Insect phenology and diversity in Malaise traps at the Veluwe

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Abstract: Five Malaise traps, used in a period of several years on an estate at the Veluwe (The Netherlands) yielded 577 insect species; most attention was given to the Aculeata, of which 240 species were found. Both for all insects combined and for Aculeata alone the annual distribution of the number of species, and the weighted diversity (averaged over all years and traps) fluctuated strongly, peaking in the first week of July. In contrast, the daily Shanon-Wiener diversity remained fairly constant, and relatively high, throughout the season. For the Aculeata there is a close correlation between the daily weighted diversity and the running average of the temperature. Over all 249 insect species (excluding social and semisocial species) of which data for both sexes were available, the proterandry amounted to 7.6 days.

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Introduction

In the period 1975-1984 five Malaise traps were operated throughout large parts of the year in the estate ''De Vennen'' near Nunspeet. Much of the material collected by these traps has been quantitatively identified by the following persons: B. van Aartsen, L. H. M. Blommers, L. Botosaneanu, W. N. Ellis, D. Geyskes, T. Gijswijt, V. S. van der Goot, W. Hogenes, G. Kruseman, Th. van Leeuwen, H. J. G. Meuffels, A. W. M. Mol, P. Oosterbroek, H. Overbeek, J. de Rond, R. Schouten, L. E. N. Sijstermans, R. T. Simon Thomas, R. L. Veenendaal, H. Wiering, and J. H. Woudstra.

The material that has been identified is not a balanced sample of the total entomofauna that was collected; in particular the Aculeata have been strongly emphasised, and Parasitica and Diptera are decidedly underrepresented. Nevertheless we think it worthwhile to present a brief summary of the phenological conclusions that can be derived from the available data.

Locality and methods

The estate ''De Vennen'' is located 3 km SE of the village of Nunspeet (kilometer square 27, 41, 14) and has a surface of 34 ha. It is situated on nutrient-poor consolidated Pleistocene drift sand; the soil is podsolic. The water table is approximately 10 m below the surface.

A large part of the area (20 ha) is covered by an 80 years old wood of badly growing *Pinus sylvestris* L., with an undergrowth of *Sorbus aucuparia* L., *Prunus serotina* Ehrh., and some *Amelanchier lamarckii* Schroeder and *Rhamnus frangula* L. (fig. 1). Parts of the wood have been badly hit by the devastating storms of 1972 and 1973 and rotten stumps of fallen trees, mostly dating from that period, still abound.

The largest continuous surfaces of deciduous wood consist a large stretch of *Quercus rubra* L. (just to the north of the area mapped in fig. 1), and of *Fagus sylvatica* L. without undergrowth; isolated patches consist of *Amelanchier* and *Betula pubescens* Ehrh., and, bordering the ponds, *Salix aurita* L., *S. cinerea* L., and their hybrids.

Two natural ponds owe their existence to a shallow hardpan; most of the 1.0 ha of their surface consists of open water. In the border zone *Juncus effusus* L., *Molinia caerulea* (L.) Moench, *Menyanthes trifoliata* L., *Sparganium erectum* L., *Phragmites australis* (Cav.) Trin. ex Steud., *Carex* spp., and some *Sphagnum* may be found. In the open water *Nymphaea alba* L., *Nuphar luteum* Sm., and

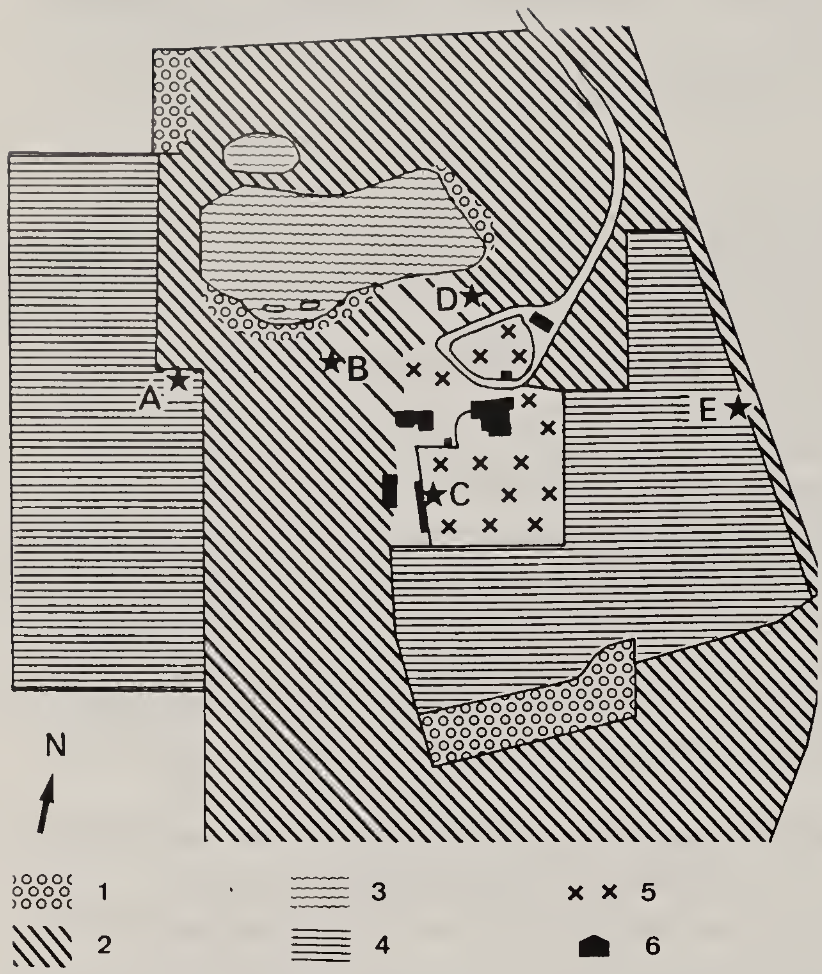

Fig. 1. Sketch map of the central part of the estate with major vegetation types and location of the traps (A-E); the width of the map is 425 m. The vegetation types are: 1, deciduous wood; 2, fir wood; 3, natural pond; 4, meadow; 5, garden; 6, buildings.

Nymphoides peltata (Gmel.) O. Kuntze occur.

The garden complex is bordered by old and large *Rhododendron ponticum* L. and *Thuja occidentalis* L. Part of it is used as a fruit and vegetable garden. Between the gardens and the pond an area has been almost cleared by the storm, and has not been replanted.

The meadows to the south and east of the house were at the time of the research extensively grazed by a few ponies; the western meadow is abandoned, and consists of a coarse grass vegetation with many perennial plants like *Plantago lanceolata* L., *Malva moschata* L., *Linaria vulgaris* Mill., *Achillea millefolium* L., *Rumex acetosa* L. and *Hypochaeris radicata* L. The trap at location A (fig. 1), at the fringe of the wood and overlooking the abandoned meadow was most productive by far. Trap B was much less productive, probably because it was situated in a part of the wood that consisted of little *Pinus* and much *Sorbus* and *Prunus*, that cast much shade in the second half of the season. Trap C was situated in a disused vegetable garden. Trap D was located in a clearing, caused by the big storms mentioned above, and trap E next to a hedge of *Abies grandis* Ldl. bordering a grazed meadow.

The insects were killed in the traps with an mixture of trichlorethylene and ethyl acetate, and were kept dry. In the months June-August the traps were emptied every two days; at other times they were emptied once or, mostly, twice a week.

Trap A produced material in the periods 8.iv-28.x.1976, 6.iv-3.xi.1977 and 26.iv-17.x.1984; trap B: 12.vi-10.viii.1975 and 8.iv-13.x.1976; trap C: 10.iv-24.ix.1976; trap D: 2.iv-16.x.1977; and trap E: 24.vi-3.vii.1977. In several cases; the material from two or more traps had already been pooled. Because of this reason, and also because of the relatively close proximity of the traps no attempts have been made to treat the catches of individual traps separately, and we will not go into much detail concerning the individual traps.

During the seasons 1976 and 1977 daily rainfall and maximal shadow temperatures were recorded at the estate.

Calculations were based on the number of specimens per species, irrespective of trap, sex or caste. The calculations started from a table of the number of specimens per species against the collecting dates (unless stated otherwise, summed over all years and traps). Dates were conversed to day numbers (1..365). As a first step, the numbers per species were evened out by calculating a running average over 9 days.

Based on these averaged values, we calculated daily values of the following values: 1) the diversity *D*, i.e., the number of species present on any calendar day, 2) *M*, the weighted diversity: the sum, over all species, of the daily number of a species, divided by the maximal daily number of that species, and 3) *N'*, the Shannon-Wiener index of diversity. A somewhat more formal definition of these values is given at the end of the paper.

As it turned out, the daily diversity (*D*) and the daily weighted diversity (*M*), when plotted in a graph, did not behave very differently. We also calculated for all species, for each sex separately, the calendar day when they

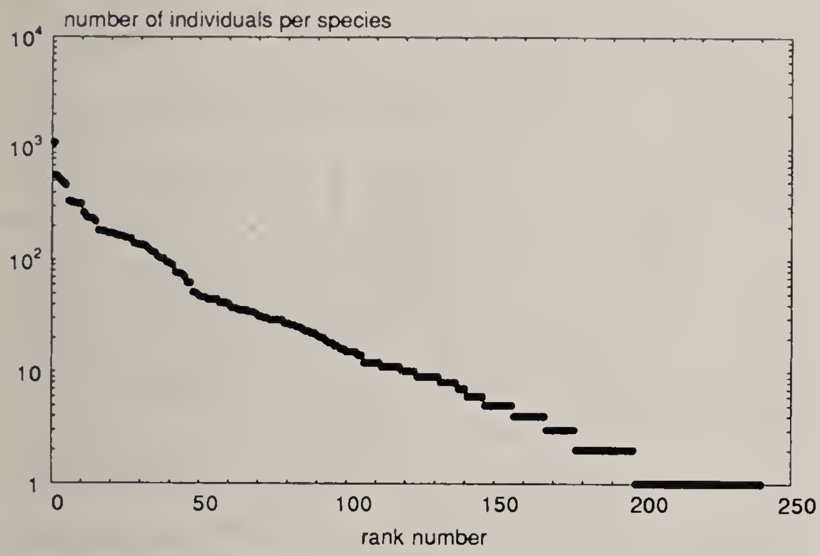

Fig. 2. Distribution of the number of individuals per species for the Aculeata ("Whittaker plot").

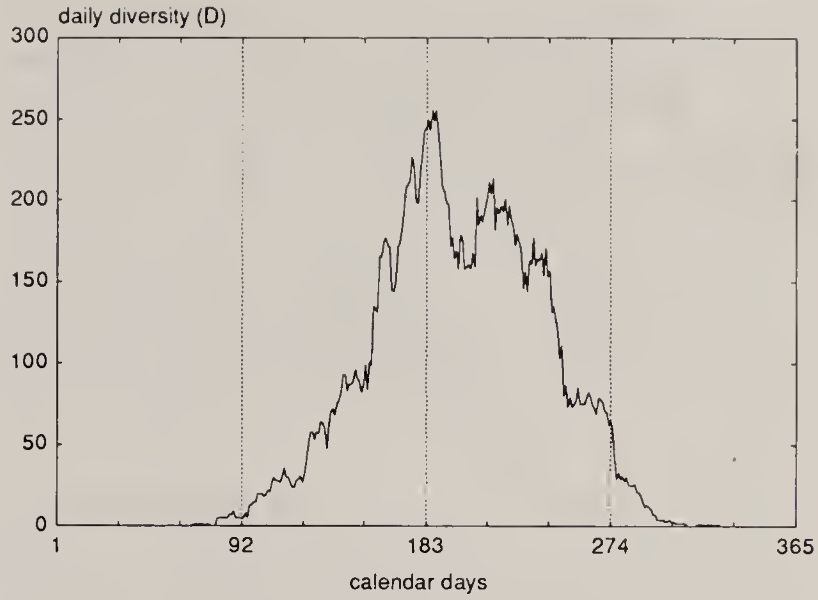

Fig. 3. Distribution of the number of species per day (*D*) for all insect species over all years.

reached their first quartile; i.e. the day that the running total of its daily scores reached 25% of the total value of that species. In this calculation the eventual occurrence of multivoltinism was not taken into account.

Results

Total diversity

The collected material (as far as it was identified) amounted to 19,046 specimens in 577 species, 240 of them Aculeata. This does not fully exhaust the entomological diversity of the estate, because many more species have been collected only by net-catches; these are not taken into account here. A list specifying all 942 species known to date from the estate (both Malaise material and hand catches), with some summarily phenological details, will be separately published, and will be available from the second author.

Fig. 2 shows the distribution of the number of individuals for all of the Aculeata species; the average value is 2.42 (± 0.116 standard error). Because the data, when plotted against a logarithmic axis, fall fairly well on a straight line, we may assume that the species numbers are distributed according to the lognormal distribution model (Krebs, 1989). If this model would indeed fully explain the distribution of numbers, it would enable us to calculate the number of species that would be found under an exhaustive search. Following the procedure outlined by Krebs (l.c.), this would lead to a total number of 395 species of Aculeata, more than half of the 782 species that comprise the Aculeata fauna of The Netherlands (Th. Peeters, unpublished).

Daily diversity

Because of our use of a running average, and of the large number of species and data points, we had expected *D* to follow a fairly smooth course, but as is shown in fig. 3, the converse is true. The curve fluctuates rather strongly, with a very well-delimited peak in the first days of July. Noteworthy are two dips, one around the end July, another around the mid of August; the steeply descending trend in the end of August is followed by a slight resurgence in September.

Since Aculeata were identified exhaustively, a separate graph of the same data for the Aculeata might be interesting. Rather than showing again the distribution of the daily number of species, we present here the value *M* (fig. 4). It shows roughly the same pattern as fig. 3; the sharp peak in the value of *M* in begin July stands out even more clearly. The maximal value of *M*, 93.4, falls on day 188, and exactly coincides in time with the maximal value of *D*, which is 146.

Contrary to the daily number of species or the daily weighted diversity, the value of *N'* does not strongly fluctuate; in fact, during

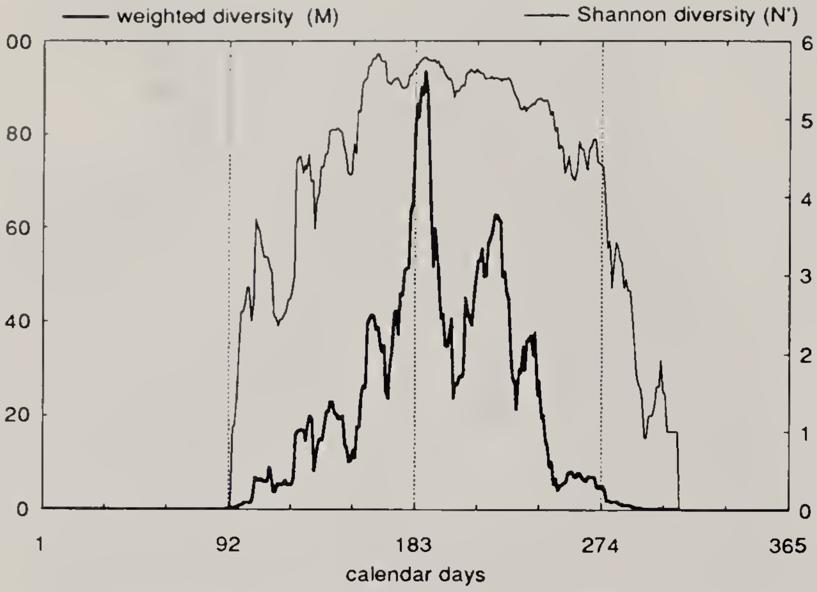

Fig. 4. Distribution of the weighted diversity (*M*, left vertical axis) and (Shannon-Wiener diversity (*N*', right vertical axis) for the Aculeata over all years.

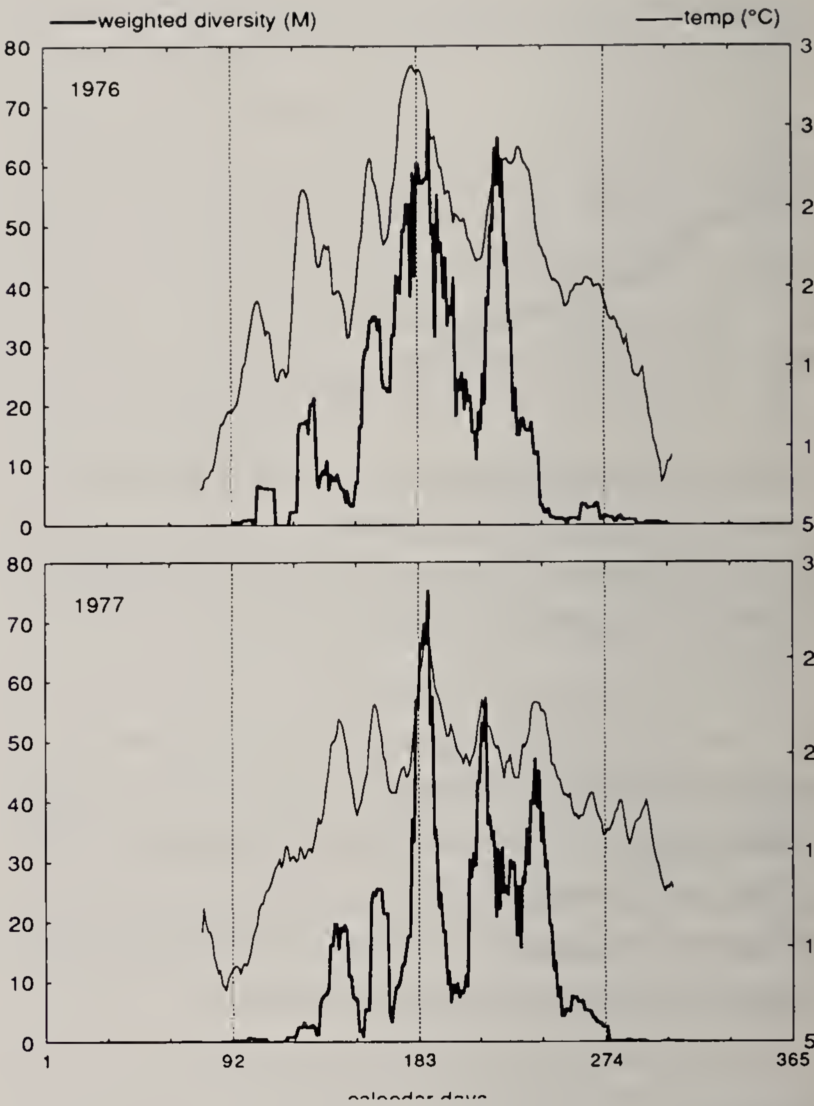

Fig. 5. Distributions of the weighted diversity (*M*) for the Aculeata with running average (over 9 days) of the temperature (°C) in 1976 (top) and 1977 (bottom).

most of the insect season, in the period of June through September, the value of *N'* remains more or less the same.

It is interesting to note that the value of *N'* throughout this period is comparatively high. Because the theoretical maximum of $N' = \log(D)$, the theoretical limit of *N'* on, for example, day 188 is 7.19, whereas the actual value is 5.79.

1976 versus 1977

The records for Aculeata for the years 1976 and 1977 are well comparable. By coincidence, the two years climatologically differed appreciably: over the period March 19 - November 4, the temperature sum rose in 1976 to 4785, in 1977 to 4010 °C; the cumulated rainfall in this period amounted to 269 mm in 1976, against 417 mm in 1977. Fig. 5 shows the curve of the value *M* for the two years, as well as that of the running average of the temperature (calculated, again, over 9 days). The correlation between both values, in both years is evident. In fact, the Spearman rank correlations of the running average of the temperature with *D*, *M*, and *N'* are as high as 0.898, 0.877, and 0.876, respectively ($N = 462$, $p < 0.000$).

Proterandry

It is a well known fact that in many insect groups the males become adult and active some time before the females. The obvious advantage brought about by this strategy is that it enhances each male's chance of meeting virgin females for mating. This phenological difference between the sexes is known as proterandry (Fagerström & Wiklund, 1982).

We chose as the reference date to phenologically compare the two sexes not so much the date of first occurrence of either sex (because this would entail much observational error), but rather the date that each sex reached its first quartile.

We calculated the proterandry, after leaving out the social insects and the semisocial Halictidae genera *Halictus* and *Lasioglossum*. There remained 249 species of which we had data for both males and females. Taking the simple average of the proterandry over these 249 species resulted in a value of 4.5 ± 1.55 days; however, by weighting by the total number of individuals per species the more reliable estimate of 7.6 ± 1.50 days is obtained.

Discussion

For a phenological study, the value N' is relatively uninteresting, because its value remains more or less the same from May/June to September. At the other hand, the value of D, and even more clearly M, points to a strongly marked peak in both unweighted and weighted diversity. This sharply delimited maximum, relatively late in the season, may partly be explained by the fact that the best sampled group, Aculeata, as a whole is relatively thermophilous. It would be interesting to compare our results with those obtained, for instance, for Parasitica or a more complete array of Diptera.

The correlation between M and the averaged temperature is so strong that we hesitate to attach much importance to the exact shape of the graphs of M (or, for that matter, D). It seems quite probable that another sequence of warm and cold spells might bring about a different pattern. It cannot even be decided if the coincidence of the peaks of M in both years in the first week of July is real or spurious (it might be relevant as well that this period also has the longest duration of daylight). As it stands, and allowing for the vicissitudes of the Dutch weather, our best suggestion for an entomologist planning a collecting trip (or a Society's field meating) in our region must be to book in the first weekend of July.

Acknowledgement

We wish to stress that this short paper is primarily the result of the dedicated assistance of the many entomologists who have taken the burden of sorting and identifying the large material that the traps produced.

References

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Appendix

S = the total number of species observed in the group under study.

n_{ds} = the number of individuals of species s observed at day d (after the calculation of the running average). Unless stated otherwise, n_{ds} is the total over all years and traps.

$$k_{ds} = 0 \text{ if } n_{ds} = 0,\ 1 \text{ if } n_{ds} > 0;\ D_d = \sum_{s=1}^{S} k_{ds}.$$

$$M^0_s = \text{maximum } (n_{ds}, d = 1 \,..\, 365);\ M_{ds} = n_{ds}/M^0_s;\quad M_d = \sum_{s=1}^{S} M_{ds}.$$

$$W_d = \sum_{s=1}^{S} n_{ds};\ \rho_{ds} = n_{ds} / W_d;\ N'_d = -\sum_{s=1}^{S} \rho_{ds}\ {}^2log\rho_{ds}.$$

$$T^{sex}_s = \sum_{d=1}^{365} n^{sex}_{ds},\ sex = \text{male, female; } Q^{1sex}_s \text{ is defined}$$

$$\text{by } \left(\sum_{d=1}^{Q^{1sex-1}} n^{sex}_{ds} < 0.25T^{sex}_s,\ \sum_{d=1}^{Q^{1sex}} n^{sex}_{ds} \geq 0.25T^{sex}_s\right).$$