences between those parameters for colonies of this species of wasp established in natural places and buildings. However, the correlation between the number of cells and combs in the nest, and the number of individuals in the colony are very strong correlated (Figs. 28 and 29).

As can be inferred from these analyzes, the location of the slot is the primary determinant of colony size for large societies of wasps, including the European Hornet. Numbers of cells are especially strongly correlated (all $r > 0.7$) with the counts of individuals in a wasp colony.

Proportions of castes

Based on the data obtained from the quantitative assessment of nests and societies, including the abundance of individual castes, the comparative analysis of proportions between *gynes* and young males (*drones*) of the studied species of wasps was conducted (Fig. 30).

The statistical analysis of proportions between reproductive castes *gynes* / *drones* in the nests of the studied wasp species, showed homogeneity of variances (Levene's test).

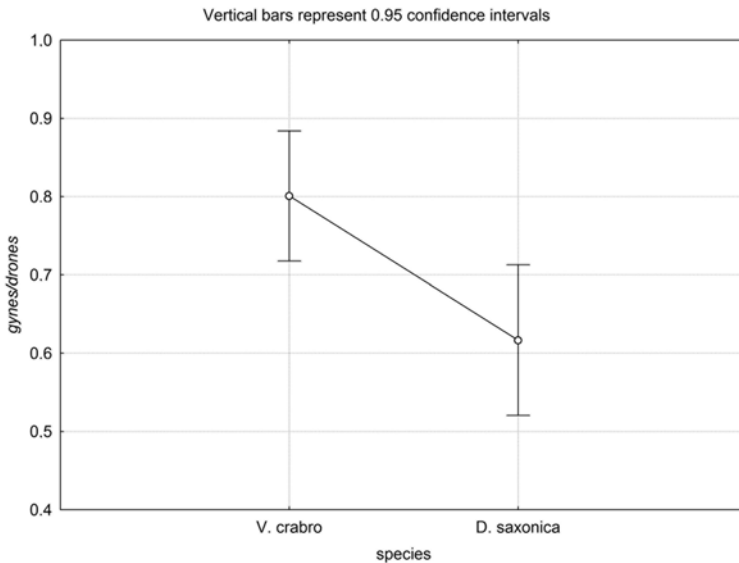


Fig. 30. The comparison of proportions between reproductive castes: *gynes* / *drones* in the nests of the studied species of wasps (*Vespa crabro* and *Dolichovespula saxonica*). ANOVA single-factor ($F_{1,19} = 9.22$, $p = 0.007$)

The differences between the mean values of these proportions are statistically significant (Fig. 30). These proportions between the colonies of the same species, both of the European hornet and Saxon wasp were not statistically significant. The obtained values of these proportions (about 0.8) for each colony of *Vespa crabro* are proving that *drones* have a small quantitative advantage over the *gynes*. In case of societies of *Dolichovespula saxonica* these proportions are different (about 0.6) from hornet because the count of young males in the Saxon wasps is increased. It should be assumed that this is one more proof of the limited 'worker policing' observed in this species (Foster, Ratnieks 2001; Foster et al. 2001). The correlation between the total number of workers and the number of *drones* and *gynes* together in the nests of *Vespa crabro*, established in buildings were very strong ($N = 11$; $r = 0.82$; $p < 0.05$) but there is no correlation between the total number of workers and the number of *drones* and *gynes* together in the nests of hornet, established in natural places. For the Saxon wasp, correlations between the number of large cells and the number of workers both from "natural" and "building" places were strong ($N = 27$; $r = 0.62$; $p < 0.05$) (Cohrn 1988).

The presented results of the analysis between the number of large cells and the number of workers in nests of *Vespa crabro* and *Dolichovespula saxonica* indicate no correlation of these variables in nests of *V. crabro* located in natural places and strong correlation in nests in buildings and for all colonies of *D. saxonica*. This confirms the assumption of smaller structure stability of nests of hornet caused among other things by 'technical problems' occurring in colonies established in places too "cramped" for this species. In case of *D. saxonica*, the small sizes of nests of this wasp do not cause problems with locating the colony in a freely chosen place.

DISCUSSION

A large city is a specific ecosystem which, like no other, undergoes continuous changes resulting from constant, planned or accidental human intervention. As an environment, it is characterized by exceptional mosaics and diversity of microhabitats. The dynamic process accompanying these changes in result of which we may observe loss of some species and inflow of others may sometimes lead to the increase of species diversity within certain animal groups. According to Wanat (1987), in suburban part of Łódź, species diversity of

weevils (Coleoptera, Curculionidae) can be comparable or even larger than that found in Białowieski National Park.

Previous studies on the presence of different groups of animals in Łódź show a decrease in their diversity in the direction of town centre. However, the specific character of downtown habitats is tolerated relatively well by some groups of hymenopterans (*Hymenoptera*) especially by forest species (Markowski *et al.* 2004). Because of large, located near each other houses, a specific microclimate is created, which stands out due to reduced amplitude of temperature and humidity, even when compared with directly neighboring areas devoid the urban infrastructure. These conditions are multiplied especially inside buildings due to the presence of heating and air conditioning, heating pipes, sewage system, culverts of various types, wells, tunnels and cellars. This situation makes it possible for thermophilic species to exist in a city (Banaszak 1978), for whom survival during the winter in conditions outside the city would be difficult or impossible.

The study of Aculeata in the Warsaw agglomeration has shown that social insects are a group that relatively easily, as it seems, overcomes the barrier of urban pressure (Banaszak 1978; Skibińska 1978). Some representatives of Aculeata have long been using human houses and homesteads to form colonies in them, and certainly many times all of us have found in attics and lofts of houses traces of their existence as active or already empty and abandoned nests. However, the only urban conditions have created a new quality that allowed for a much larger scale existence of many representatives of this group of insects in the immediate vicinity of people. The species, which 'were able' to adapt their biology to urban environment using the existing food resources and the infrastructure abundant with places for nesting, began their expansion at an unparalleled scale, as it seems (Skibińska 1982, Skibińska 1987; Nadolski 2000b; Nadolski 2001).

Both studied species the Saxon wasp - *Dolichovespula saxonica* and European hornet *Vespa crabro* are species which, as is clear from these research, often form colonies in the city, but the size of the *D. saxonica* nests and its societies is always rather small. Besides the breeding boxes for birds, the presence of its colonies was recorded in different places in residential and utility buildings. The colonies of the European hornet, which because of its size, builds large nests and there is a species most often recorded in forests (Dvořák 2007b;

Pawlikowski 2009), maybe not in large counts, but also were found inside residential and utility buildings, within the very centre of Łódź. However, it builds its nests most often in suburban zone. Furthermore, analysis of the spatial distribution of *V. crabro* nests showed no clear preference in the selection of Łódź area by this species (Nadolski unpublished). Reproductive success of European hornet in urban conditions is achieved by ability of efficiently creating large colonies by this wasp and skills of efficient using of specific conditions of “housing”, which were made by man. In the city of Łódź, even in places most similar to “natural”, *Vespa crabro* prefers “buildings” as a place for the development of its colonies. Interestingly, apart from isolated cases, not been demonstrated, that colonies of European hornet were created several times in the same places, even in cases of nests formed in breeding boxes for birds. So unlike in Poznań studies have shown (Langowska *et al.* 2010). Perhaps this is due to surplus of potential nest sites in urban area.

It seems that the key element conditioning reproductive success of Vespinae is the choice of place to build a nest, made in the spring by the young queen. These studies demonstrated undoubtedly (table 1) that urban populations of both species prefer places in residential and utility buildings and other accompanying urban infrastructure. It may be understandable because the number of ‘natural’ places for nests is usually limited in urban area, while in ‘buildings’ is plenty of them. This seemingly obvious as it might seem cause, should fully explain the observed trends. However, there are situations that cannot be unambiguously explained this way. This applies especially as species as the Saxon wasp which, according to their biology, usually can build their nests on the branches of trees and the European hornet as the ‘tree hollow’ species prefers attics of buildings and sheds than neighboring nest-boxes for birds. The cause of these observed trends is not probably only a limited number of available natural places on the nest, but rather their quality. Places in ‘buildings’ provide relatively stable temperature and protection from precipitation, predators. Wasp colonies ‘installed’ in buildings in majority of cases may reach much larger sizes (tables 2 and 7) than those from natural places and at the same time achieve definitely bigger reproductive success. The number of all individuals of a given society is closely correlated with the nest size (Figs. 24-26 and 28-29), which is also confirmed by studies of Jeanne and Bouwma (2002), and size of the nest built depends on the volume

of the place chosen for its establishment. Limitations to the size of the nest resulting from the volume of the place of its location are compensated by the wasp society using the same cells many times. However, the beginning of final stage of colony development forces the society to build large cells which are used for the development of reproductive castes only once. In consequence, the number of large cells being built, limited by the volume of the place, is a few times smaller than in nests of colonies which do not have such problems, i.e. located in buildings (Fig. 27).

Urban conditions make it possible to form exceptionally large societies of Vespinae and the parameters of their nests recorded in the city of Łódź were sometimes impressive (table 6). It is worth adding that the largest nest of *Vespa crabro* found in Łódź, which was located in an attic of a residential building, was 70 cm in diameter and its volume including envelopes was about 180 dm³. However, it is difficult to compare it with the size of colonies of other species of hornet (Seeley & Seeley 1980; Star & Jacobson 1990), especially perennial societies (Pickett *et al.* 2001).

Based on the results of statistical analyses of nests of two species of social wasps, it can be considered, that the differentiation of cells in nests of Vespinae into small, medium and large can be a universal feature (Figs. 1 and 2). The conducted analysis of nest structure distinguished two types of workers' cells, of which the smaller ones described as small are formed mainly in the period of initiation of the nest and in the first comb are built by the queen. Later they are seen in the central areas of the first three combs (Figs. 3- 5) and as a result of the analysis of meconium, are often used twice for the development of larvae, rarely three times. Small cells are sometimes built later as well, by 'reproductive' workers, which sometimes lay eggs in these cells and from which develop only small *drones*. Thus, the described types of cells can not to be synonymous to the development stages of nests: QN, LS and LC (Pawlikowski & Pawlikowski 2003; Nadolski 2004). Their characteristics are based on cell size in combs, with respect to the period of their building at a given stage of development of insect societies and therefore not by their location in the comb and sizes, but since their time of formation. Small cells are also observed in the areas of nest whose structure was disturbed by parasitoids. In the latter case, formed empty combs, sometimes are not positioned parallel to other combs but are set in relation to them almost at right angles (photo 6) (author's own

observations). This may testify to the disorder of the system of the assessment of spatial position of nest, which conditions its proper structure, including combs and envelopes, characteristic of individual species (Wenzel 1991) and conditioned by various factors (Karsai & Péntzes 1993; Karsai & Péntzes 1996; Karsai & Péntzes 1998), including the phenomenon of gravity (Ishay *et al.* 2008). Disturbances of the nest structure can certainly have a negative impact on its internal homeostasis, which determines the normal development of larvae and pupae (Ishay *et al.* 2002a; Ishay *et al.* 2002b; Klingner 2006). Workers' larger cells, described here as medium are located in the areas of combs which are added gradually. This is the largest group of cells occurring in a nest, some of which are used twice, very rarely, only in cases of nests of species with large societies (e.g. *Vespa crabro*) formed in cramped with too low volume places, three times (e.g. in breeding boxes).

The position of cells in the nests of both species of wasps exhibits some regularity. Along with the formation of successive combs are increased the size of small cells (Figs. 3-5 and 12-15), however, no significant differences in the width of these cells in the same type of combs (eg, the first or the second) between various nests (Figs. 5 and 15). In colonies of *Dolichovespula saxonica* differences in size of small cells between nests is bigger, especially when the structure of the nest is disturbed by "reproductive" workers (limited "worker policing") (Foster *et al.* 2001; Wenseleers *et al.* 2005a) (Fig. 13). Parameters of medium cells are also variable depending on combs on which they occur (Figs. 6-7 and 16-17), but these differences are greater between different nests (Figs. 8 and 18). Differences in depth between small cells and between medium cells in different combs and nests in both colonies of *Vespa crabro* and *Dolichovespula saxonica* are not statistically significant. Cells large, regardless of their location have a high stability of these parameters for both species (Figs. 9-11 as well 19-21). These cells are built mainly in the last combs or on the periphery of earlier built ones and this depend on the location place of the nest. If the spatial conditions make it impossible for the nest to develop along its axis, and in consequence forming new combs, the wasp society builds the nest in the transverse direction by forming new rings of cells in combs of existing ones. Cells for *gynes* and *drones* are not isolated from one another, although there are some homogeneous clusters of the same type of cells for reproductive of the same caste. Presence of "reproductive" workers causes

produce of males also in other areas of the nest. However, in this case, the medium cells (sometimes small) are used and *drones* developed from them are always significantly smaller than those of large cells (author's own observations). Nests parameters, especially the number of cells, are highly correlated with the size of the wasp's societies. This gives grounds for assessing the size of the society based on the volume of the nest (Figs. 24 and 25), although this dependency may be fraught with error because of the possibility of using these same cells twice or three times in the case of societies, limited by small volume of the place where the colony is located. Still, this estimate may be used effectively when analyzing most nests; especially those, that already have been deserted. Sometimes observed deviations from these general principles of the construction of nests may be due to disturbances of its structure caused by various external factors. It may be the size of the place of the nest location, or technical obstacles (photo 5) as well as the presence of parasitoids (photo 6), and the death of the queen and the action of usurpers.

The results of the analysis of number of particular castes are also worth thorough discussion. The differences in proportions between reproductive castes and workers between of the studied species did not prove to be statistically significant and this parameter exhibits relatively high changeability even between different colonies of the same species. Thus, it may be assumed that the number of workers may have no influence on the number of 'produced' males and queens.

The analysis of nest structure showed, that the number of large cells in nests of *Vespa crabro* is correlated with the number of the rest of cells only for colonies established in buildings and for colonies of *Dolichovespula saxonica*. This correlation, though it is not high occurs in both types of places for nests (natural and buildings). Interestingly, the proportions between the number of *gynes* and *drones* in societies *Vespa crabro* (about 0.8) are constant for different colonies and nests places. Reducing of the value of *Dolichovespula saxonica* to about 0.6 is probably related to the more frequent presence of egg-laying workers in this species (Foster *et al.* 2001) in connection with the limited control of male reproduction by the workers - "queen or worker policing" (Foster & Ratnieks 2000; Foster *et al.* 2000; Foster & Ratnieks 2001; Foster *et al.* 2001; Foster *et al.* 2002; Takahashi *et al.* 2004; Wenseleers *et al.* 2005a; Wenseleers *et al.* 2005b) which is typical for wasps belonging to the genus *Dolichovespula*

(Rohwer, 1916). The research of hornet nests (*Vespa* sp. Linnaeus 1785) in Japan done by Matsuura (Yamane & Makino 1977) demonstrated for species of large and numerous societies, similar proportions between drones and gynes and twice bigger number of males than future queens in small nests of *Vespa analis insularis* Dalla. Thus, it is difficult to assess the causes and adaptive nature of these proportions, which in the case of nests *Vespa crabro*, give only the result of about 10-20% more drones than gynes.

Briefly summarizing these considerations, it should be noted that the city is a special kind of environment that creates for wasp societies very good living conditions, which are far better than the outside of cities. Buildings and the entire infrastructure in urban areas, allow the formation of nests, in many larger and generally much more favorable places for wasps. Therefore, urban societies of studied Vespinae are often definitely larger, more numerous and they have better reproductive success than colonies outside the urban areas.

REFERENCES

- Ahrné, K., 2008. Local Management and Landscape Effects on Diversity of Bees, Wasps and Birds in Urban Green Areas. Doctoral Thesis, Swedish University of Agricultural Sciences.
- Banaszak, J. & K. Kasprzak. 1978. Przegląd badań nad fauną bezkręgowców terenów miejskich. [A review of studies on the fauna of invertebrates in urban areas] *Przegląd Zoologiczny*. 22,3: 239-249.
- Brian, M.V. 1965. Social insect population. London and New York Academic Press.
- Bunn, D.S., 1988: The nesting cycle of the hornet *Vespa crabro* L. (Hym., Vespidae). *Entomologist's Monthly Magazine*. 24: 117-122.
- Christie, F.J. & D.F. Hochuli. 2008. Responses of wasp communities to urbanization: effects on community resilience and species diversity. *Journal. Insect Conservation* 13(2): 213-221
- Chudzicka, E. & E. Skibińska. 1994. An evaluation of an urban environment on the basis of faunistic data. *Memorabilia Zoologica*. 49: 176-185.
- Cohen, J. 1988. Statistical power analysis for the behavioral sciences (2nd Ed.) Hillsdale, NJ: Erlbaum: 569 ss.
- Czechowski, W. 1979. Urban woodland areas as the refuge of invertebrate fauna. *Bulletin of the Polish Academy of Sciences Seria Biology* 27: 179-182.
- Dubaniewicz, H. 1990. Skład chemiczny opadów atmosferycznych na obszarze Łodzi. [in] Zimny H. (ed.) *Funkcjonowanie układów ekologicznych w warunkach zurbanizowanych*. [Chemical composition of precipitation in the area of Łódź *In: The functioning of ecological systems in urban conditions*] *SGGW AR, Warszawa*, 58: 35-41.

- Foster, K. R. & F.L.W. Ratnieks. 2000. Social insects: Facultative worker policing in a wasp. *Nature* 407: 692-693.
- Foster, K. R., F.L.W. Ratnieks & A.F. Raybould . 2000.: Do hornets have zombie workers? *Molecular Ecology*. 9: 735-742.
- Foster, K.R. & Ratnieks F. L.W. 2001. Paternity, reproduction and conflict in vespine wasps: a model system for testing kin selection predictions. *Behavioral Ecology and Sociobiology*. 50: 1-8.
- Foster, K.R., Ratnieks F. L.W., Gyllenstrand N., Thoren P.A., 2001: Colony kin structure and male production in *Dolichovespula* wasps. *Molecular Ecology* 10: 1003-1010.
- Foster, K.R., J.Gulliver & F.L.W. Ratnieks . 2002. Worker policing in the European hornet *Vespa crabro*. *Insectes Sociaux* 49: 41-44.
- Haeseler, V.1982. Amais, Wespen und Bienen als Bewohner gepflasterter Bürgersteige, Parkplätze und Straßen (Hymenoptera: Aculeata). *Drosera* 82(1): 17-32.
- Haeseler, V. 1997. A nest of the vespineae *Dolichovespula media* (Retzius, 1783) with a vestibule of 19.5 cm length (Hymenoptera, Vespidae), *Entomofauna Zeitschrift fur Entomologie*, 18, 23: 393-400.
- Hermes, M.G. & A. Köhler. 2006. The flower-visiting social wasps (Hymenoptera, Vespidae, Polistinae) in two areas of Rio Grande do Sul State, southern Brazil. *Revista Brasileira de Entomologia* 50(2): 268-274.
- Ishay, J.S., L. Litinetsky, V. Pertsis, D. Linsky, V.Lusternik & A.Voronel A. 2002a. Hornet silk: thermophysical properties. *Journal of Thermal Biology* 27: 7-15.
- Ishay, J.S., V.Pertsis, L. Litinetsky, E. Rosenzweig, V. Lusternik & A.Voronel . 2002b. Thermoelectric conversion and specific heat of hornet combs. *Journal of Optoelectronics Advanced Materials* 4(1): 135-145.
- Ishay J.S., Barkay Z., Eliaz N., Plotkin M., Volynchik S., Bergman D.J., 2008: Gravity orientation in social wasp comb cells (Vespinae) and the possible role of embedded minerale. *Naturwissenschaften* 95: 333-342.
- Jeanne, R.L. & A.N. Bouwma . 2002. Scaling in nests of a social wasp: a property of the social group. *The Biological Bulletin* 202: 289-295.
- Karsai, I. & Z. Péntzes. 1993. Comb building in social wasps: selforganization and stigmergic scripts. *Journal of Theoretical Biology* 161: 505-525.
- Karsai, I. & Z. Péntzes. 1996. Intraspecific variation in the comb structure of *Polistes dominulus*: parameters, maturation, nest size and cell arrangement. *Insectes Sociaux* 43: 277-296.
- Karsai, I. & Z. Péntzes. 1998. Nest shapes in paper wasps: can the variability of forms be deduced from the same construction algorithm. *Proceedings of the Royal Society of London Series B* 265: 1261-1268.
- Klingner R., Richter K., Schmolz E., Keller B., 2005: The role of moisture in the nest thermoregulation of social wasps. *Naturwissenschaften* 92: 427-430.
- Klingner, R. & K. Richter & E. Schmolz. 2006. Strategies of social wasps for thermal Homeostasis in light paper nests. *Journal of Thermal Biology* 31: 599-604.

- Kowalczyk, J.K. 1991. Materiały do znajomości żądłówek (*Hymenoptera, Aculeata*) Łodzi. [Materials to the knowledge of *Aculeata (Hymenoptera)* in Łódź] Acta Universitatis Lodzianensis, Folia zoologica and anthropologica 7: 67-114.
- Kowalczyk, J.K. & T. Kurzac. 2005. Żądłówki (*Hymenoptera, Aculeata*) Ogrodu Botanicznego w Łodzi. [Aculeata (Hymenoptera) of the Botanical Garden in Łódź] Biuletyn Ogrodów Botanicznych 14: 101-113.
- Kowalczyk, J.K. & J. Nadolski. 2007. Żądłówki (*Hymenoptera, Aculeata*) terenów kolejowych w Łodzi. [Aculeata (Hymenoptera) of railway areas in Łódź] Wiadomości Entomologiczne 26 (4): 279-288.
- Kowalczyk, J.K. & K. Szczepko. 2008. Actual list of Aculeata (Hymenoptera) of Łódź city. Acta Universitatis Lodzianensis, Folia Biologica et Oecologica 4: 127-146.
- Kuziel, S. & B. Halicz. 1979. Występowanie porostów epifitycznych na obszarze Łodzi. [Occurrence of epiphytic lichens in the area of Łódź] Sprawozdanie z czynności i posiedzeń Łódzkiego Towarzystwa Naukowego [Report on the activities and meetings of the Łódź Scientific Society] 33(3): 1-7.
- Langowska, A., A. Ekner, P. Skórka, M. Tobolka, & P. Tryjanowski. 2010. Nest-site tenacity and dispersal patterns of *Vespa crabro* colonies located in bird nest-boxes. Sociobiology 56 (2): 375-382.
- Leathwick, D.M. & P.L. Godfrey. 1996. Overwintering colonies of the common wasp (*Vespula vulgaris*) in Palmerston North, New Zealand, New Zealand Journal of Zoology 23: 355-358.
- Markowski, J., Z. Wojciechowski, J.K. Kowalczyk, E. Tranda, Z. Śliwiński & B. Soszyński. 1998. Fauna Łodzi. [Fauna of Łódź] Fundacja „Człowiek i Środowisko”, Łódź.
- Markowski, J., J.K. Kowalczyk, T. Janiszewski, Z. Wojciechowski, K. Szczepko & J. Domański. 2004. Fauna Łodzi – stan poznania, zmiany, gatunki chronione i zagrożone. In Indykiewicz P., Barczak T. (eds). Fauna miast Europy Środkowej 21. wieku. [Fauna of Łódź – the state of knowledge, changes, protected and threatened species. In Urban Fauna of Central Europe in the 21st Century]. LOGO, Bydgoszcz: 19-36.
- McGain, F., J. Harrison & K.D. Winkel. 2000. Wasp stinging mortality in Australia. The Medical Journal of Australia 173 (4): 198-200.
- Nadolski, J. 2000a. Zróżnicowanie własności toksycznych jadu wybranych żądłówek społecznych (*Hymenoptera, Aculeata*). [Differentiation of toxicity properties of some social Aculeata venoms (Hymenoptera, Aculeata)] Acta Universitatis Lodzianensis, Folia zoologica 4: 3-24.
- Nadolski, J. 2000b. Gniazda szerszenia (*Vespa crabro*) na obszarze Łodzi – wstępna analiza rozmieszczenia. [Hornet nests (*Vespa crabro*) in the area of Łódź – preliminary analysis of the distribution] Acta Universitatis Lodzianensis, Folia zoologica 4: 57-63
- Nadolski, J., D. Majczyna, B. Loga, & A. Stańczyk-Lutz A. 2000. Szerszeń (*Vespa crabro*) w Łodzi – wstępna ocena epidemiologiczna. [Hornet (*Vespa crabro*) in Łódź, preliminary estimate of epidemiology] Acta Universitatis Lodzianensis, Folia zoologica 4: 47-56.

- Nadolski, J. 2001. Gniazda os społecznych na terenie Łodzi. *In*: Indykiewicz P., Barczak T., Kaczorowski G. (eds). „Bioróżnorodność i ekologia populacji zwierzęcych w środowiskach zurbanizowanych” [Nests of social wasps and hornets in Town area of Łódź. *In*: Biodiversity and ecology of animal populations in urban environments]. NICE Bydgoszcz: 89-93.
- Nadolski, J. 2004. Gniazda os społecznych (*Hymenoptera: Vespinae*) w skrzynkach lęgowych dla ptaków na obszarze Łodzi – wstępne wyniki badań. *In*: Indykiewicz P., Barczak T. (eds). Fauna miast Europy Środkowej 21 wieku”. [Nests of social wasps (*Hymenoptera: Vespinae*) in breeding Bowes for birds in the town area of Łódź – preliminary results of investigation. *In*: Urban Fauna of Central Europe in the 21 st Century]. LOGO, Bydgoszcz, pp 83-93.
- Nadolski, J., M. Michalski & B. Loga. 2011. Paper wasps (*Hymenoptera; Polistinae*) in the city of Łódź. *In*: Indykiewicz P, Jerzak L., Böhner J., Kavanagh B. [eds]. Urban fauna, Studies of Animals biology, ecology and conservation in European cities. UTP Bydgoszcz, pp 209-215.
- Nakamura, M. & S. Sonthichai S. 2004. Nesting habits of some hornet species (*Hymenoptera, Vespidae*) in Northern Thailand. *Kasetsart Journal Natural Science*, 38(2): 196-206.
- Pawlikowski, T. & M. Osmański. 1998: Atrakcyjność środowisk miejskich dla os Społecznych (*Hymenoptera: Vespinae*) na obszarze Torunia. [Attractiveness of city environments for social wasps (*Hymenoptera: Vespinae*) in the area of Toruń] *Wiadomości entomologiczne*. 17 (2): 95-104.
- Pawlikowski, T. & K. Pawlikowski 2003. Zasiadlanie skrzynek lęgowych dla ptaków przez osę saksońską *Dolichovespula saxonica* (Fabr.) (*Hymenoptera: Vespidae*) w Puszczy Boreckiej. [Wasp *Dolichovespula saxonica* (Fabr.) (*Hymenoptera: Vespidae*) settling wooden breeding boxes for birds in the Borecka Forest] *Wiadomości Entomologiczne* 22 (4): 201-210.
- Pawlikowski, K., T. Pawlikowski, & E. Szaławicz. 2005. Fenologia lotów os społecznych (*Hymenoptera: Vespidae*) na obszarze miasta Torunia w latach 1981-2000. [Phenology of flight of social wasps (*Hymenoptera: Vespidae*) in the city of Toruń in the years 1981 -2000] *Biblioteka Monitoringu Środowiska*, Poznań: 495-500.
- Pickett, K.M., D.M. Osborne, D. Wahl, & J.W. Wenzel. 2001. An enormous nest of *Vespula squamosa* from Florida, the largest social wasp nest reported from North America, with notes on colony cycle and reproduction. *Journal of the New York Entomological Society* 109(3-4): 408-415.
- Seeley, T.D. & R.H. Seeley. 1980: A nest of a social wasp *Vespa affinis*, in Thailand (*Hymenoptera: Vespidae*). *Psyche* 87: 299-304.
- Skibińska, E. 1978. Influence de la pression urbaine sur les groupements de *Vespidae*. *Memorabilia Zoologica* 29: 173-181.
- Skibińska, E. 1982. Wasps (*Hymenoptera, Vespidae*) of Warsaw and Mazovia, *Memorabilia Zoologica* 36: 91-102.

- Skibińska, E. 1987. Structure of wasp (*Hymenoptera, Vespidae*) communities in the Urban Green of Warsaw. *Memorabilia Zoologica* 42: 37-54.
- Starks, P.T. & N.H. Fefferman. 2006. *Polistes* nest founding behaviour: a model for selective maintenance of alternative behavioral phenotypes. *Annales Zoologici Fennici* 43: 456-467.
- Star, C.K. & R.S. Jacobson. 1990. Nest structure in Philippine Hornets (Hymenoptera, Vespidae, *Vespa* spp.). *Japanese Journal of Entomology* 58 (1): 125-143.
- Strassmann, J.E. 1989. Early termination of brood rearing in the social wasp, *Polistes annularis* (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society* 62(3): 353-362.
- Takahashi, J., J. Nakamura, S. Akimoto & E. Hasegawa. 2004. Kin structure and colony male reproduction in the hornet *Vespa crabro* (Hymenoptera: Vespidae). *Journal Ethology* 22: 43-47.
- Tibbetts, E.A. 2004. Complex social behaviour can be selected for variability in visual features: a case study in *Polistes* wasps. *Proceedings of the Royal Society of London Series B* 271: 1955-1960.
- Wanat, M. 1987. Ryjkowce (Coleoptera, Curculionidae) Łodzi. [Curculionidae (Coleoptera) of Łódź] *Acta Universitatis Lodzianae, Folia zoologica and anthropologica* 5: 27-86.
- Wenseleers, T., N.S. Badcock, K. Erven, A. Tofilski, F.S. Nascimento, A.G. Hart, A.T. Burke, M.E. Archer & F.L.W. Ratnieks. 2005a. A test of worker policing theory in an advanced eusocial wasp, *Vespula rufa*. *Evolution*, 59(6) 1306-1314.
- Wenseleers, T., A. Tofilski & F.L.W. Ratnieks. 2005b. Queen and worker policing in the tree wasp *Dolichovespula sylvestris*. *Behavioral Ecology and Sociobiology* 58: 80-86.
- Yamane, S. & S. Makino. 1977. Bionomics of *Vespa analis insularis* and *V. mandarinia latilineata* in Hokkaido, northern Japan, with notes on vespine embryo nests (Hymenoptera: Vespidae). *Insecta Matsumurana (N.S.)* 12: 1-33.

