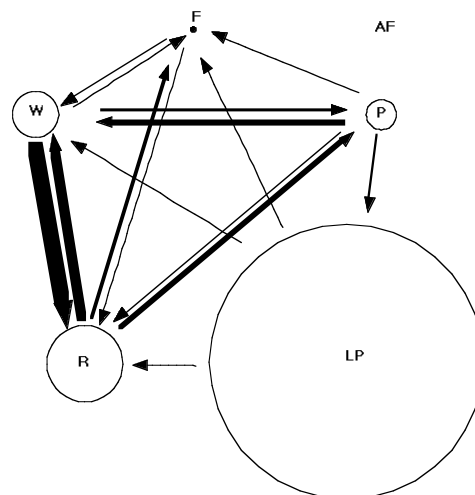


Quantifying Behaviour Sequences of Winged Aphids on Potato Plants for Virus Epidemic Models

T. Nemecek, A. Fischlin, O. Roth & J. Derron



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Eidgenössische Technische Hochschule Zürich ETHZ
Swiss Federal Institute of Technology Zurich

Departement für Umweltnaturwissenschaften / Department of Environmental Sciences
Institut für Terrestrische Ökologie / Institute of Terrestrial Ecology

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Adressen der Autoren / Addresses of the authors:

Dr. T. Nemecek, Dr. J. Derron
Station fédérale de recherches agronomiques Changins
CH-1260 Nyon
SWITZERLAND

Dr. A. Fischlin
Systemökologie ETH Zürich
Institut für Terrestrische Ökologie
Grabenstrasse 3
CH-8952 Schlieren/Zürich
SWITZERLAND

e-mail: fischlin@ito.umnw.ethz.ch

Dr. O. Roth
Widenstr. 3
CH-8302 Kloten
SWITZERLAND

Quantifying Behaviour Sequences of Winged Aphids on Potato Plants for Virus Epidemic Models

Thomas Nemecek¹, Andreas Fischlin², Olivier Roth³ and Jacques Derron¹

¹ Federal Agricultural Research Station of Changins, 1260 Nyon, Switzerland

² Systems Ecology, Institute of Terrestrial Ecology, Swiss Federal Institute of Technology, Grabenstr. 3, 8952 Schlieren, Switzerland

³ Widenstr. 3, 8302 Kloten, Switzerland

SUMMARY

Behaviour sequences of *Myzus persicae* SULZER (potato colonizing) and *Aphis fabae* SCOP (noncolonizing) were observed in a climatic chamber and in the field. Three behaviour types were derived by visually comparing the sequences: host-rejection behaviour, searching behaviour and settling behaviour. *A. fabae* showed host-rejection behaviour more frequently than *M. persicae*. The proportion of settling behaviour increased with age. *M. persicae* was only able to fly during three days after hatching, while *A. fabae*, forced to live on potato plants, was able to fly until death. The behaviour in the climatic chamber differed from that in the field. The behaviour sequences became stationary after the first two to three minutes. Parameters for a Markov chain describing the behaviour sequences of alatae vectors on potato plants were estimated for use in virus epidemic models. *A. fabae* changed behaviour twice as frequently as *M. persicae* and showed higher flight, walking and probing frequencies than *M. persicae*.

Keywords: epidemiology, Markov chain, simulation models

Introduction

Epidemics of aphid-transmitted virus diseases are driven by the amount of inoculum, the host plant susceptibility and vector intensity (Irwin & Ruesink 1986). Vector intensity can be decomposed into three factors: *vector abundance*, *vector propensity* (the 'ability' of virus transmission) and *vector behaviour*. Most models and forecasting systems of vector-borne virus epidemics do not take vector behaviour into account and could be improved by including the latter (Harrington, Govier & Gibson 1986). Vector abundance and propensity are quantified for many systems. Many aspects of aphid behaviour and the aphid-plant interaction have been extensively studied, but none of these studies provides data that can be used to describe relevant vector behaviour in virus epidemic models. Some authors consider vector behaviour to be even more important for virus epidemiology than abundance (Rochow 1974; Harrewijn 1989).

In this study, parameters describing winged aphid behaviour sequences on potato plants were estimated that can be used for virus epidemic models in potatoes, with special emphasis on the nonpersistently transmitted potato virus Y (PVY), the major virus problem in potatoes. The behaviour study was concentrated on alatae populations, which are likely to come from their (primary or secondary) hibernation hosts into a potato field during the spring migration. These populations probably contribute most to PVY spread in the temperate zones.

Alatae *Myzus persicae* SULZ. and *Aphis fabae* SCOP. were observed from May to July 1989. The former is a potato colonizing (or resident) species, the latter a noncolonizing (or non-resident) one. These two species were used as model species for the respective groups. Two other species (*Aphis nasturtii* KALT. - colonizing and *Brachycaudus helichrysi* KALT. - noncolonizing) were also observed to verify whether the behaviour of *M. persicae* and *A. fabae* could be considered as representative for the respective groups.

To reduce the amount of information contained in the behaviour sequences and to allow easy comparisons between species and age classes the sequences were visually grouped into three behaviour types characterizing the aphid-host plant relationship.

A Markov chain model was chosen to quantify the behaviour sequence, since such models are simple and have often been successfully applied to describe behaviour sequences (Cane 1978). Following behaviour states were distinguished for the model: flight, walking, resting, probing and 'long penetration'. Observations were performed with alatae of known age to compare young with old individuals in respect to virus epidemiology. The estimated Markov chain matrices were used to calculate behaviour in steady state.

Material and Methods

Aphid Material

Alatae aphids used in the experiments were collected as nymphs with the aid of a fine brush either on leaves of primary hosts or from a rearing on secondary hosts in a climatic chamber. *M. persicae* originated from colonies on *Sinapis arvensis* L. collected in March 1989 and were reared on chinese cabbage (*Brassica chinensis* L.). *A. fabae* were collected on the primary hosts *Evonymus europaea* L. and *Viburnum opulus* L. or in a rearing on *Vicia faba* L., which was started with colonies taken from the primary hosts *E. europaea* and *V. opulus*. *A. nasturtii* was taken from the primary host *Rhamnus catharticus* L. and *B. helichrysi* from the primary host marian plum (*Prunus cerasifera x munsoniana x angustifolia*).

The nymphs were kept in plastic petri dishes on leaves of the plant species, where the individuals had been sampled, underlaid with wet filter paper. The dishes were kept at daylight at a mean temperature of 20 °C and a mean rel. humidity of 60 %. Hatched alatae were collected and transferred every evening to another petri dish, containing leaves of the plant species, where they had been sampled. The alatae stayed overnight in these dishes, which ensured that they had passed a teneral period of at least 12 h, necessary for alatae to be able to fly (Robert 1987). The following day the alatae were transferred to petri dishes without leaves, where they stayed for 2 h. According to Klingauf (1976), a fasting period has similar effects on aphid behaviour as a distance flight. The alatae were thus in a state corresponding to the state after a distance flight.

Observation of the Sequences of Behaviour under Controlled Conditions

Potato plants of the Bintje variety were grown in plastic pots (diameter 14 cm) in a greenhouse and used for aphid behaviour observations 10 to 15 days after plant emergence. The aphids were transferred one by one to these plants enclosed in a cylindrical cage of plexiglass (diameter 30 cm, height 50 cm). The observations were performed at a temperature of 22°C and a rel. humidity of 75% in a climatic chamber illuminated by 11 40W-neon tubes. An aphid was observed during 15 min with the aid of a glass and a dentist's mirror. Any change of the aphid's behaviour state was recorded together with the corresponding time (time resolution 1 s) using a programmable event-recorder (PSION Organiser II, Model XP). This corresponds to a complete record according to Slater (1978). The data were later transferred to an Apple™ Macintosh™ computer for further analysis. Six behaviour states were distinguished in the observations (according to Lehmann, Klaus & Karl 1975, modified):

- Flight
- Walking
- Resting (aphid remains motionless, usually with rostrum directed backwards)
- Wing beating (movement of the wings, often followed by flight)
- Tapping (aphid touches the plant surface with the tip of the rostrum, *the antennae are directed upwards*)

- Penetration (according to Tarn & Adams 1982, stylets penetrate into plant tissue, includes probing and feeding. The rostrum is perpendicular to the plant surface, *the antennae are directed backwards and motionless*)

For the analysis tapping and wing beating was counted as resting, because aphids in these three behaviour states do not contribute to virus dissemination. Tapping and wing beating often occurred in sequence with resting.

After the first observation, performed immediately after the hunger period, the aphids were kept singly in petri dishes on potato leaves with wet filter paper and subjected to further observations (whenever possible three times a week) until death. The ethograms of the behaviour sequences were plotted using a colour plot program to compare them visually.

Observation of the Sequences of Behaviour in the Field

The same observation method as under controlled conditions was applied in the field experiments, except that no cage was used and the individuals were observed only once (most individuals were lost due to flight). The experiments were performed in a field with the variety Bintje, planted on May 3rd at distances of 75 x 33 cm. The alatae were observed immediately after the hunger period, or stored in groups on potato leaves with wet filter paper in the laboratory until observation. Each aphid was observed until it was lost during flight, or penetrated longer than 15 min. In the latter case, the aphid's location was marked with a pin and controlled in 15 min intervals as long as possible. If the aphid was still penetrating and had not changed its location, it was assumed that it had been in state 'long penetration' during the whole interval. Otherwise, the end of the penetration was estimated with the midpoint between the last two controls. The behaviour sequences recorded in the field had varying durations, contrary to those recorded under controlled conditions.

Splitting Penetration into Probing and 'Long Penetration'

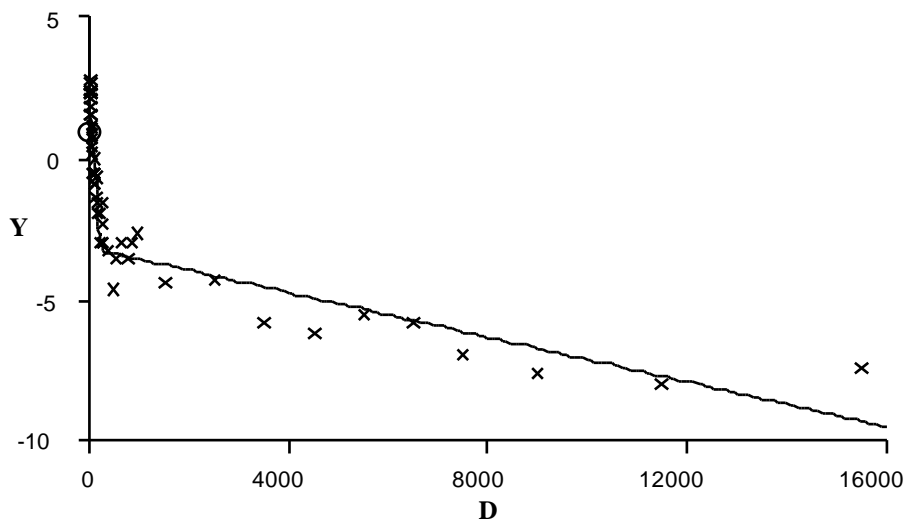


Fig. 1: Logarithmic frequency plot of the penetration act durations in the field. D = duration in seconds, Y = natural logarithm of the number of acts N per interval, weighted by the interval length ($Y = \ln \frac{N}{(D_u - D_l)}$, where D_u and D_l are the upper and lower limits of the respective interval $[D_l, D_u]$). The first point (circle) was excluded from the analysis. The line represents the fitted nonlinear function.

Simulation studies of the Markov models showed that it was not possible to satisfactorily describe the behaviour sequence with only one state 'penetration' with an expo-

ponential distribution of the durations. An exponential distribution of durations is inherent to Markov chains (Metz *et al.* 1983). The frequency distribution of the penetration durations indicated that a better description of the sequences might be achieved by splitting penetration acts into short penetrations (probing) and 'long penetrations' (Fig. 1). A statistical criterion was chosen, based on the duration of the acts, because visual observation does not allow to distinguish these two behaviour states. A nonlinear model was fitted to the log frequency data (Fig. 1, Sibly, Nott & Fletcher 1990). The Quasi-Newton method was used to minimize the least squares of the deviations. The threshold was determined with the criterion minimizing the number of acts assigned to the wrong state, the so-called misassigned acts (Sibly *et al.* 1990).

Estimation of the Transition Matrices and Statistical Tests

In a first step, the parameters for a discrete Markov model were estimated, since statistical methods are much better developed for this model class. In a second step, the discrete Markov matrices were transformed into continuous Markov matrices. Continuous Markov models are better suited for simulation studies (the time step can be easily changed).

The transition probabilities for a stationary first order Markov chain (discrete time) were estimated after Anderson & Goodman (1957) by the proportion of individuals being in state i and passing to state j in the following step:

$$\hat{p}_{ij} = \frac{\sum_{k=a}^{b-1} n_{ij}(k)}{\sum_{k=a}^{b-1} n_i(k)} \quad (1)$$

where \hat{p}_{ij} is the estimated probability to pass from state i to state j in the time interval $[a, b]$, k is the time, $n_{ij}(k)$ is the number of transitions from state i (at time k) followed by j (at time $k+1$), $n_i(k)$ is the number of occurrences of state i at k .

To test the Markov chains for stationarity, i.e. the constancy of the transition probabilities in time, the number of state transitions was calculated for the time intervals: 0-300 s (I_1), 300-600 s (I_2) and 600-900 s (I_3) after the begin of the record. A log-linear model was fitted to the observed number of transitions (according to Bishop, Fienberg & Holland 1975):

$$\ln(m_{ijt}) = \mu + \lambda_i + \lambda_j + \lambda_t + \lambda_{ij} + \lambda_{it} \quad (2)$$

where m_{ijt} is the expected number of transitions from state i to state j in time interval t . μ is the natural logarithm of the overall mean and λ_i , λ_j and λ_t are the 'main effects'. Two second order interaction terms (λ_{ij} and λ_{it}) are included. The model omits the second order interaction term λ_{jt} for the different time intervals, thus testing whether the model still fits the data with $\lambda_{jt} = 0$. If the expected numbers of transitions m_{ijt} (Eq. 2) do not significantly deviate from the observed cell counts, the null hypothesis that the t intervals have the same transition probabilities will be retained and the Markov chain is assumed to be stationary in the tested time intervals. If the null hypothesis is rejected, the Markov chain is considered as not stationary, i.e. different transition matrices must be used for the different time intervals. The following transitions were treated as structural zeros (expected cell count = 0) for the test: flight 'long penetration', walking- 'long penetration', resting 'long penetration' and 'long penetration' probing, because these transitions could not occur by definition of the state 'long penetration'. The log-linear model was fitted after having added 0.5 to all cell counts (otherwise the number of degrees of freedom would have been too small for the test, due to the zero values). The likelihood ratio values (G^2) were used to test for significance.

The estimated discrete Markov matrices were transformed into continuous Markov matrices, using the equations given by Jeffers (1988). The continuous Markov chain model is a linear differential equation system:

$$\frac{d p_j}{dt} = \sum_{i=f}^l p_i q_{ij} \quad j \in \{f, w, s, p, l\} \quad (3)$$

where p_i is the proportion of individuals in state i , q_{ij} is the transition rate from state i to state j , f to l stand for the behaviour states flight f , walking w , resting r , probing p and 'long penetration' l . The steady state of the system (proportions of states after infinite time) were calculated by matrix operations (Snell 1989). The frequency f_j of state j is given by:

$$f_j = \sum_{\substack{i=f \\ i \neq j}}^l p_i q_{ij} \quad (4)$$

Probing frequency was calculated differently, taking into account only the occurrences of the state probing, not followed by 'long penetration'. For nonpersistently transmitted viruses this value can be considered as the epidemiologically relevant probing frequency, since the transmission probability declines with increasing probing duration (Völk 1959; Zettler 1967; Katis & Gibson 1985).

The mean residence time r_i of state i (mean time spent in state i) is given by:

$$r_i = -\frac{1}{q_{ii}} \quad (5)$$

where q_{ii} is the transition rate $i \rightarrow i$.

Statistical tests were calculated with the statistical package SYSTAT™ on Apple Macintosh™ computers.

Results

Splitting Penetration into Probing and 'Long Penetration'

The log frequency plot according to Sibly *et al.* (1990) showed that the penetration acts were probably not due to a single process with an exponential distribution of the durations (all points would lie on a line), but to at least two processes (Fig. 1). A threshold duration of 179.2 s was estimated. For further analysis a penetration act was assumed to be probing until 3 min and to switch to 'long penetration' afterwards. Note that due to this definition the state 'long penetration' can only be reached via the state probing and that probing cannot follow immediately after 'long penetration'.

Classification of Behaviour Sequences

Table 1: Definition of the behaviour types under controlled and field conditions.

Behaviour type	Controlled conditions	Field	Name
	>50% of time on cage or at the end of the observation on cage	lost by flight	
	>50% of time on plant, but not in state 'long penetration' at the end of the observation	on plant at the end of the observation, but not in state 'long penetration'	
	in state 'long penetration' at the end of the observation	in state 'long penetration' at the end of the observation	

The plotting of the sequences with the colour plot program revealed that similar behaviour sequences existed (Nemecek 1993). The sequences were repeatedly rearranged and finally three behaviour types were derived (Table 1), named according to the aphid-plant relationship. Aphids showing type *I* behaviour typically took off from the plant after a few probes. Type *II* behaviour was characterized by frequent probes interrupted by walking, type *III* by initiation of 'long penetration' after a few probes.

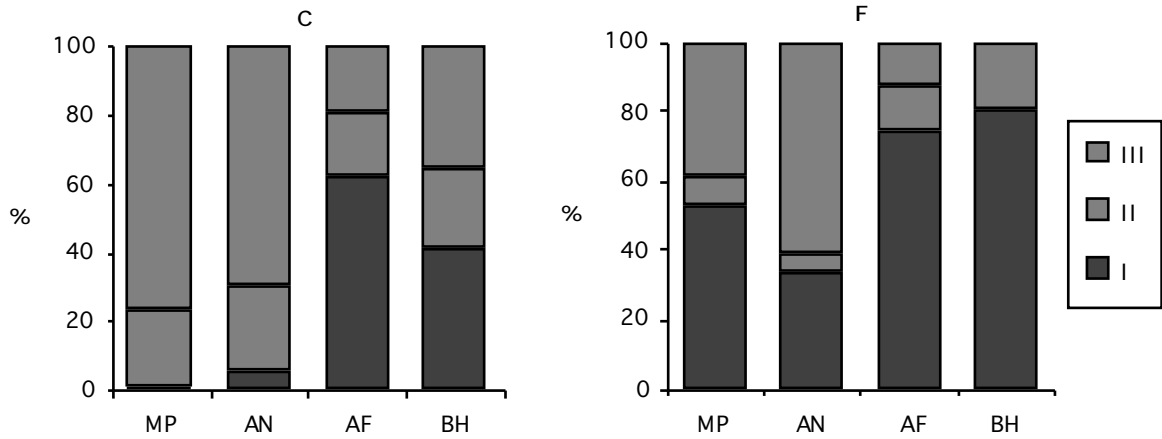


Fig. 2: Proportions of sequences observed under controlled conditions (C) and in the field (F) classified by the three behaviour types (*I*, *II*, and *III*) of the following species (number of observations given in brackets): *MP* = *M. persicae* (C: 202, F: 61), *AN* = *A. nasturtii* (C: 36, F: 14), *AF* = *A. fabae* (C: 72, F: 42), *BH* = *B. helichrysi* (C: 17, F: 8).

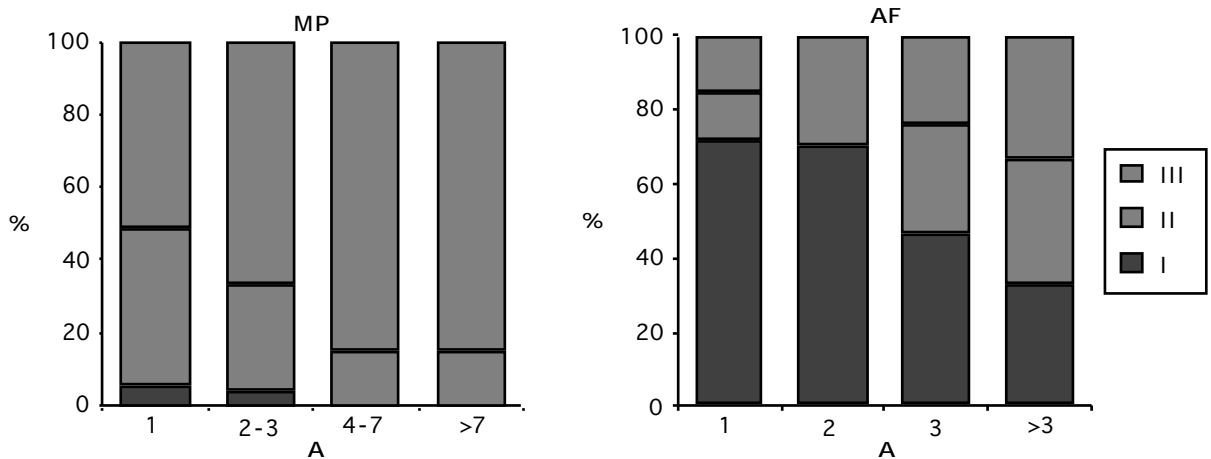


Fig. 3: Proportions of sequences observed under controlled conditions classified by the three behaviour types (*I*, *II*, and *III*) in function of aphid age (*A* = days after hatching) of the following species (number of observations in the four age classes in brackets): *MP* = *M. persicae* (35, 27, 67, 73), *AF* = *A. fabae* (39, 10, 17, 6).

Colonizing species showed predominantly settling behaviour (Fig. 2, *III*), non-colonizing species mainly host-rejection behaviour (Fig. 2, *I*), i.e. they left the plant and spent most time on the cage. Only those field sequences were classified, where the final behaviour state had been recorded. Marked differences between the laboratory and field sequences were found. Particularly flight and host-rejection behaviour (*I*) was less fre-

quent for colonizing species under controlled conditions than in the field. These differences were similar but less marked for noncolonizing aphids. The differences in behaviour within the groups of colonizing resp. noncolonizing species were smaller than the differences between the groups.

The age classes were chosen differently for the two species due to the much shorter longevity of *A. fabae*. The proportion of host-rejection behaviour (Fig. 3, *I*) was highest in young individuals and decreased with age. The proportion of settling behaviour (*III*) increased, whereas the proportion of searching behaviour (*II*) decreased with age in *M. persicae*.

M. persicae performed flights only during the first two days in the climatic chamber and during the first three days in the field. Yet, most *A. fabae* remained able to fly until death. Even the oldest *A. fabae* (seven days) were able to fly.

Markov Matrices

Only sequences observed in the field of the first two age classes, i.e. 1-3 days for *M. persicae* and 1-2 days for *A. fabae*, were used for the following analyses. The stationarity of the sequences was tested to eliminate the initial phase, when the aphids might be disturbed by the handling procedure. The transition probabilities differed significantly at the 5 % level between the intervals I_1 (0-300 s) and I_2 (300-600 s), but not between intervals I_2 and I_3 (600-900 s). The transition probabilities for the time interval $I_2' = [D_k, D_k+300]$ were recalculated several times, changing D_k in steps of 25 s, and compared with I_3 , to determine the threshold D_k , where the sequences became stationary. The smallest value D_k , for which I_2' did not differ from I_3 at the 5% significance level was 125 s for *M. persicae* and 200 s for *A. fabae*. For following analyses, only the stationary part of the sequences ($k \geq D_k$) was retained.

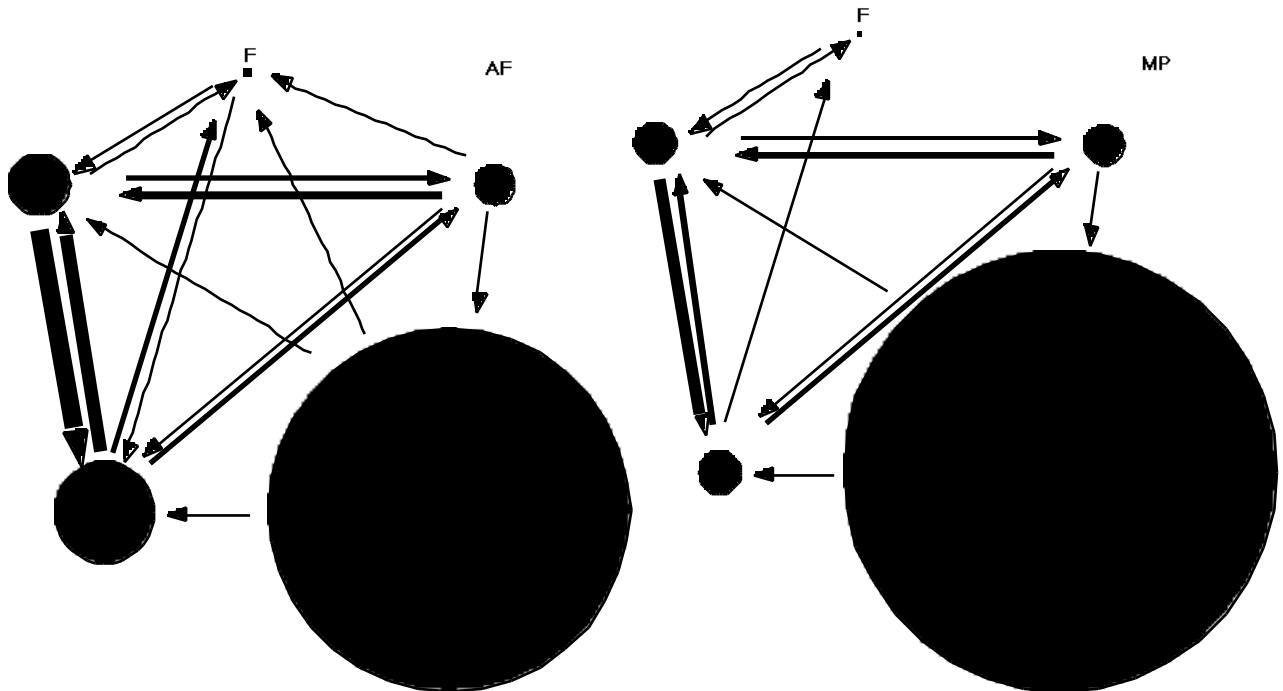


Fig. 4: Kinematic graphs of the stationary part of the behaviour sequences of *A. fabae* (AF) and *M. persicae* (MP) observed in the field. The widths of the arrow lines are proportional to the observed transition frequencies and the diameter of the circles to the proportion of total time spent in the behaviour state. Broken lines indicate sparse transitions (< five times observed). *F* = flight, *W* = walking, *R* = resting, *P* = probing, *LP* = 'long penetration'.

The kinematic graphs (Fig. 4) are a representation of the transition frequencies between behaviour states and the proportion of the total time spent in a state, which has not to be confounded with the mean residence time. It seems that the behaviour sequences of the two species were qualitatively similar, but that there existed quantitative differences. *M. persicae* spent most time in state 'long penetration'. The same was true for *A. fabae* but the proportion of time spent in other states was higher. *A. fabae* showed the behaviour states walking, resting and flight more frequently than *M. persicae*.

To test the ergodicity of the Markov matrices, higher order powers of the discrete Markov matrices were calculated. The resulting matrices had nonzero values in all cells, indicating that it is possible to reach any state in a finite number of steps from any other state (Snell 1989). The transition matrices are thus ergodic for both species, i.e. no absorbing state exists and the matrices are not periodic. Therefore the proportions of the states will converge towards a steady state with increasing time.

The continuous Markov chain matrices for the field observations in the first two age classes of *M. persicae* and *A. fabae*, calculated from the discrete matrices, are given in Table 2.

Table 2: Transition rate matrices of behaviour sequences for a continuous Markov chain. The given values are the transition rates [d^{-1}] from state i (shown in the left column) to state j (shown in the top row). The matrices were estimated for the age of 1-3 days (*M. persicae*, 68 sequences) and 1-2 days (*A. fabae*, 46 sequences) after hatching, and the stationary part of the sequences, (k 125 seconds for *M. persicae* and k 200 seconds for *A. fabae*).

	Flight	Walking	Resting	Probing	'Long penetration'
Flight	-3366 [#]	3366	0	0	0 [†]
Walking	32	-1799	1307	460	0 [†]
Resting	123	717	-1410	570	0 [†]
Probing	0	771	92	-1207	344
'Long penetration'	0	8.4	3.8	0 [†]	-12.2
	Flight	Walking	Resting	Probing	'Long penetration'
Flight	-3366 [#]	3029	337	0	0 [†]
Walking	49.8	-1808	1476	282	0 [†]
Resting	169	548	-987	269	0 [†]
Probing	25.4	939	152	-1421	304
'Long penetration'	2.8	11.1	2.8	0 [†]	-16.7

[#] Parameter estimated indirectly from the mean flight distance of alatae assuming a mean flight speed of 0.5 m/s (Nemecek *et al.* in press).

[†] Impossible transition by definition.

Ethograms of sequences, simulated with the estimated transition matrices were compared visually with the observed sequences. The simulated sequences were similar to the observed ones.

Simulation studies of the continuous Markov models showed that the steady state was nearly reached after 1 h. Simulation studies have also shown that the results were little affected, if the system was assumed to be in steady state. Using the proportions of the states in steady state instead of variable proportions will greatly simplify epidemic models. In steady state, *M. persicae* spent nearly 90 % of the total time in state 'long penetration' (Fig. 5, P). *A. fabae* spent a higher proportion of time flying, walking, resting and even probing than *M. persicae*.

Marked differences between the walking, probing and especially flight frequencies of the two species were found (Fig. 5, F). The total frequency of behaviour state changes (= sum of all frequencies) was twice as high for *A. fabae* (375 d^{-1}) than for *M. persicae*

(175 d⁻¹), which confirms that noncolonizing species are in fact more 'restless' than colonizing ones.

The mean residence times seem to be similarly long in the two species, except that *M. persicae* had a longer mean residence time of 'long penetration' (Fig. 5, D).

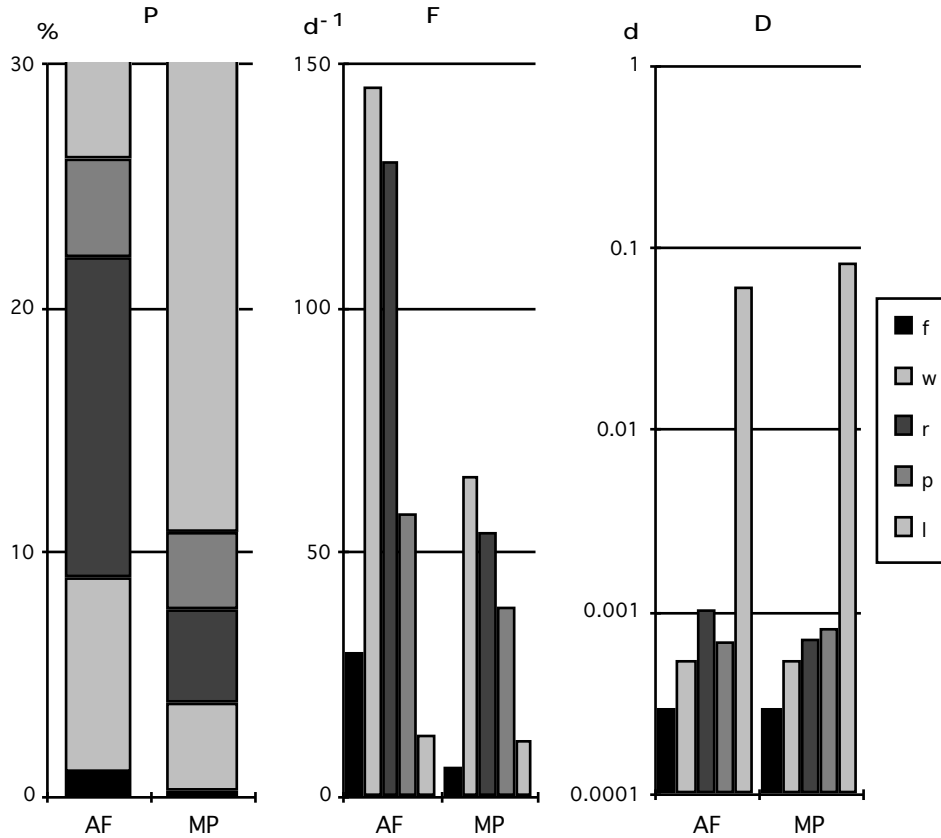


Fig. 5: Proportions P , frequencies F and mean residence times D (logarithmic scale) of the five behaviour states in steady state of the Markov model: f = flight, w = walking, r = resting, p = probing, l = 'long penetration' for *A. fabae* (AF) and *M. persicae* (MP).

Discussion

The penetration acts could be divided into short penetration (probing) and 'long penetration', which allowed an appropriate description of the behaviour sequences by the Markov model. The biological meaning of 'long penetration' is unclear. It cannot be equal to phloem feeding for two reasons: 'long penetration' started after 3 min, but aphids need longer to reach the phloem (Klingauf 1987). Moreover, some *A. fabae* also performed long penetrations (Fig. 2, III and Fig. 4), although aphids seem not to ingest phloem sap from nonhosts (McLean & Kinsey 1968). It is possible that some individuals were not able to recognize the plant as unsuitable host during short probes. Another explanation is that the handling procedure had increased the aphid's tendency to settle (Johnson 1969). *M. persicae* in the state 'long penetration' penetrated towards the phloem and either started feeding or retired the stylets before reaching the phloem. Separating short and 'long penetrations' could also be useful in an epidemic model, because nonpersistent viruses are transmitted with a higher probability by short probes.

The three behaviour types that could be derived by summarizing similar behaviour sequences seem to give classes that can be interpreted in relation to nonpersistent virus epidemiology. Host-rejection behaviour (*I*) is probably the most important, since the alatae disperse by flight and can transmit viruses over longer distances, if they probe before take-off and after landing. Successful virus transmission would require that an aphid visits other potato plants in the proximity of the source, which is likely to occur (Nemecek *et al.* in press). Searching behaviour (*II*) can be relevant, if the aphids walk onto another plant or stem. Since walking over long distances is unlikely (Ferrar 1969), mainly the neighbouring plants can be infected by aphids showing behaviour type *II*. Settling behaviour (*III*) will rarely lead to virus transmissions, because the aphids are most time performing 'long penetrations' and hardly change to other behaviour or location.

The significance of the three types for the epidemiology of persistently transmitted viruses (e.g. potato leafroll virus, PLRV) is different. Host-rejection behaviour (*I*) hardly can contribute to virus spread, since these individuals seem not to penetrate long enough on the plants. Searching behaviour (*II*) and settling behaviour (*III*) could potentially contribute to persistent virus dissemination. The frequency of transmission will probably be low, since individuals showing searching behaviour rarely feed and those showing settling behaviour rarely move from plant to plant. Hence alatae immigrating in the field are probably of little importance for persistent virus transmission. Unlike for PVY, probably winged and wingless aphids developing on infection source plants in the field are more important for PLRV.

The experiments have shown that behaviour observation under controlled conditions can yield results substantially different from field observations (Fig. 2). The laboratory sequences could thus not be used for the parameter estimations, as intended in the beginning. The differences in flight frequency could be explained by the fact that the air was completely calm in the cages, whereas in the field, there was always some air motion. Kennedy (1990) has shown that more aphids take off in slight wind and in sequences of wind and calm than in continuous calm. Behaviour observations in a climatic chamber should always be compared with field observations.

Fig. 2 suggests that the differences in behaviour within the group of the colonizing and within the noncolonizing group are relatively small. It seems possible to extrapolate the results of *M. persicae* to other colonizing and that of *A. fabae* to other noncolonizing species.

Older alatae moved less and were more likely to settle than younger individuals (Fig. 3). Settled aphids of many species, among them *A. fabae* and *M. persicae*, autolyse their wing muscles and become unable to fly after two to three days (Johnson 1957 & 1959). Later they can disperse only by walking. Alatae on host plants therefore contribute to virus spread only during few days. As settled aphids rarely move, they can be ignored in epidemiological studies of nonpersistently transmitted viruses. Unsettled *A. fabae* on potato plants (nonhost) were able to fly until death. Their wing muscles were apparently not autolyse, because they could not find a suitable host. Aphids remain thus potential vectors, until they settle on a suitable host. Older *A. fabae* were excluded from the parameter estimations, since their behaviour might be unnatural, due to starvation in petri-dishes during days. The estimated transition matrices can be considered as representative for the epidemiologically relevant behaviour of unsettled alatae of the two species on potato plants.

The procedure of taking the aphids from a petri dish and transferring them to a potato plant in the field is artificial. Disturbance can increase the probability of flight (Dixon & Mercer 1983) and the handling procedure the tendency of settling (Johnson 1969). Taking only the stationary parts of the sequences can eliminate such effects, so that the matrices probably represent average behaviour sequences on potato plants.

Markov models are simple models and probably rough simplifications of the behaviour sequences of aphids. Nevertheless, they have often been successfully applied to behaviour sequences (Cane 1978; Metz *et al.* 1983). Comparison of observed and simulated sequences indicated that the underlying assumptions of the Markov model (stationarity, exponential distribution of the residence times and single-step dependence) were consistent with the data.

The estimated transition matrices (Table 2) represent behaviour of young alatae on potato plants relevant for nonpersistent virus epidemiology. They can be used to study the effects of differences between colonizing and noncolonizing species on virus epidemiology and the also the effects of changes in vector behaviour induced by man or by the environment. They were used for these purposes to model epidemics of PVY in potatoes (Nemecek 1993).

Although the behaviour sequences of the two model species seem to be qualitatively similar (Fig. 4), there exist important quantitative differences. *A. fabae* showed more frequently the relevant behaviour sequences for epidemiology, namely probing (walking, resting) flight (walking, resting) probing and a higher frequency of behaviour state changes. The same is indicated by the occurrences of behaviour types (Fig. 2), where the noncolonizing species showed more often the epidemiologically relevant behaviour types *I* and *II*. Similar differences have also been observed for other aphid-host systems (Kennedy *et al.* 1959; McLean & Kinsey 1968). Many authors (e.g. Romanow 1985; Carter & Harrington 1991) suggest that higher activity (mainly interplant movement frequency and probing frequency) leads to faster virus spread. Provided this is true, the restlessness of noncolonizing aphids would enable the noncolonizing species to transmit nonpersistent viruses more frequently than colonizing species.

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