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Long-term dynamics of structure changes of the social wasp community (*Hymenoptera: Vespinae*) in agricultural landscape of the Kujawy Region

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Abstract. Studies were carried out for 14 years (1981–1994) on the structure of the social wasp community (6 species) in the agricultural landscape of the Kujawy Region. It was assumed that the most important mechanism of changes in abundance of a multispecies community of social wasps was described by M.E. Archer. In this paper demonstrated that in the 2-year cycle of changes the increase of abundance occurred in even-number years. The cycle itself was affected by favourable or unfavourable weather conditions.

Key words: *Hymenoptera*, *Vespinae*, social wasps, dynamics of community changes, agricultural landscape, the Kujawy Region.

Introduction

Social wasps are among the most efficient predatory insects, which particularly prefer anthropogenic environments (Edwards 1980; Matsuura & Yamane 1990; Pawlikowski 1990, 1993). In agricultural areas they are the principal reducers of *Diptera*. They also consume carbohydrates from various sources (Edwards 1980; Kemper & Döhring 1967). While searching for them, they often visit sites with food products or food waste. By visiting such places they become vectors of pathogenic microorganisms and thus can constitute sanitary concern. Furthermore, being active and aggressive stingers, they also constitute a considerable allergo-toxicological threat to local residents. However, anthropogenic factors of the agricultural landscape, which determine their social wasp development success, are still insufficiently understood.

Archer (1998) worked out a model of intraspecies regulation of abundance in social wasp colonies, underlying the 2-year periodic changes of abundance in local populations (fig. 1). As the main mechanism of that model he adopted the competition among queens for environment resources. Taking this into consideration, it was decided to consider this interaction as a parallel mechanism shaping the structure of the multi-species *Vespinae* community. As demonstrated in studies carried out simultaneously at several sites of the urban area of Toruń, the multispecies social wasp complex competed mainly for sites for effective nesting with sufficient food supply for the offspring (Pawlikowski & Przybylska 2001). Such sites occurred mainly in areas with predominantly arboreal and shrub vegetation (Pawlikowski & Osmański 1998).

The main object of this work was to present the long-term dynamics of the *Vespinae* community structure in the typical agricultural landscape of the Kujawy Region. Moreover, it was undertaken to assess the functional usefulness of the Archer model for the description of changes in the main parameters of this community structure in the agricultural landscape of Central Poland.

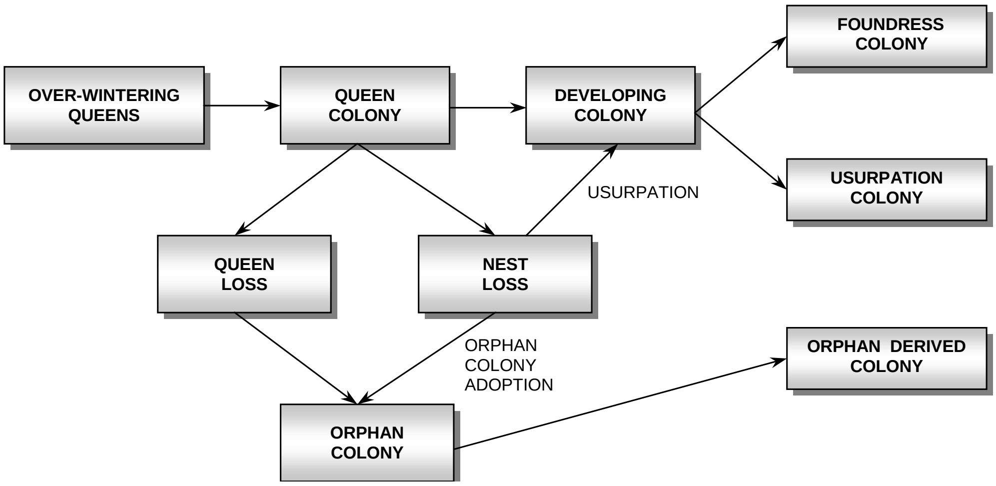

Figure 1. Types of life histories of the *Vespinae* colony (according to Archer 1997)

Material and methods

Research on social wasps in the agricultural landscape of Kujawy was conducted about 20 km south of Inowrocław (the cultural capital of the Region) in the period of full development of their colonies, i.e. from August until October, in the years 1981–1994. The computational unit (a representative sample – Pawlikowski 1990) was the number of individuals observed (or sometimes caught) in the course of a 30-min passage under optimal weather conditions (10^{00}–17^{00} CET, clear sky, air temperature 19^0–25^0C) in all main habitats of the villages Stodólno, Kraszyce, Książ, Strzelno Klasztorne. The area was situated in square CD13 of the UTM grid. All individuals were collected while performing their activities, i.e. hunting, nectar collecting, search for food, collecting material for nest building (roadsides, hedges, wooden fences), as well as at various sites containing carbohydrate food (gardens, orchards, farm service and food stores). The captured wasps were identified to the species level in the field using a magnifying glass (x20), and after that they were released. All collected individuals were used to determine the community structure of social wasps in particular growing seasons.

The community structure was described by the number of species (S), the mean number of individuals observed (and caught) in a 30-min passage (A), the general species diversity index (H') and the potential species diversity (J'). Differences between values of A in particular years were worked out statistically using the t-test. The general species diversity index was adopted after Shannon & Weaver (1963): $\mathbf{H' = \Sigma p_i \log_2 p_i}$, where $p_i = n_i / N$, which denotes the species „i" fraction in a community consisting of S number of species, and n_i denotes the abundance of species „i" in a community with the total abundance of individuals N. The potential species diversity index, also called the index of evenness of relative species abundance in the community structure, was adopted after Pielou (1966): $\mathbf{J' = H'/ \log_2 S}$, where

$\log_2 S$ denotes the maximum possible value of the index H' (H'_{max}). The index J' takes values within the range $0 < J' < 1$, and its value decreasing towards 0 denotes an increasing superdomination tendency, while increasing towards 1 denotes an increasing codomination tendency. The statistical significance of differences between values of the index H' was calculated according to Hutcheson (1970), the significance of the difference (P) was accepted at the level of significance not exceeding 0.05.

Description of weather conditions in particular years of studies was based on the data supplied by the Meteorological Station in Inowrocław, the nearest one to the study areas. The data considered in the description were: the mean air temperature and total rainfall. The analysis of total rainfall was carried out in 7 classes based on the criterion of Kaczorowska (1962), where a given year is considered:

1 – extremely wet, when excess of rainfall exceeds 50% of the long-term mean total, i.e. the total rainfall exceeds 150% of the standard,
2 – very wet, when excess of rainfall amounts to 26–50% of the long-term mean total, i.e. the total rainfall is 126–150% of the standard,
3 – wet, when the rainfall excess is 11–25% of the long-term mean total, i.e. the total rainfall amounts to 111–125% of the standard,
4 – moderate, when deviation from the long-term mean does not exceed 10%, i.e. the total rainfall comes within the limits of 90–110% of the standard,
5 – dry, when the rainfall shortage is from 11 to 25% of the long-term mean total, i.e. the total rainfall is 75–89% of the standard,
6 – very dry, when the rainfall shortage ranges from 26 to 50% of the long-term mean total, i.e. the total rainfall is 50–74% of the standard,
7 – extremely dry, when rainfall shortage exceeds 50% of the long-term mean rainfall, i.e. the total rainfall drops below 50% of the standard.

Basing on mean temperature values, the seasons were classified into 11 classes according to the criterion of Lorenc (1998), applying the formula: $ST = \sqrt{1/n\sum(t_2 - T)}$, where ST – standard deviation of mean temperature values, t_2 – deviation from the mean of a given year, T – long-term mean, n – number of years considered in the present study. The thermic classification was based on the mean annual air temperature, whose variability measure was the standard deviation value (ST):

1 – extremely cold year, when $t_2 < T - 2.5ST$,
2 – abnormally cold, when $T - 2.5ST \le t_2 < T - 2.0ST$,
3 – very cold, when $T - 2.0\,ST \le t_2 < T - 1.5\,ST$,
4 – cold, when $T - 1.5ST \le t_2 < T - 1.0ST$,
5 – lightly cold, when $T - 1.0ST \le t_2 < T - 0.5ST$,
6 – moderate, when $T - 0.5ST \le t_2 < T + 0.5ST$
7 – slightly warm, when $T + 0.5ST \le t_2 < T + 1.0ST$,
8 – warm, when $T + 1.0ST \le t_2 < T + 1.5ST$,
9 – very warm, when $T + 1.5ST \le t_2 < T + 2.0ST$,
10 – abnormally warm, when $T + 2.0ST \le t_2 \le T + 2.5ST$,
11 – extremely warm, when $t_2 > T + 2.5ST$.

Description of weather conditions for the studied area of Kujawy in the years 1980–1996, based on the adopted classification is presented in tab. 1.

Results

In 14 years period of studies in the Kujawy Region, 6 *Vespinae* species were found (tab. 2), i.e. all social nest building species and 70% of all species (including kleptoparasites) found in Poland. The most commonly found was *Vespula germanica* (F.), which constituted 64–99% of the total number of wasps (92.20% throughout all years – superdomination). Another fairly common species was *Dolichovespula saxonica* (F.) (4.24% – subdomination). The number of species found in particular years ranged from 3 to 6.

The mean abundance ranged from 1.75 to 19.3 individuals in a 30-min passage; the lowest values mostly on odd-number years and the highest ones on even-number years (fig. 2). This resembled oscillations with a recurring, mostly 2-year, cycle for statistically different values ($P \le 0.05$), particularly in the years 1982–1993, except 1990, when instead of an increase in the mean abundance a decrease was observed.

The qualitative and quantitative structure of the wasp community was described using the indices of general (H') and potential (J') species diversity (tab. 3). In the course of years the general species diversity ranged from 0.06 to 1.46 bits, depending on the increase or decrease in abundance of the predominant species (*V. germanica* and *D. saxonica*) in the community structure with the significant ($P \leq 0.05$) diversity of H' values. Whereas values of J' denoted the degree of potential species diversity proportional to the number of species and their abundance in the community. Over the years, H' and J' values displayed mostly cyclic fluctuations. The lowest H' values were observed most frequently in even-number years, which was related to the growing abundance of *V. germanica* towards superdomination.

Table 1. Characteristics of weather conditions in Western Kujawy (according to Inowrocław Meteorological Station) during 1980–1996

Year	Winter		Spring		Summer		Autumn		Year		
	TS÷TP	PS÷PP	TS÷TP	PS÷PP	TS÷TP	PS÷PP	TS÷TP	PS÷PP	TS÷TP	PS÷PP	ET+EP
1980	5	6	3	1	5	2	6	1	4	2	6
1981	6	2	6	5	5	2	5	1	6	2	8
1982	6	5	6	4	8	7	9	6	7	6	13
1983	7	2	5	5	7	6	6	4	7	5	12
1984	6	6	6	2	5	4	7	6	6	4	10
1985	3	5	6	4	5	3	6	4	4	4	8
1986	4	4	7	4	5	5	8	3	6	4	10
1987	3	4	4	3	5	2	8	2	3	2	5
1988	6	1	7	6	6	4	6	4	7	4	11
1989	9	6	7	7	7	7	8	4	9	6	15
1990	9	6	8	4	5	4	8	4	9	4	13
1991	6	6	6	3	6	6	6	4	6	5	11
1992	7	4	7	5	8	5	6	5	7	5	12
1993	6	2	8	6	4	2	5	3	6	3	9
1994	6	2	6	2	10	5	7	4	8	4	12
1995	7	4	7	5	8	3	4	7	7	5	12
1996	3	6	6	2	4	3	6	7	3	4	7

TS–TP – evaluation of seasonal air temperature according to Lorenc (1996) in evaluation classes: 1 = extremely cold, 2 = abnormally cold, 3 = very cold, 4 = cold, 5 = lightly cold, 6 = moderate, 7 = lightly warm, 8 = warm, 9 = very warm, 10 = abnormally warm, 11 = extremely warm

PS–PP – the seasonal total of precipitation according to Kaczorowska (1962) in evaluation classes: 1 = extremely wet, 2 = very wet, 3 = wet, 4 = moderate, 5 = dry, 6 = very dry, 7 = extremely dry

ET+EP – the sum of evaluation classes of air temperature and precipitation

Discussion and conclusions

In the years 1981–1994 studies were carried out on the changes in abundance of the *Vespinae* community in the agricultural landscape of Kujawy. In principle, there was a two-year cycle of changes significantly influenced by weather conditions (fig. 2). Analysis of materials indicated that dry and warm weather, creating good environmental conditions (GEC) for colony development, somehow increased the habitat resources needed for nesting, which reduced the nesting competition among queens, and consequently decreased the number of usurping queens and orphan colonies. On the other hand, wet and cool weather (BEC = bad environmental conditions) by curbing the colony development somehow diminished habitat resources, which kept production of a young queen at the low level irrespective of effects of competition among mothers. If fluctuations of seasonal weather conditions coincided with the two-year cycle then they stimulated it in direct proportion to abundance changes. If bad conditions occurred in several consecutive seasons (1982–1985 and 1989–1991), then the amplitude of cycle oscillations was reduced or even the cycle was disturbed (1990). However, when in the course of parallel studies in the area of Toruń (Pawlikowski, Przybylska 2001) favourable years alternated with unfavourable ones, the cycle extended even up to four years ($R^2 = 0.81$, $P = 0.05$). Taking this into account, it was proposed to modify the population mechanism (according to Archer 1998) concerning the long-term changes in abundance of social wasp populations (fig. 3).

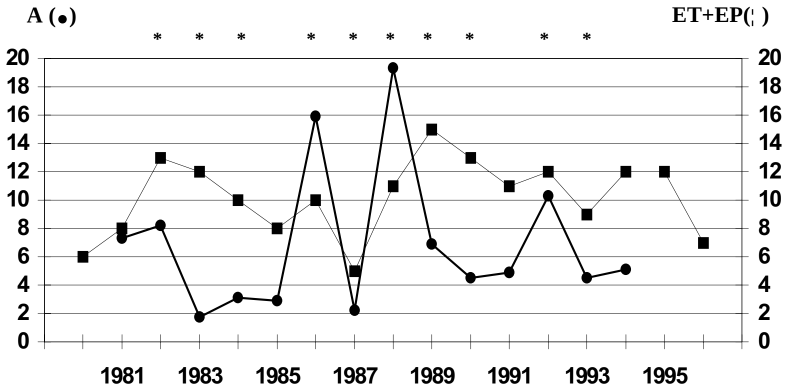

Figure 2. Abundance of *Vespinae* wasps (A = number of specimens per 30 min) and characteristics of weather conditions (ET+EP = sum of evaluation classes of air temperature and precipitation, as in tab.1); asterisks mean value changes with the significance level P ≤ 0.05

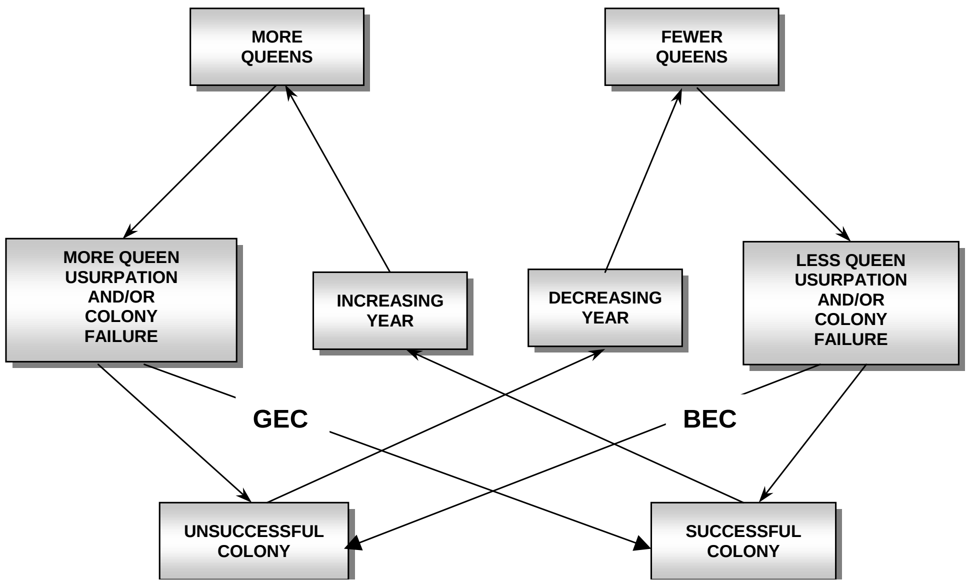

Figure 3. Endogenous mechanism of the two-year cycle of colony abundance of *Vespinae* wasps (Archer 1997) modified by good environmental conditions (GEC) or bad environmental conditions (BEC)

Generally speaking, the main mechanism affecting the abundance of colonies in a social wasp community is the intrapopulation two-year cycle of numerical changes predicted by Archer (1998), associated with the competition among queen-mothers (of a given species as well as of different species in a community) for habitat resources in the nesting period. That mechanism, however, is under a strong impact of weather conditions, which modify its effect. That modification is possible when weather conditions become the main factor(s) affecting habitat resources (i.e. suitable nesting

Table 2. Domination of *Vespinae* wasps in the agricultural landscape of Western Kujawy during 1981–1994: n – number of samples, ni – number of specimens

SPECIES	INVESTIGATION IN YEARS																													
	1981 n=23		1982 n = 35		1983 n = 12		1984 n = 15		1985 n = 15		1986 n = 15		1987 n = 16		1988 n = 31		1989 n = 20		1990 n = 15		1991 n = 13		1992 n = 14		1993 n = 13		1994 n = 16		19811994 n = 293	
	ni	%N	ni	%N	ni	%N	ni	%N	ni	%N	ni	%N	ni	%N	ni	%N	ni	%N	ni	%N	ni	%N	ni	%N	ni	%N	ni	%N	ni	%N
1) *Vespula germanica* (F.)	157	94.58	274	94.81	22	75.86	50	92.60	27	64.29	186	81.94	35	89.75	601	95.10	147	97.35	72	94.75	60	81.08	150	98.68	55	84.62	79	86.81	1915	92.20
2) *Vespula vulgaris* (L.)	2	1.21	3	1.04	1	3.45	2	3.70	2	4.76	3	1.32	1	2.56	3	0.47	2	1.33	2	2.63	1	1.35	1	0.66	1	1.54	3	3.30	27	1.30
3) *Dolichovespula saxonica* (F.)	4	2.41	4	1.38	2	6.90	1	1.85	10	23.81	26	11.45	2	5.13	20	3.16	1	0.66	1	1.31	12	16.22	1	0.66	9	13.84	5	5.49	88	4.24
4) *Dolichovespula sylvestris* (Scop.)	3	1.80	6	2.08	4	13.79	1	1.85	3	7.14	12	5.29	1	2.56	6	0.95	1	0.66	1	1.31	1	1.35	0	0	0	0	1	1.10	40	1.92
5) *Vespa crabro* (L.)	0	0	2	0.69	0	0	0	0	0	0	0	0	0	0	2	0.32	0	0	0	0	0	0	0	0	0	0	1	1.10	5	0.24
6) *Dolichovespula media* (Ret.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2.20	2	0.10
Total *Vespinae* (N)	166	100	289	100	29	100	54	100	42	100	227	100	39	100	632	100	151	100	76	100	74	100	152	100	65	100	91	100	2077	100

Table 3. Characteristics of the *Vespinae* community structure in the agriculture landscape of Western Kujawy during 1981–1994

PARAMETERS	INVESTIGATION IN YEARS													
	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
H'	0.39	0.39	1.13	0.49	1.38	0.90	0.63	0.35	0.22	0.38	0.84	0.11	0.69	0.83
TH'	=	↑	↓*	↑*	↓*	↓n	↓	↓n	↑n	↑*	↓*	↑*	↑n	
J'	0.19	0.17	0.57	0.25	0.69	0.45	0.32	0.15	0.11	0.19	0.42	0.07	0.44	0.32
TJ'	↑	↓	↑	↓	↑	↑n	↑	↑n	↓n	↓	↑	↓	↑	

H' – the species diversity index
TH' – tendency of H' value changes with the significance level $P \leq 0.05$ (*): = – no changes, ↓ – decrease, ↑ – increase, n – not typical
J' – the evenness index
TJ' – tendency of superdomination of *Vespula germanica* according to J' value changes: ↓ – decrease, ↑ – increase, n – not typical

sites and food) for social wasp populations. In that case we observe (1) an increase or decrease in the amplitude of oscillation fluctuations of the cycle by favourable or unfavourable weather conditions, or (2) a prolongation of the oscillation period of the cycle by extending favourable or unfavourable weather conditions in consecutive years.

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