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## RESEARCH ARTICLE - WASPS

### Phenology of European Hornet, *Vespa crabro* L. and Saxon Wasps, *Dolichovespula saxonica* Fabr. (Hymenoptera: Vespidae): the Influence of the Weather on the Reproductive Success of Wasps Societies in Urban Conditions

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#### Abstract

In subsequent years, changes in the period of colonies activity for both species of wasps were observed as well as the longer period of development of wasp societies in the city than in the forest. There was not found a clear influence of weather conditions in winter on date of colonies initiation. However, low temperatures and rainfall in May caused a delay in the initiation of nesting. The temperature in winter had a little impact on the number of queens that survived the winter and established their colonies in spring, but the humidity in winter had influence on the count of queens and thereby on the number of future nests especially in the forest area.

#### Introduction

The presence of different species of social wasps (Vespidae) in urban habitats is commonly known (Edwards, 1980; Matsura & Yamane, 1984; Haesler, 1982; Ahrnè 2008), also in the cities from Poland (Skibińska, 1987; Kowalczyk, 1991; Nadolski et al., 2011). Previous studies determined the species composition of these insects, their proportions and structures of nests and sizes of their colonies (Nadolski, 2012), including their parasitoids, parasites, pathogens and other microorganisms accompanying their nests (Nadolski, 2013) as well as the dynamics of quantitative changes in the urbanized areas (Christie & Hochuli, 2008). However, it is still difficult to determine which factors have important impacts on the effective colonization of cities by many species of social wasps. The most characteristic features of these areas are a warmer and more stable microclimate than in other variable environments, and abundant food resources and a large variety of niches to be used (Christie & Hochuli, 2008). Wasp colonies in cities

are mostly established in buildings such as roofs, attics, and within the walls of houses, and their nests are larger and societies are more numerous than those from rural or forested areas (Nadolski, 2012). Subjects concerning the biology of social wasps have been the basis of many studies (Matsura, & Yamane, 1984; Starr & Jacobson, 1990; Leatwick & Godfrey, 1996; Haesler, 1997; Nakamura & Sonthichai, 2004), but only a few are directly related to the phenology of this group of insects in Poland (Pawlikowski et al., 2005; Tryjanowski et al., 2010). However previous studies were based only on observed of wasp flight activity, which method does not always correctly characterizes the current stage of development of the colony.. The purpose of this study was to determine the phenology and the duration of reproductive periods of two wasp species - the European hornet *Vespa crabro* Linnaeus, 1758 and Saxon wasp *Dolichovespula saxonica* (Fabricius, 1793) based on the study of whole colonies and nests in the Łódź city in Poland and to determine whether meteorological factors may have an impact on their reproductive success.



## Materials and Methods

### Study sites

The study was conducted in the city of Łódź (51°45'N 19°28'E) in central Poland. The climate of Łódź is intermediate between the continental climate – Eastern European and maritime climate – Western European. The study of phenology of two species of social wasps (Vespinae), the European hornet *Vespa crabro* (Linnaeus, 1758) and Saxon Wasp *Dolichovespula saxonica* (Fabricius, 1793) was carried out in two 10 km-distant areas in different habitat types. The first of these, The Botanic and Zoological Gardens, was located at a parkland habitat (51°45'N 19°24'E) with the area about 84 ha. It is located in the western part of the city. The whole area, a remnant of an ancient deciduous forest, is dominated by hornbeam *Carpinus betulus* and oaks *Quercus robur* and *Q. petraea* as well as Scots pines *Pinus silvestris*, birches *Betula* sp. and different exotic tree and shrub species. South and south-east sides of these gardens directly border on big residential area with numerous blocks of flats and with population over one hundred thousand. The other study area, a woodland habitat, was the Łagiewniki Forest (51°50'N 19°29'E). It is a rich deciduous forest of considerable size about 1250 ha that is a remnant of the former of primeval forest and which was partly chopped down 70 years ago and reforested later. It is located in north-eastern part of Łódź, a few kilometers from the city centre. Because of its exceptional nature and landscape, part of this forest was turned into a nature reserve 'Las Łagiewnicki' with the area of 69.85 ha; whose main object of protection is a complex of natural phytocenoses with oak and hornbeam.

### Collecting data

This study was conducted between 2000 and 2009. The data concerning of the establishing of nests (the day of initiation nesting) were gathered based on the regular weekly recording of wooden nest boxes and other places (tree hollows, branches, outbuildings) where studied species could potentially form their nests by the young queen. Wooden nesting boxes had dimensions of 13 x 13 x 36 cm and an entrance hole with 29 mm of diameter located 29 cm above the bottom of the box. The arising colonies were then regularly monitored, every two weeks, until the moment when reproductive castes (gynes and drones) left the nest. During each season the boxes occupied by wasps were observed and their colonies were studied for the presence of particular castes. The data obtained in this way, concerning both the date of initiation nesting and the appearing of castes, especially reproductive ones, gave ground to phenological analyses of biology of studied species. For the statistical analyses, the system of specification of dates was simplified by standardizing them. Dates were coded as numbers, starting with April 1st as num-

ber 1 of the given year (so that May 1st = 31, June 1st = 62 and so on). These activities were correlated with the studies on breeding of Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major* in Łódź (Alabrudzińska et al., 2003; Marciniak et al., 2007; Bańbura et al., 2010). Together 200 boxes during years 2000-2001 (110 located in the woodland site and 90 in the parkland site), 300 in years 2002- 2003 (180 located in the woodland site and 120 in the parkland site) and 450 during the years 2004-2008 (250 located in the woodland site and 200 in the parkland site) were located on studied areas. After each season all the boxes were cleaned of all organic waste, including the remains of birds and nests of wasps as well as other impurities.

Weather data were obtained from Historical Weather Records published on a website <http://www.tutiempo.net/en/Climate/europe.htm>. Graphics and statistical analyses were conducted using STATISTICA 9 package (StatSoft, Inc. 2010).

## Results and Discussion

### Phenology of the establishment of a nest

A total of 182 colonies of *Vespa crabro* and 347 colonies of *Dolichovespula saxonica* were investigated on studied areas in the city. The dynamic of development stages of colonies of *V. crabro* and *D. saxonica* are showed in the Fig 1. For analysis, introduced designations (QN, and E) where QN (the queen) it is the nest of queen without workers yet, and E (the end) it is the nest ending the development, where been able to already observed the presence of first reproductive castes (gynes - young queens and drones). Analysis ANOVA non-parametric, Kruskal-Wallis test: (H 3,529 = 448.03 p = 0.00) and p-values for multiple comparisons showed statistical significance between ranks all of analyzed variables (p < 0,05) except ranks of QN period for both studied species (p = 1.0) (Fig 1).

Figures 2 and 3 present the results of statistical analysis of initiation nesting dates (the period of QN without larvae and pupae yet) for *D. saxonica* (ANOVA nonparametric, Kruskal-Wallis test: H 9,189 = 94.5 p = 0.00) and *V. crabro* (ANOVA nonparametric, Kruskal-Wallis test: H 9,84 = 56.0 p = 0.00) in particular years. Worthy of note are the minimum and maximum values which demonstrate the differences in dates of initiating nest-building in a given year although for some of multiple comparisons p-values were higher than 0.05.

### Influence of urban conditions and weather on the reproductive success of social wasps (Vespinae).

Means values of ranks of nest initiation dates, between two studied areas (parkland and woodland) were analyzed. Fig 4 presents the mean value of standardized dates for establishing nests by *Vespa crabro* in both studied areas - habitats (the

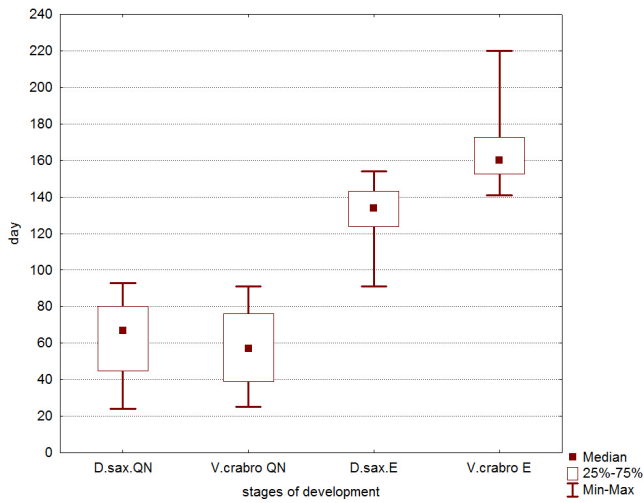


Fig 1. Stages of development for *Dolichovespula saxonica* and *Vespa crabro* colonies in Łódź in 2000-2009. D.sax.QN – the stage of Queen for *Dolichovespula saxonica*, V.crabro.QN – the stage of Queen for *Vespa crabro*, D.sax.E – the ending stage of development for *Dolichovespula saxonica*, V.crabro.E – the ending stage of development for *Vespa crabro*

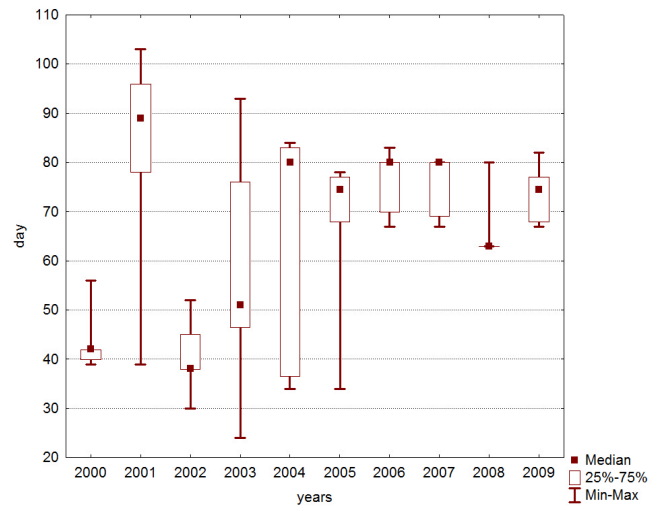


Fig 2. Date of initiation for *Dolichovespula saxonica* nests in Łódź in 2000-2009.

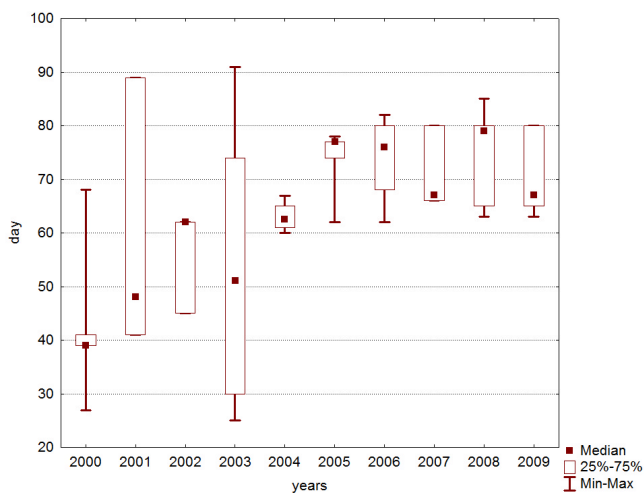


Fig 3. Date of initiation of *Vespa crabro* nests in Łódź in 2000-2009.

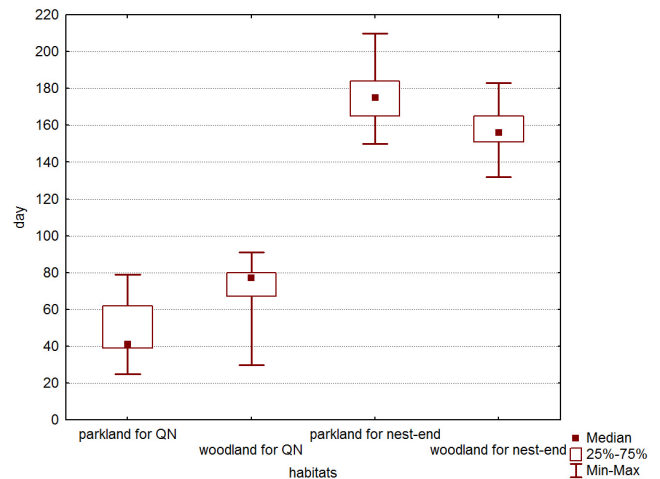


Fig 4. Date of initiation of nests by queens and time of appearing of reproductive castes for *Vespa crabro* nests in two habitats in Łódź, in 2000-2009.

first - residential areas with parkland and the second - woodland). The analysis ANOVA nonparametric Kruskal-Wallis test ( $H_{3,203} = 163.5$   $p = 0.00$ ) demonstrated statistical significance between studied areas. Multiple comparisons showed statistical significance ( $p$ -values,  $<0.05$ ) between means values of ranks of the time of appearing of reproductive castes for both habitats. For initiation dates, these differences are not statistically significant, although the mean of dates for the parkland habitat date is lower (earlier date). In the woodland habitat males and gynes appear in the nest about a week earlier than in the parkland habitat. For *Dolichovespula saxonica* these differences were not statistically significant, probably due to the short period the full development cycle of colonies of this wasp.

The assessment of the influence of weather conditions

in the period of establishing of a nest by young queens of *D. saxonica* and *V. crabro* was conducted as well as the correlation between the number of nests in a given year and weather parameters in the winter (the average weather parameters of December, January, February and March) preceding the study season and in spring. In figures 5 and 6, correlations between the mean temperature in May and date of initiation of nests were demonstrated for nests of *D. saxonica* and *V. crabro*. Temperature, precipitation and humidity in winter practically did not affect on the date of initiation of their nests and the precipitation and humidity in June had a weak effect. Other weather factors for both species had a weak influence on date of nesting initiation by queens.

The influence of weather conditions on the count of established nests was also studied. In Table 1 are demonstrated  $r$ -values for correlations between count of established wasp nests and weather conditions in winter and spring in the studied period.

**Table 1.** The correlation between the weather conditions and the count of *Dolichovespula saxonica* and *Vespa crabro* colonies. WN - weak or none the correlation ( $r < 0.3$ ), Numbers in bold indicate  $p < 0.05$

Habitat	r-values for winter conditions			r-values for spring conditions		
	Temperature	Humidity	Precipitation	Temperature	Humidity	Precipitation
<i>Dolichovespula saxonica</i>						
Residential and Parkland	WN	WN	WN	0.30	WN	WN
Woodland	WN	<b>0.62</b>	0.32	0.35	<b>-0.65</b>	<b>-0.57</b>
<i>Vespa crabro</i>						
Residential and Parkland	WN	<b>0.52</b>	WN	WN	WN	WN
Woodland	WN	<b>0.81</b>	WN	0.37	0.35	-0.36

A large city is a specific ecosystem which, like no other, undergoes continuous changes resulting from constant, planned or accidental human intervention. The dynamic process accompanying these changes, in result of which we may observe loss of some species and inflow of others may sometimes leads to the increase of species diversity within certain animal groups. In urban habitats specific microclimate is created, which stands out due to reduced amplitude of temperature and humidity. 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. Specific character of these habitats is tolerated by some groups of Hymenoptera, including social wasps (Banaszak, 1978; Skibińska, 1978). The species, which 'were able to' adapt their biology to urban environment, began their expansion at an unparalleled scale (Skibińska, 1987). The European hornet *Vespa crabro* and Saxon wasp *Dolichovespula saxonica* are species which often form colonies in the city and sizes of their nests and their societies are different and depend on the location of their colonies (Nadolski, 2012).

Current knowledge of the phenology of Vespinae in urban condition is clearly insufficient. One of the many rea-

sons of this state of affairs are specific problems connected with the study of particular stages of the development of nests and societies, especially the time of produce particular forms and castes. A nest of Vespinae is a tightly closed structure and some kind of external interference can irritate the society of these insects and leads to their attack in defense of the colony. Monitoring of wasp societies based on observations of flight of particular forms of imago allows, as it seems, relatively accurate assessment of time of appearance and disappearance of particular forms and castes. Special attention should be paid to the work of the research centre headed by Tadeusz Pawlikowski (Pawlikowski et al., 2005; Pawlikowski & Pawlikowski, 2009; Tryjanowski et al., 2010). However, studies of phenology based only on observations of wasps' flight do not fully reflect the real phenomena occurring in their societies. Many different factors can affect the time of departure from the nest of the particular individuals, especially the weather conditions and food availability. At the same time these factors may have a different effect on the wasps inside the nest. For example, adverse weather conditions, rain and low temperatures significantly reduce the penetration of the area by the wasps, however it does not mean they are not present inside

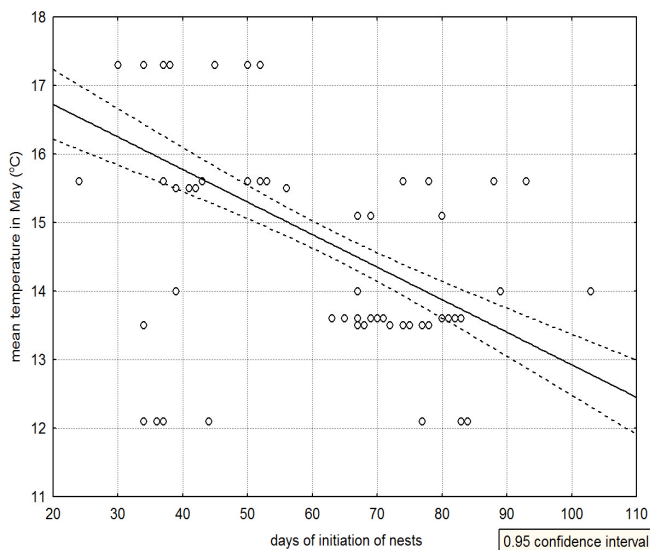


Fig 5. The correlation between the mean temperature in May and date of initiation of *Dolichovespula saxonica* nests in Łódź, in 2000-2008 (N = 180;  $r = -0.54$ ;  $p < 0.05$ ).

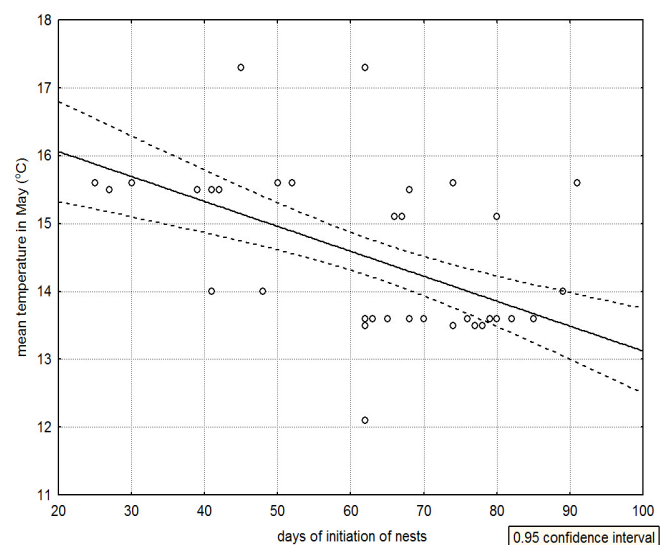


Fig 6. The correlation between the mean temperature in May and date of initiation of *Vespa crabro* nests in Łódź, in 2000-2008 (N = 53;  $r = -0.55$ ;  $p < 0.05$ ).

the nest. Availability of food may be equally important factor in accelerating or delaying the flight of wasps from their nests. Studies on *Vespa crabro* (Nadolski, unpubl.) in open breeding conditions demonstrated that when wasps have enough food (artificial feeding), neither gynes nor drones did not leave the nest even in late autumn. In autumn in natural conditions is running low on food because the number of workers that transported food are decreased both gynes and drones have to leave their nest. The effects of this phenomenon can be noticed most clearly in late autumn when reproductive castes leave nests suddenly and on mass scale. Studies of hornet's colonies conducted right before the abundant leaving of nests by wasps demonstrates large presence of gynes and drones (often few hundred) and only tens of workers. As earlier studies have shown (Nadolski, 2012) the total number of gynes and drones leaving the nest in the autumn is close to the sum of all cells, previously occupied by larvae of reproductive castes. However, the emergence of particular individuals in nest is gradual as is apparent from the analysis of distribution of larvae and pupae in combs (Nadolski, 2012) and it starts still in summer, not only in colonies of *Dolichovespula saxonica* which development is completed in July as well as in colonies of *Vespa crabro* which have active colonies in October yet (Fig 1). This indicates that probably only very few individuals of reproductive castes probably leave their nest earlier. This situation is fully understandable because, there is necessity to synchronize the departures of these castes from various colonies. Individuals which left the nest too early have little chance to find the partner. In studied years, changes in the period of activity of both species of wasps were observed (Fig 2 and Fig 3) but presence of hornets seems to be more stable. In the research of nests of both species of wasps based on the analysis of structure and the time of appearance of particular castes were demonstrated a statistically significant difference between dates of start and end of colony development. In Fig 1 it can be seen that for hornet a stage QN sometimes lasted until the turn of June and July, and F stage was beginning in mid-August. Thus, the presence or absence on the ground, the representative of reproductive castes is not equivalent to its presence or absence in the nest. It is worth paying attention to that on average, reproductive castes appear in nests for *Vespa crabro* between the standardized value 160 and 170, i.e. the beginning of September, and the first males-drones and gynes can be observed in nests already in the middle of August. The comparison of the date of nesting initiation by young queens of *Vespa crabro* and *Dolichovespula saxonica* (Fig 2 and Fig 3) demonstrated differences in particular years. However, it is difficult to compare these data with the results of studies done for many years in Kujawy region in Poland (Pawlikowski & Pawlikowski, 2009; Tryjanowski et al., 2010), because these studies were carried out on another area and with other methods. However, it can also be observed that in recent years the initiation of wasp nests is delayed and the period of time during which young queens begin to build nests is shortened

also in Łódź. The weather and urban conditions in particular years may have a significant impact on biology of wasps. The results concerning the nesting initiation for *Vespa crabro* colonies based on the analysis of their nests showed nearly a week the difference between studied habitats residential-parkland and woodland (Fig 4) although these differences were not statistically significant. It is interesting that similar results are obtained in studies of certain other groups of organisms. Observations conducted over many years in the city of Łódź showed similar phenological differentiation in vegetation of some plant species between these zones (Bańbura et al., 2010). Even more interesting is a significant difference between the periods of ending of colonies development of *Vespa crabro* in both habitats (Fig 4). In the forest a small but statistically significant accelerate the emergence of reproductive castes were observed. In conjunction with the later date of initiation of colonies this situation must result in shortening of the period of full development of society of hornets, and so consequently development of a smaller number of workers, gynes and drones and weaker reproductive success. Demonstrated differences of presence of reproductive castes in the colony from zones of Łódź, confirms assumptions that is a small but noticeable impact of urbanization degree on the time of wasps transformation. A longer period of colonies activity in urban conditions causes that wasp nests can be larger and achieve the better reproductive success. These results again confirm that urban conditions are more favorable for social wasps, than conditions outside the city (Nadolski, 2012).

In these studies a clear influence of weather conditions of the preceding winter season, on nest initiation date in the next year in both studied habitats there was not found. However the weather conditions preceding directly the time of establishing of nests by young mothers proved to be significant. The strong negative correlation (Cohen, 1988) ( $r = -0.61$ ) between the mean temperature in May and date of initiation of nests was demonstrated for nests of Saxon wasp (*Dolichovespula saxonica*) (Fig 5). For the European hornet (*Vespa crabro*), there was also found a strong negative correlation ( $r = -0.55$ ) (Fig 6) between mean temperature in May and date of initiation of nests. Other weather factors for both species had no significant effect on date of nesting initiation. These results are partly consistent with the date for the "first queen" of *Vespula germanica* (Fabricius, 1793) obtained in Kujawy region in Poland (Tryjanowski et al., 2010).

Winter weather conditions can have an effect on the number of wasp queens who have survived the winter and established colonies. Winter temperatures and temperatures in spring do not have an influence on the number of colonies of wasps in the city (Table 1). These relationships with spring temperatures are different for other social insects, such as the honey bee *Apis mellifera* (Gordo & Sanz, 2006) and Spiewok and Schmolz (2006) showed that ambient temperature has an influence on the flight performance of wasps, especially hornets. This demonstrates that the phenology of social wasps

is difficult to investigate only based on an assessment the activity of flights, because wasps are active first of all in sunny and warm days and their absence on the ground does not mean, that they are not in the nest.

In urban conditions wasps are not so strongly related to temperature for different reasons. First of all, the urban habitat can provide more comfortable and safer conditions for wintering for many groups of insects, protecting them from too low temperature during diapauses. It is different in the forest area where insects can survive the winter only in natural places in which temperature and humidity can be important. Interestingly, this study indicates that no severe frosts, but rather mild and snowless winters may have a negative impact on the survival of young queens (Table 1). In the light of current studies, it is understandable, because obtained LTemp50 values for gynes indicate that even a severe winter should not have influence on their survival (Nadolski & Bańbura, 2010). However, for both studied species were demonstrated a strong positive correlation between the level of humidity in the period preceding winters and the count of the established nests within the area of Łagiewniki Forest ( $r = 0.62$  for *Dolichovespula saxonica* and  $r = 0.81$  for *Vespa crabro*). This parameter is therefore important for the survival of gynes during diapauses in natural conditions. For *Vespa crabro*, proper humidity in winter in urban conditions is also important (Table 1). For *Vespa crabro*, the humidity in winter in the residential-parkland habitat had also strong ( $r = 0.52$ ) influence on the number of established colonies. It can be assumed that these differences between studied species may result from different places where young queens (gynes) overwinter. Queens of hornet rarely overwinter inside in buildings (author observations) in contrast to queens of the Saxon wasp.

In natural areas intense precipitation and higher humidity also in spring have a negative influence on the very process of forming a nest and its further development especially for colonies of *Dolichovespula saxonica* (Table 1). Especially nests on the branches of trees and bushes as well as colonies in breeding boxes and in tree hollows may be infected with fungi. For colonies in the urban area these factors are less important for initiation of the nest, because of the possibilities of alternative nest location in the buildings. The temperature in May had moderate influence on the count of nests of Saxon wasps (moderate positive correlation  $r = 0.30-0.35$ ) in both habitats and the weather condition in the spring had moderate influence on the count of colonies of *Vespa crabro* in forest (Table 1).

The results of these studies demonstrate a clear influence of weather conditions on the phenology and reproductive success of social wasps. However, urban conditions can significantly reduce this impact in favor of insects.

## References

- Ahrnè, 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.
- Alabrudzińska, J., Kaliński, A., Słomczyński, R., Wawrzyniak, J., Zieliński, P. & Bańbura, J. (2003). Effects of nest characteristics on breeding success of Great Tits *Parus major*. *Acta Ornithol.*, 38: 151-154.
- Banaszak, J. & Kasprzak K. (1978). A review of studies on the fauna of invertebrates in urban areas. *Przegląd Zool.*, 22 (3): 239-249. (In Polish).
- Bańbura, M., Sulikowska-Drozd, A., Kaliński, A., Skwarska, J., Wawrzyniak, J., Krul, A., Zieliński, P. & Bańbura J. (2010). Egg size variation in Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major* in relation to habitat differences in snail abundance. *Acta Ornithol.*, 45 (2): 121-129.
- Christie, F.J. & Hochuli, D.F. (2008). Responses of wasp communities to urbanization: effects on community resilience and species diversity. *J. Insect Conserv.*, 13: 213-221.
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd Ed.) Hillsdale, NJ: Erlbaum: 569 p.
- Edwards, R. (1980). *Social wasps. Their biology and control.* Rentokil, East Grinstead UK. 398 p.
- Gordo, O. & Sanz, J.J. (2006). Temporal trends in phenology of the honey bee *Apis mellifera* (L.) and the small white *Pteris rapae* (L.) in the Iberian Peninsula (1952–2004). *Ecol. Entomol.*, 31: 261–268.
- Haesler, V. (1982). Amaisien, Wespen und Bienen als Bewohner gepflasterter Bürgersteige, Parkplätze und Straßen (Hymenoptera: Aculeata). *Drosera*, 82 (1): 17-32.
- Harris, R.J., Moller, H., & Tilley, J.A. (1991). Weather-related differences in attractiveness of protein foods to *Vespula* wasps. *N. Zealand J. Ecol.*, 15: 167-170.
- Harris, R.J. & Oliver, E.H. (1993). Prey diets and population densities of the wasps *Vespula vulgaris* and *V. germanica* in scrubland-pasture. *N. Zealand J. Ecol.*, 17: 5-12.
- Kowalczyk, J.K. (1991). Materials to the knowledge of *Aculeata* (Hymenoptera) in Łódź. - *Acta Universitatis. Lodzianensis, Folia Zool. Anthropol.*, 7: 67-114 (In Polish).
- Kurowski, J.K. (ed.) (2001). *Plant Cover of the Łagiewniki Forest in Łódź.* OWR Sagalara, Łódź, p. 144. (In Polish)
- Leathwick D.M. & Godfrey, P.L. 1996: Overwintering colonies of the common wasp (*Vespula vulgaris*) in Palmerston North, New Zealand. *N. Zealand J. Zool.*, 23: 355-358.
- Marciniak, B., Nadolski, J., Nowakowska, M., Loga, B. & Bańbura J. (2007). Habitat and annual variation in arthropod

- abundance affects Blue Tit *Cyanistes caeruleus* reproduction. *Acta Ornithol.*, 42(1): 53-62.
- Matsuura, M. & Yamane S. (1984). *Biology of the Vespine Wasps*. Springer-Verlag, Berlin, p. 323.
- Nadolski, J. & Bańbura, J. (2010). A method for simple assessment of cold in insects. *Polish J. Ecol.*, 58 (1): 187-190.
- Nadolski, J., Michalski, M. & Loga, B. (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, p. 209-215.
- Nadolski, J. (2012). Structure of Nests and Colony Sizes of the European Hornet (*Vespa crabro*) and Saxon wasp (*Dolichovespula saxonica*) (Hymenoptera: Vespinae) in Urban Conditions. *Sociobiology*, 59: 1075-1120.
- Nadolski, J. (2013). Factors restricting the abundance of wasp colonies of the European hornet *Vespa crabro* and Saxon wasp *Dolichovespula saxonica* (Hymenoptera: Vespidae) in an urban area in Poland. *Entomol. Fennica*, 24: 204-215.
- Nakamura, M. & Sonthichai, S. (2004). Nesting habits of some hornet species (Hymenoptera, Vespidae) in Northern Thailand. *Kasetsart J. Nat. Sci.*, 38: 196-206.
- Pawlikowski, K., Pawlikowski, T. & Szaławicz, E. (2005). Phenology of social wasps flight (Hymenoptera: Vespidae) in the area of the Toruń city in 1981-2000. *Biblioteka Monitoringu Środowiska*, Poznań: p. 495-500. (In Polish).
- Pawlikowski, K. & Pawlikowski, T. (2009). Phenology of social wasps (Hymenoptera: Vespinae) in the Kujawy region under the influence of climatic changes 1981-2000. *Bul. Geogr. - Physical Geography Series*, 1: 125-134.
- Skibińska, E. (1978). Influence de la pression urbaine sur les groupements de Vespidae. *Mem. Zool.*, 29: 173-181.
- Skibińska, E. (1987). Structure of wasp (Hymenoptera, Vespidae) communities in the Urban Green of Warsaw. *Mem. Zool.*, 42: 37-54.
- Spiewok, S. & Schmolz, E. (2006). Changes in temperature and light alter the flight speed of hornets (*Vespa crabro* L.). *Physiol. Biochem. Zool.*, 79: 188-193.
- Starr, C.K. & Jacobson, R.S. (1990). Nest structure in Philippine Hornets (Hymenoptera, Vespidae, *Vespa* spp.). *Jap. J. Entomol.*, 58: 125-143.
- Tryjanowski, P., Pawlikowski, T., Pawlikowski K., Banaszak-Cibicka, W. & Sparks, T.H. (2010): Does climate influence phenological trends in social wasps (Hymenoptera: Vespinae) in Poland? *Europ. J. Entomol.*, 107: 203-208.

