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Demography of the cereal rust mite *Abacarus hystrix* (Acari: Eriophyoidea) on quack grass

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Abstract. Demography parameters of the cereal rust mite *Abacarus hystrix* (Nalepa) on quack grass were studied to investigate its potential capacity of population increase in conditions of initially low density. The experiment was maintained under laboratory conditions at a constant temperature of 19.5–20.5 °C and 94 ± 1% RH. Life-history data were used to calculate duration of developmental stages, survival of adults and rates of population increase. A new method of estimation of age-dependent fecundity is proposed. On average, eggs required 7.98 ($n = 33$, 95% CI: 7.68–8.21) days to develop into adults. Life expectancy of females was longer than that of males (9.72 and 5.41 days, respectively). The mean sex ratio, expressed as the proportion of females, was 0.80 ($n = 122$, CI: 0.71–0.86). The reproductive output for females was age-dependent and daily egg production reached a peak (3.83 eggs/day, CI: 2.50–5.15) on the 5th day, and then decreased steeply. The net reproductive rate (R_0) was 10.12 female progeny per female per generation, the generation time (T) was 11.31 days, the intrinsic rate of increase (r) was 0.20 female progeny per female per day, and the finite rate of increase (λ) was 1.23 female progeny per day. These estimates showed that *A. hystrix* has a great potential capacity for rapid population increase when colonising new hosts and its density is low. Therefore, we conclude that the population of the cereal rust mite on quack grass may rapidly build up to very high densities and can be a reservoir population, which may easily disperse and infest other, including cultivated, grasses.

Introduction

The cereal rust mite *Abacarus hystrix* (Nalepa 1896) is a common pest of cultivated and wild grasses, widely distributed in Eurasia, North America, temperate regions of Africa, Australia and New Zealand. Its occurrence has been reported from at least 40 grass species. The mite has a vagrant life style, inhabits the laminar furrows on the upper surface of leaves, and disperses passively on air currents. Its feeding causes symptoms of discoloration and inhibition of development of grass ears. It is also known to transmit ryegrass mosaic virus (RMV), a serious disease of temperate grasslands, and agropyron mosaic virus (AMV), a minor disease of wheat and quack grass (Amrine and Stasny 1994; Frost and Ridland 1996; Lindquist and Oldfield 1996; Oldfield and Proeseler 1996). During the years 1998–2001, a survey of the eriophyoid fauna on grasses in Poland revealed, that *A. hystrix* was one of the most abundant and frequent species (Skoracka 2002). Considering the importance

of *A. hystrix* as a pest, information on the life-history parameters of this species is needed for understanding its population dynamics.

To date, little is known about the demography of *A. hystrix*, or of any of the grass-inhabiting eriophyoids. Boczek and Chyczewski (1975) observed the development of *A. hystrix*, *Aceria tulipae* Keifer and *Aculodes mckenziei* (Nalepa) on quack grass. Naidu and ChannaBasavanna (1986) determined the developmental time of *Aceria cymbopogonis* (Mohanasundaram et Subramaniam) on Lemon grass. Rosario and Sill (1964) gave information about female fecundity and developmental time of *A. tulipae*.

Abacarus hystrix has a wide host range, high extensity of infestation on ephemeral plants and great dispersal abilities. These features facilitate easy dispelling amongst hosts, and thus induce the foundress effect. The aim of our study was to determine the cereal rust mite's potential population increase when its (initial) density is extremely low. For this purpose the mite population arising from few females was observed and demographic parameters of *A. hystrix* were estimated. For our study quack grass was chosen as a host plant for its economic importance as a weed in cultivation.

Material and methods

Abacarus hystrix was reared on quack grass (*Agropyron repens* (L.) P. Beauv.). Our earlier observation indicated that, amongst all grasses in Poland, quack grass is the most frequently and intensively infested by the cereal rust mite. Prevalence of cereal rust mite infestation on quack grass was 62.6% (95% CI: 59.3–65.8%), and its intensity was 109.6 (95.0–127.4) specimens per shoot (Skoracka 2002).

Quack grass cultivation and the stock mite colony

A quack grass cultivation was prepared for maintaining the stock population. Rhizomes of *A. repens* were put in boxes with sandy soil and kept at room temperature. Boxes were covered with nylon taffeta fastened to the wooden frame to protect the plants from infestation by mites, insects or fungi. When grown–up these plants were used for the trials.

The stock colony of mites was established with individuals collected on *A. repens* from the study plot in north-eastern Poznań, Poland (16°55′E, 52°25′N), during April 2001. Plants were examined under a stereomicroscope, and mites were transferred by the use of human hair. Females of this species could be easily recognised under the stereomicroscope by the distinct dorsal ridge. Moreover, several mites collected from the study plot and mites used for experiments (after the experiments' termination) were prepared for phase contrast microscopic examination by mounting them in Heinze solution (Boczek 1994). The stock colony was maintained in the controlled-environmental chamber at 19.5–20.5 °C, $94 \pm 1\%$ RH and photoperiod of 16–17/7–8 (L:D) for 1 month. Afterwards, mite specimens were used for the trial.

Experimental set-up

Quack grass shoots from the cultivation were examined under stereomicroscope to verify that they were not infested, and transplanted to flower-plots. There was only one grass shoot in each flower-plot. Each shoot had only two medium leaves, others were removed. This procedure reduced the time spent searching for mites during surveys. Three to five females from the stock colony were placed on leaves of one quack grass shoot. Females used for trials were 1-day-old (only specimens shortly after emergence were used) and probably fertilised (females of *A. hystrix* pick spermatophores deposited around them immediately after emergence – personal observations). Each flower-plot was covered with nylon taffeta and maintained in a controlled-environment chamber. The mite population maintained on one quack grass plant was defined as an experimental group. Demographic parameters were calculated using data obtained from six experimental groups. Duration of experiments and sample sizes used for calculation of the various estimates are summarised in Table 1. Each trial was terminated when the colony was so numerous that the mites started to migrate (i.e., they were walking along shoots or cumulated at the leaf tops showing dispersal position) and accurate counting was no longer possible.

Plants were examined with the mean interval of 1.10 days (95% CI: 0.91–1.29) using stereomicroscope and 'cold light'. Numbers of adults, larvae, nymphs and eggs were counted. Additionally, the position of eggs on the leaf was mapped, which helped to record hatching.

Data processing and analysis

Egg detectability

Eriophyoids eggs are small, about 20–60 μm in diameter, and often difficult to notice, as they may be colourless or translucent (Manson and Oldfield 1996). Due to the possible problems with detection, the detectability (D) of eggs was calculated as follows. For each census eggs were counted, giving the number of eggs detected. From the number of larvae in the subsequent counts it was possible to infer, how many eggs should have been found that day to give this particular number of larvae. For instance, if three eggs were found during the first count, and seven larvae during the subsequent count, it was assumed, that four eggs were missed during the first census. Numbers of eggs detected and larvae hatched were summed over all the days of the censuses for each experimental group and subsequently used for estimation of detectability. We defined detectability as the number of eggs detected divided by the number of larvae hatched. When the population became numerous and generations started to overlap, the method became ambiguous and unreliable. Thus, detectability estimates were restricted and usually refer to the F1 generation. For this reason, sample sizes used for detectability estimation differ from those used for estimation of demographic parameters (Table 1).

Table 1. Duration of experimental trials and sample sizes used for estimation of demographic parameters.

Experiment No.	Duration [days]	No. of individuals used for estimation								
		Adult survival		Duration of developmental stages				Egg detectability (no. larvae)	Sex ratio (F1 only, all adults)	Female fecundity (female-days)
		Males	Females	Egg	Larva	Nymph	Egg-adult			
1	22	12	3	31	92	19	8	86	11	48
2	18	28	5	37	60	28	0	71	28	32
3	16	39	6	11	54	39	11	66	39	9
4	18	28	11	32	63	33	6	101	34	35
5	10	2	1	16	27	0	0	34	0	0
6	11	10	2	11	33	11	8	41	10	0
Total	95	119	28	138	329	130	33	399	122	124

Duration of developmental stages

The time of moulting or death was recorded on the basis of daily censuses. In the cases when a 1-day interval had occurred between counts, the value of 0.5 was added to the developmental time (assuming that an event occurred halfway an interval between two censuses). To avoid underestimation of developmental time of eggs (due to problems with their detection), only eggs detected at least twice were used for calculations.

Survival, fecundity and sex ratio of adults

Survival curves were estimated for adult stages only, for each sex separately. Data setup of the form (t_i, u_i) was used, where t_i is the observed survival time of an adult mite and $u_i = 0$ if the observation was censored (i.e., the mite was not further observed and its fate was unknown) or $u_i = 1$ if death was stated (Kleinbaum 1996).

Age-dependent fecundity of females was calculated using the method presented in Appendix 1. Sex ratio (SR) was estimated as the proportion of females in F1 generation.

Population parameters

The net reproductive rate (the total number of female progeny produced by an average female over their lifetime, R_0), the intrinsic rate of natural increase (the per capita instantaneous rate of increase of a population, r), the finite rate of increase (the daily growth rate, λ) and the generation time (average age of mothers giving birth, T) were calculated accordingly to Stearns (1992). Life expectancy was calculated accordingly to Krebs (1989). The number of female progeny of females being at age x (b_x) was calculated using the estimated overall fecundity (i.e., no. of progeny of both sexes, f_x) and the estimated sex ratio in F1 generation: $b_x = f_x \times \mathrm{SR}$. In all calculations, survivorship of eggs, larvae and nymphs were assumed to be 100%.

Throughout the text, means are given with 95% confidence intervals (CI). To avoid violations of assumptions of parametric statistics (non-normal distributions, non-homogeneity of variances, dependence of observations) randomisation tests were used for testing differences between means. For testing differences between proportions, we used the criterion of their CI overlapping. Confidence limits for proportions (sex ratio and detectability) were calculated directly from the binomial distribution. CI for other estimates (duration of developmental stages) were computed using the bootstrap method (Efron and Tibshirani 1993).

Results

Egg detectability

The minimum estimate of egg detectability ranged from 84 to 100%, with the mean 89% (CI: 86–92%). Differences in detectability between groups were not significant (confidence limits overlap in all cases).

Table 2. Duration (in days) of the immature stages of *A. hystrix* on *A. repens*. The test statistics (F) of the ANOVA of differences between experimental groups and their randomised significances (p) are given.

Stage	Mean	95% CI	Range	n	F	p
Egg	3.74	3.68–3.80	3.5–5.0	138	8.1	0.0001
Larva	1.34	1.29–1.39	1.0–2.0	329	9.9	0.0001
Nymph	3.55	3.41–3.68	2.0–5.5	130	6.1	0.0002
Total (egg-adult)	7.98	7.68–8.21	6.5–9.0	33	4.6	0.0112

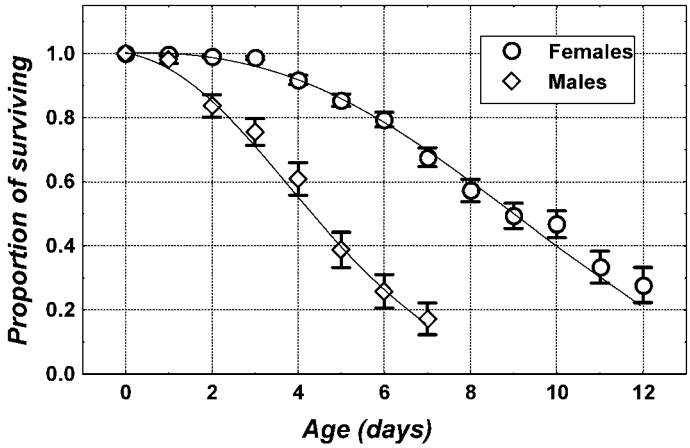

Figure 1. Survival curves of adults of *A. hystrix*. Bars represent standard errors. Lines represent Weibull model fitted to the hazard estimates.

Developmental time

Developmental times for all stages are summarised in Table 2. Duration of all stages differed significantly between experimental groups.

Adult survival, reproduction and sex ratio

Survival curves of adults are shown in the Figure 1. For females, maximum longevity was 12 days, for males 7 days. The mean life expectancy was 9.72 days for females and 5.41 days for males.

Sex ratio (expressed as the proportion of females) ranged from 0.68 to 0.87 for different experimental groups. These values did not differ between experimental groups (confidence limits overlapped). Overall, 97 of the 122 adults hatched were females (0.80, CI: 0.71–0.86).

Mean reproductive output for females is age-dependent. The pre-oviposition period (from adult emergence to egg laying) lasted 1 day. Oviposition began at the

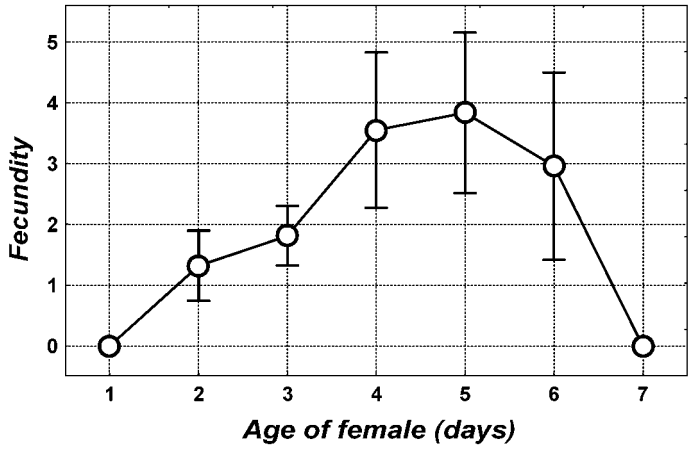

Figure 2. Age-dependent fecundity of *A. hystrix*. Bars represent 95% CI around means.

2nd day of life and the daily egg production reached a peak on the 5th day, and then decreased (Figure 2). The mean number of larvae produced by a single female during a lifespan was 13.5.

Rate of population increase

Demographic parameters of *A. hystrix* were estimated as follows: generation time $T = 11.31$ days, the net reproductive rate $R_0 = 10.12$ female progeny per female per generation, the intrinsic rate of natural increase $r = 0.20$ female progeny per female per day, the finite rate of increase $\lambda = 1.23$ female progeny per day.

Discussion

Amongst grass-infesting eriophyoids, two were reported to be of serious agricultural significance, that is, *Aceria tosichella* Keifer and *A. hystrix*, particularly owing to their ability of vectoring plant viruses (Frost and Ridland 1996; Oldfield and Proeseler 1996). In spite of their economic importance the information on their life histories is scarce. We believe that the results of our study will help to fill this gap and may be useful in future research of *A. hystrix* biology and ecology. We found a short oviposition period, high fecundity, short developmental time, female-biased sex ratio, etc. These estimates indicate, that *A. hystrix* has a great potential capacity for rapid population increase. However, it was reared under conditions of very low population density, low competition, optimal abiotic conditions and absence of predators. After several generations more, under conditions of higher competition and higher density, demography parameters will probably shift.

There are no data in literature regarding the duration of the developmental time of respective stages of *A. hystrix*. In the present study eggs developed slowest and larvae fastest. These results correspond to those found for *Epitrimerus gibbosus* (Nalepa) on blackberry (Shi 2001) and *Aceria mississippiensis* Chandrapatya et Baker on wild gerianium (Chandrapatya and Baker 1986) at similar temperatures. Many others reported that nymphs developed fastest (eggs were always slowest), for example, *Epitrimerus piri* (Nalepa) on pear (Easterbrook 1978), *Aculus schlechtendali* (Nalepa) on apple (Easterbrook 1979; Kozłowski and Boczek 1989) and *Cecidophyes caroliniani* (Chandrapatya et Baker) on wild geranium (Chandrapatya and Baker 1986).

Interestingly, there were significant differences among experimental groups in developmental time of all stages. All trials were maintained under the same controlled conditions. However, particular shoots of host plants could differ from each other in many ways (e.g., in their physiological age or other respects, unknown). Therefore, individual differences between shoots could influence mites development. Connin (1956) reported that degree of maturity of grasses may influence their suitability as hosts for *Aceria tosichella*. These results may be an indication for future observations on the biology of plant-feeding mites. Possibly, for such studies, shoots of the same age and maturity, or even originating from one rhizome, should be used.

The percentage of females of laboratory reared *A. hystrix* was 80%. Sabelis and Bruin (1996) reported that the sex ratio of eriophyoid mites depends on their life style. The strong female-biased sex ratio was reported for bud and gall-forming eriophyids, for example 95% of females for *Acalitus phloeocoptes* (Nalepa) (Sternlicht et al. 1973); 86% for *Eriophyes emarginatae* Keifer (Oldfield 1969), 78% for *Aceria sheldoni* (Ewing) (Sternlicht and Goldenberg 1971). On the contrary, mites which are vagrants on leave surfaces have a sex ratio closer to 50% or slightly female-biased, for example, *A. mississippiensis*: 64%, *Cecidophyes caroliniani*: 51% (Chandrapatya and Baker 1986), *Rhyncaphytoptus ficifoliae* Keifer: 54% (Abou-Awad et al. 2000), *Phyllocoptruta oleivora* (Ashmead): 57% (Swirski and Amitai 1959). These differences could be explained by theory of local mate competition (Hamilton 1967; Taylor and Blumer 1980). It is important to remark that eriophyoids are arrhenotokous, that is, unmated females produce only male offspring, and thus they may control egg fertilisation. Generally, a few females produce colonies in buds and galls, therefore daughter–son mating inside the colony and female-biased sex ratio are expected. Otherways, mating among free-living mites is probably more random, thus expected sex ratio is closer to 1:1. The sex ratio of *A. hystrix* was slightly higher than of other free-living eriophyoids. We suppose that it could be affected by experimental conditions, that is, arising of population from 4 to 5 foundresses females, similarly to that in galls. Our results suggest that the sex ratio of free-living and easily dispersing eriophyoids is female-biased, when they infest new plants. However, the sex ratio of *A. hystrix* population developing on the same host during a longer period of time will probably be closer to 1:1.

The net reproductive rate R_0 (the per-generation rate of multiplication of a population) of *A. hystrix* was rather high ($R_0 = 10.12$), compared to values estimated for eriophyoids reared under similar temperature, for example, *Epitrimerus*

gibbosus on blackberry ($R_0 = 4.5$) (Shi 2001), and *Phyllocoptruta oleivora* on citrus ($R_0 = 3.2$) (Li et al. 1989).

The *r*-values of many eriophyoid species were estimated by Sabelis and Bruin (1996) to explore the relationships between the life histories of mites and habitats they use. They divided mites into three groups that represented different life styles: (1) vagrant, (2) refuge-seeking (infesting leaf sheaths, buds, etc.), and (3) gall-making. Their results show, that the highest *r*-values occur among the vagrants and the lowest among the gall-makers. The authors hypothesised, that when coping with predation pressure, mites have different strategies to maintain a balance between reproduction and predation. Galls, buds, erinea and sheaths offer refuges from predation, but less favourable conditions for reproduction, due to higher food scarcity or food competition (lower *r*-values). Alternatively, vagrant mites are exposed to the higher predation risk and they have better opportunities to produce offspring (higher *r*-values). The intrinsic rate of natural increase of a vagrant *A. hystrix* in the present study ($r = 0.20$/day) is higher than that determined for free-living eriophyoids, for example, *Phyllocoptruta oleivora*: 0.084–0.114/day (Allen et al. 1995) and 0.16–0.21/day (Li et al. 1989), and *Aculus schlechtendali*: 0.109–0.216/day (Kozłowski and Boczek 1989). However, it is also much higher than the *r* found for refuge-seeking mites, for example, *Epitrimerus gibbosus*: 0.077–0.079/day (Shi 2001), and *A. tulipae*: 0.04–0.05/day (Sabelis and Bruin 1996). These observations generally support the hypothesis of habitat dependence of life-history traits of eriophyoids. Dingle (1981) pointed out that the intrinsic rate of natural increase is higher in high migratory insects than in low ones. Similarly, the *r*-values of tetranychid species that are forced to migrate frequently because of frequent habitat deterioration are high, compared to those of species with a more stable environment (Gotoh 1983). The high *r*-value of *A. hystrix* may therefore also be related to its great dispersal ability, which may be influenced by the broad range of accessible hosts and unstable character of hosts.

The value of $r = 0.20$, as found for *A. hystrix* in this study, might be considered to be rather high compared to literature data ranging from 0.05 to 0.2–0.25, obtained for eriophyoid mites at 20–30 °C and high humidity (Sabelis and Bruin 1996). It also seems rather high when compared to values ranging from 0.13 to 0.33 reported for tetranychid mites – the most important economically plant pests (Sabelis 1985, 1991). This indicates that *A. hystrix* has a high capacity of rapid population increase on quack grass. However, the mite's potential role as control agent of this important weed is reduced, due to its high dispersal ability and its wide range of host plants, many of which are cultivated grasses (Nault and Styer 1969; Frost and Ridland 1996). The cereal rust mite may rapidly build up to very high densities on quack grass, forming a reservoir population from which mites may easily disperse and infest other grasses.

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Appendix 1

Calculation of age-dependent female fecundity

Due to problems with egg detection, a female's fecundity was defined as the number of larvae produced by a female. We assumed age-dependent fecundity and estimated it for each day separately of a female's life.

The number of progeny (no. of larvae, L) observed each day (taking into account the time lag resulting from developmental time) in each experimental group is a sum of products of number of females in age x and the mean fecundity of females in this age. This can be written as a set of linear equations:

$$\begin{aligned} &a_{11}f_1 + a_{12}f_2 + \cdots + a_{1x}f_x = L_1 \\ &a_{21}f_1 + a_{22}f_2 + \cdots + a_{2x}f_x = L_2 \\ &\cdots \\ &a_{q1}f_1 + a_{q2}f_2 + \cdots + a_{qx}f_x = L_q \end{aligned}$$

where a_{qx} is the subsequent observation (q) of number of females being in day x of their life; f_x the fecundity of females in the age of x days; L_q the subsequent (q) observation of number of larvae (with the time lag of three days resulting from rounding the mean developmental time of an egg and larvae); $1 \ldots q$ the index of subsequent observation (i.e., each observation day in each experimental group); $1 \ldots x$ the female age in days.

Note that f_x is not the same as b_x from previous equations, because f_x also takes male progeny into account.

The above set of linear equations can be rewritten in matrix form:

$$Af = l$$

where A is the matrix of dimensions $q \times x$ containing numbers of females in subsequent observation days in different experimental groups at age x; f the row array of length x of females fecundity in each age class; l the column array of length q of numbers of larvae observed three days later.

The above set of equations cannot be solved unambiguously, because the number of equations is greater than the number of coefficients ($q > x$). Thus, it becomes a linear problem:

$$l = Af + \varepsilon \tag{1}$$

where ε is an array of errors, assumed to be distributed normally with the mean zero and standard deviation δ.

Equation (1) can be solved using the least squares method by finding a vector f, minimising the residual sum of squares $\varepsilon\varepsilon'$, where ε' means ε transposed.

CI for fecundity estimates were computed in a standard way from the *t* distribution (Sokal and Rohlf 1995).

Solving Equation (1) was conducted in two steps. First, the vector *f* minimising the residual sum of squares was found. Then, all elements of this vector which were not significantly different from zero (i.e., if their 95% CI included zero) were set to zero. Afterwards, Equation (1) was resolved with above constraints.

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